

UNIVERSITÉ DU QUÉBEC À MONTRÉAL

LES DYNAMIQUES INTERHÉMISPHÉRIQUES RÉVÉLÉES PAR LE TEMPS
DE RÉPONSE DANS LE PARADIGME DE DIMOND

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DU DOCTORAT EN PSYCHOLOGIE

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RÉSUMÉ

L'objectif principal de la thèse était de clarifier l'interprétation d'une mesure comportementale, l'avantage unilatéral ou bilatéral en temps de réponse, liée à la communication entre les deux hémisphères du cerveau. L'avantage unilatéral ou bilatéral est une différence obtenue dans des tâches demandant une comparaison entre deux stimuli (paradigme de Dimond) en soustrayant le temps de réponse obtenu lorsque les deux stimuli apparaissent dans la même moitié du champ visuel (présentations unilatérales) du temps de réponse obtenu lorsque les deux stimuli apparaissent dans des moitiés opposées du champ visuel (présentations bilatérales). Trois champs d'investigation principaux ont été abordés : la validité de l'avantage unilatéral en tant qu'index de la latence du transfert d'information visuelle dans des tâches simples, la validité d'une interprétation anatomique d'un effet d'orientation des paires de stimuli sur l'avantage unilatéral, et le lien entre l'avantage unilatéral et un autre index de la communication interhémisphérique, la différence croisé - non-croisé.

L'article présenté au chapitre II proposait un modèle selon lequel l'avantage unilatéral ou bilatéral est formé de deux composantes, c'est-à-dire de deux sources de latence différentes. La première composante est associée au traitement de l'information par les hémisphères cérébraux, la latence entraînée par ce traitement étant plus courte pour les présentations bilatérales grâce au traitement en parallèle de l'information par les deux hémisphères. Son allongement entraîne alors un avantage bilatéral plus grand. La seconde composante est associée au transfert d'information par le corps calleux lors des présentations bilatérales. Son allongement entraîne un avantage unilatéral plus grand reflétant une efficacité moindre du transfert interhémisphérique. L'étude visait plus spécifiquement à identifier des caractéristiques des tâches visuelles susceptibles d'influencer chacune des deux composantes de l'avantage unilatéral ou bilatéral. Pour rejoindre ces objectifs, une revue quantitative de la littérature a été effectuée. 75 paires de conditions expérimentales montrant un changement de l'avantage unilatéral et bilatéral ont été trouvées, soit 26 paires pour lesquelles la croissance de la composante liée au transfert interhémisphérique dominait et 49 paires pour lesquelles la croissance de la composante liée au traitement intrahémisphérique dominait. Des analyses par régression multiple ont trouvé deux caractéristiques de la tâche susceptibles de révéler un changement de la latence de la composante de transfert, soit une manipulation de la similarité des stimuli devant être comparés et une absence de conditions demandant un traitement langagier des stimuli visuels. Les analyses statistiques ont aussi trouvé deux facteurs susceptibles de révéler un changement de la latence de la composante de traitement, soit la charge attentionnelle des distracteurs visuels et l'augmentation de la complexité du critère de sélection. Les résultats ont été

interprétés comme une validation de l'utilisation des tâches de Dimond pour l'étude de la composante de transfert, et comme une confirmation de l'hypothèse selon laquelle des changements à la complexité des tâches de Dimond entraînent un allongement de la composante de traitement.

L'article présenté au chapitre III visait à clarifier l'interprétation de l'effet d'une manipulation de l'orientation de la paire de stimuli sur l'avantage unilatéral dans la tâche de Dimond. Plusieurs études scientifiques avaient obtenu un avantage unilatéral plus grand pour des paires obliques que pour des paires horizontales. L'explication proposée pour cet effet se basait sur l'homotopie des fibres du corps calleux reliant ensemble des neurones traitant l'information provenant de parties des champs visuels qui sont symétriques par rapport au méridien vertical. Cependant, l'effet pouvait aussi être attribué à des concordances entre l'orientation des paires de stimuli et l'orientation des stimuli eux-mêmes. Une paire d'expériences ont été réalisées avec un total de 48 participants dans le but de tester cette dernière interprétation. Lors de la première expérience, l'effet de l'orientation des paires de stimuli sur l'avantage unilatéral a été obtenu avec des stimuli en forme de disques, favorisant ainsi l'explication anatomique. Cet effet n'a pas été obtenu lors de la seconde expérience, lors de laquelle trois niveaux d'orientation ont été systématiquement manipulés. Une diminution de l'avantage unilatéral avec le temps a aussi été obtenue lors des deux expériences, ce qui a été attribué à un effet possible de plasticité calleuse.

L'article présenté au chapitre IV visait à clarifier le lien entre l'avantage unilatéral et un autre estimé de la latence du transfert interhémisphérique, la différence croisé - non-croisé. Celle-ci est obtenue en soustrayant deux temps de réponse, soit la latence obtenue lorsqu'une stimulation visuelle dans un hémichamp visuel doit être suivie d'une réponse par la main contralatérale (essais croisés) et lorsque la réponse est faite par la main ipsilatérale (essais non-croisés) à l'hémichamp visuel. L'hypothèse de départ proposait que l'avantage unilatéral reflète la latence d'un transfert d'information visuelle alors que la différence croisé - non-croisé reflète la latence d'un transfert d'information prémotrice. Lors d'une paire d'expériences réalisées avec un total de 24 participants, ces deux mesures ont été obtenues alors que deux caractéristiques de la tâche, soit l'orientation des paires de stimuli et la fréquence du changement de la main de réponse, ont été manipulées. L'avantage unilatéral changeait selon l'orientation des paires de stimuli, mais pas selon la fréquence du changement de mains. La différence croisé - non-croisé changeait selon la fréquence du changement de mains, mais pas selon l'orientation des paires de stimuli. Aucune corrélation entre les deux mesures comportementales de la communication interhémisphérique n'a été trouvée. Les résultats supportaient l'interprétation de l'avantage unilatéral en tant qu'index de la latence du transfert d'information visuelle à travers le corps calleux. Les résultats supportaient aussi une interprétation de la différence croisé - non-croisé en tant qu'index d'un transfert interhémisphérique.

d'une commande prémotrice accompagnée d'effets de concordance entre la position du stimulus visuel et la position de la réponse motrice.

Mots clés : Corps calleux, homotopie, avantage unilatéral, avantage bilatéral, différence croisé - non-croisé, temps de transfert interhémisphérique.

CHAPITRE I

INTRODUCTION

1.1.Contexte théorique

1.1.1. Communication interhémisphérique et tâches visuomotrices

Le corps calleux est la principale commissure reliant ensemble les deux hémisphères cérébraux. Plus précisément, il est formé d'environ 200 à 300 millions d'axones (Aboitiz, Scheibel, Fisher, & Zaidel, 1992) permettant la formation de synapses entre des neurones des hémisphères cérébraux gauche et droit. Une série d'élégantes démonstrations réalisées par Sperry avec des chats et des singes (Sperry, 1961), puis avec des humains (Gazzaniga, Bogen, & Sperry, 1962) dont le corps calleux a été sectionné ont démontré de manière convaincante le rôle important du corps calleux dans le transfert d'information nécessaire à la réalisation de tâches visuomotrices. L'observation des caractéristiques de ce transfert d'information par des mesures comportementales chez des participants neurotypiques constitue l'objet du projet de recherche présent.

Deux paradigmes expérimentaux basés sur des mesures comportementales ont été créés, au fil des années, afin d'étudier la communication entre les deux hémisphères cérébraux (Poffenberger, 1912; Dimond, 1969) lorsque le corps calleux est intact. Les deux paradigmes proposent que la différence entre les temps de réponse lors d'une situation où un transfert d'information d'un hémisphère à l'autre et une seconde situation ne nécessitant pas ce transfert peut servir comme un estimé de la part du temps de réponse qui peut être attribuée à ce transfert. Pour créer ces deux situations, ces deux paradigmes expérimentaux qui seront subséquemment décrits en détail basent leurs inférences sur la connaissance de certaines particularités de l'anatomie latéralisée des systèmes visuel et moteur.

1.1.1. Anatomie latéralisée des systèmes visuel et moteur

La nécessité du transfert d'information sensorielle et prémotrice par le corps calleux provient tout d'abord du fait que chaque hémisphère possède un rôle distinct dans le traitement sensoriel et dans le contrôle moteur. Dans le système visuel, chaque hémisphère reçoit et traite l'information provenant de la moitié contralatérale, ou opposée, du champ visuel. Par exemple, lorsqu'une scène visuelle est observée, l'information visuelle est tout d'abord encodée par les cônes et bâtonnets de la rétine. L'information sensorielle passe alors par le nerf optique de chaque œil pour ensuite atteindre le chiasme optique, où les deux nerfs optiques se rencontrent. À cet endroit, une décussation partielle se produit : les fibres nerveuses des deux yeux liés aux capteurs rétiniens traitant le côté gauche du champ visuel se dirigent dans le tractus optique droit, et vice-versa.

Ainsi, tout stimulus visuel qui apparaît dans la moitié gauche du champ visuel est traité dans le corps genouillé latéral et l'aire visuelle primaire de l'hémisphère droit, et vice-versa, à l'exception des stimuli se trouvant près du méridien vertical du champ visuel : ces derniers sont traités à la fois dans les hémisphères gauche et droit. La fusion des deux moitiés du champ visuel, nécessaire pour l'expérience subjective d'un champ visuel unifié, est ensuite produite par un échange d'information visuelle entre les deux hémisphères par l'entremise du corps calleux (Berlucchi, 1981; Saint-Amour, Lepore, Lassonde & Guillemot, 2004). La largeur de la bande verticale autour du méridien vertical du champ visuel, à l'intérieur de laquelle des stimuli peuvent être traités par les deux hémisphères, a été estimée entre 0.5 et 3 degrés (Bourne, 2006).

Le contrôle moteur est aussi organisé de façon topographique, le cortex moteur primaire gauche contrôlant la motricité du côté droit du corps et vice-versa. La voie corticospinale, principale voie de l'information motrice reliant le cortex moteur primaire à la moelle épinière, croise en effet au niveau des pyramides du tronc cérébral pour créer le contrôle cortical contralatéral du mouvement. Ainsi, il y a une

spécialisation hémisphérique liée au cortex moteur qui peut aussi être utilisée dans le but d'étudier la manière dont les deux hémisphères du cerveau communiquent.

1.1.2. Les paradigmes de Poffenberger et de Dimond

Poffenberger (1912) a été le premier à soulever l'idée de présenter brièvement des stimuli visuels à gauche ou à droite d'un point de fixation et de demander aux participants de répondre le plus rapidement possible avec la main gauche ou la main droite. Lorsque l'hémisphère recevant l'information visuelle était le même que l'hémisphère chargé de la réponse motrice, un essai « non-croisé » avait lieu : aucun transfert d'information visuelle ou motrice n'était strictement nécessaire pour pouvoir répondre. Lors d'essais « croisés », pour lesquels l'hémisphère recevant l'information visuelle différait de l'hémisphère chargé de la réponse, un tel transfert d'information d'un hémisphère à l'autre était strictement nécessaire pour permettre une réponse motrice. La différence croisé - non-croisé obtenue grâce à cette méthode était donc une première mesure permettant d'estimer le temps de transfert de l'information par le corps calleux. Deux méta-analyses des nombreuses recherches réalisées avec la méthode de Poffenberger a révélé des temps de réponse plus courts pour les essais non-croisés dans toutes les études sélectionnées (Marzi, Bisiacchi, & Nicoletti, 1991 ; Braun, 1992). La taille de cette différence croisé - non-croisé était estimée entre 2 et 4 millisecondes. Cependant, l'inférence de Poffenberger ne permettait pas de déterminer si l'information transférée précisait la nature du stimulus ou n'était qu'une commande motrice.

Dimond (1969) a été le premier à créer un paradigme permettant d'étudier le transfert interhémisphérique d'une information de nature spécifiquement non-motrice. Cette méthode consistait à présenter deux stimuli visuels simultanément, soit dans la même moitié du champ visuel ou dans les moitiés opposées, et à demander une comparaison

entre ces deux stimuli. Lorsque les deux stimuli étaient présentés dans le même hémichamp visuel, la comparaison pouvait être faite sans transfert d'information puisque le même hémisphère recevait l'information sensorielle liée aux deux stimuli. Lorsque les deux stimuli étaient présentés dans des hémichamps opposés, aucun des deux hémisphères ne pouvait initialement comparer les deux stimuli et créer une commande motrice. L'information qui passait par le corps calleux pouvait alors être de nature visuelle (par exemple, la forme du stimulus) ou cognitive (par exemple, l'appartenance d'un stimulus à une catégorie). La commande motrice ne pouvait être créée qu'après ce premier transfert d'information.

1.1.3. Importance du corps calleux dans les tâches de Poffenberger et Dimond

L'importance du corps calleux dans les tâches visuomotrices faisant appel aux deux hémisphères a été démontrée plusieurs fois lors de recherches réalisées avec des individus sans corps calleux. Certains patients sont atteints d'une agénésie du corps calleux : il s'agit d'une anomalie du développement qui fait en sorte que les individus atteints naissent sans corps calleux. D'autres patients subissent plutôt une callosotomie, c'est-à-dire une section chirurgicale d'une partie ou de la totalité du corps calleux, souvent dans le but d'empêcher une crise épileptique dont le ou les foyers initiaux se trouvent dans un seul hémisphère de se généraliser à l'hémisphère opposé.

La performance de patients sans corps calleux aux essais croisés de la tâche de Poffenberger était clairement anormale. Un groupe de quatre tels patients ont obtenu une différence croisé - non-croisé moyenne d'environ 80 millisecondes (Aglioti, Berlucchi, Pallini, Rossi, & Tassimari, 1993), ce qui correspond à quelques dizaines de fois la latence du transfert interhémisphérique estimée par la même méthode chez

des participants neurotypiques. Cependant, les patients demeuraient capables de réussir la tâche de Poffenberger en réalisant un minimum d'erreurs.

L'importance du corps calleux dans les tâches visuomotrices demandant un transfert d'information visuelle d'un hémisphère à l'autre a aussi été démontrée dans des tâches de Dimond simples. Dans une telle tâche, un groupe de participants ayant un corps calleux non-développé ou complètement sectionné obtenait plus d'erreurs pour les présentations bilatérales. Trois individus sur cinq obtenaient aussi des temps de réponse plus longs pour les présentations bilatérales (Brown, Jeeves, Dietrich, & Burnison, 1999). L'agénésie partielle, quant à elle, entraînait des anomalies moindres de la performance, reflétant le fait que la section du corps calleux n'était pas complète.

Ces résultats laissent penser que le corps calleux n'est pas strictement nécessaire pour combiner l'information provenant de deux hémisphères lors des tâches de Poffenberger et de Dimond. Par ailleurs, Savazzi & al. (2007) ont proposé que la commissure reliant les colliculi supérieurs peut assurer le transfert interhémisphérique d'information visuelle en l'absence du corps calleux, ce qui est en théorie suffisant pour obtenir des taux de succès plus élevés que ceux obtenus avec une stratégie de réponse aléatoire. Cependant, le ralentissement de la performance lors des essais croisés de la tâche de Poffenberger et des essais bilatéraux lors de la tâche de Dimond en l'absence du corps calleux laisse penser que celui-ci assure bel et bien le transfert hémisphérique d'information dans ces mêmes tâches chez l'humain neurotypique. Cette inférence ouvre la porte à l'étude des caractéristiques fonctionnelles de cette commissure chez l'humain neurotypique à l'aide des tâches de Poffenberger et de Dimond.

1.1.4. Tâche de Poffenberger : transfert d'information visuelle ou prémotrice?

Les inférences liées à la tâche de Poffenberger proposent qu'un transfert d'information entre les deux hémisphères est nécessaire pour réussir les essais croisés, et qu'un seul transfert d'information est suffisant. Cependant, les données électroencéphalographiques et d'imagerie cérébrale disponibles indiquent clairement que les transferts d'information entre les deux hémisphères sont nombreux. En effet, des mesures du transfert interhémisphérique d'information pendant la tâche de Poffenberger ont été obtenues dans les cortex occipitaux, mais aussi dans les cortex pariétaux et pré moteurs des deux hémisphères. Il y a donc un doute sur la partie du corps calleux par lequel le transfert indexé par la méthode de Poffenberger passe d'un hémisphère à l'autre, et donc sur le type d'information dont le transfert détermine la différence croisé - non-croisé.

L'état présent des recherches sur le transfert d'information qui crée la différence croisé - non-croisé suggère que celle-ci reflète un transfert d'information pré motrice entre les deux hémisphères. Un premier argument en faveur de l'importance d'un transfert d'information pré motrice est basé sur les effets relativement faibles ou nuls des modifications aux stimuli dans la tâche de Poffenberger. Une comparaison métanalytique de 49 expériences dans le paradigme de Poffenberger (Braun, 1992) révèle bien des effets de la luminance des stimuli et de l'excentricité des stimuli par rapport au point de fixation, mais aucune expérience seule n'est parvenue à trouver des effets de luminance et d'excentricité significatifs. En particulier, une manipulation de la distance des stimuli par rapport à la fovéa (Miniussi, Maravita, & Marzi, 2003) ne modifiait pas la différence croisé - non-croisé, même si le temps de transfert hémisphérique mesuré dans les aires visuelles par une méthode électroencéphalographique était plus long lorsque l'excentricité du stimulus était plus élevée.

Des mesures électroencéphalographiques du temps de transfert calleux ont en effet été utilisées dans le but d'obtenir une mesure cérébrale de ce transfert, mais aussi de mieux comprendre les particularités des méthodes de Poffenberger et de Dimond. La méthode d'estimation du temps de transfert par potentiels évoqués est basée sur le fait qu'un écho aux potentiels évoqués survient dans l'hémisphère cérébral ipsilatéral aux stimuli visuels, quelques millisecondes après avoir été détectés dans l'hémisphère contralatéral à l'hémichamp visuel dans lequel les stimuli sont présentés (Lines, Rugg, & Milner, 1984; Rugg, Lines, & Milner, 1985). La latence séparant le potentiel évoqué et son écho est alors utilisée comme un estimé du temps de transfert interhémisphérique. Cet écho des potentiels dans l'autre hémisphère représente fort probablement un transfert d'information par le corps calleux et non un artefact de la méthode de potentiels évoqués, puisqu'il est absent chez des patients ne possédant pas de corps calleux (Brown, Jeeves, Dietrich, & Burnison, 1999). Deux équipes de chercheurs ont ainsi pu déterminer que la latence du transfert interhémisphérique dans les aires postérieures du cerveau était de 10 à 20 millisecondes (Lines, Rugg, & Milner, 1984; Rugg, Lines, & Milner, 1985; Saron & Davidson, 1989). Dans des aires cérébrales antérieures dans lesquelles un transfert d'information prémotrice survient, cependant, la latence du transfert interhémisphérique était estimée à environ 3 millisecondes (Lines, Rugg, & Milner, 1984). L'existence d'un transfert plus court dans des aires plus antérieures fournissait un argument contre l'idée que la latence du transfert d'information visuelle est reflétée par la mesure de Poffenberger.

Contrairement à la mesure comportementale de Poffenberger, la mesure de temps de transfert par potentiels évoqués occipitaux s'est aussi révélée sensible à l'intensité du stimulus (Lines, Rugg, & Milner, 1984), suggérant que les deux mesures n'indexent pas le même type de transfert d'information.

De plus, Thut & al. (1999) ont comparé les données électroencéphalographiques temporelles et topographiques tirées d'une tâche de Poffenberger avec des simulations représentant un transfert d'information à divers moments et endroits. Ils

ont ainsi trouvé une concordance des données réelles plus forte avec un modèle selon lequel la transmission d'information cruciale pour déterminer le temps de transfert se produit tardivement, dans les aires frontales. Comme les aires prémotrices sont antérieures tandis que les aires visuelles sont postérieures, ils ont aussi conclu que l'information transférée dans la tâche de Poffenberger chez le participant neurotypique est prémotrice. D'ailleurs, deux études tentant de lier la mesure de Poffenberger et la mesure du temps de transfert interhémisphérique par potentiels évoqués occipitaux ont trouvé des corrélations nulles entre celles-ci (Saron & Davidson, 1989; Friedrich & al., 2017). Deux études en imagerie par résonance magnétique fonctionnelle (Tettamanti & al., 2002, Iacoboni & Zaidel, 2004) ont aussi supporté l'importance d'un transfert d'une information prémotrice plutôt que visuelle dans la tâche de Poffenberger.

Finalement, la mesure de Poffenberger s'est montrée plus sensible à des manipulations des contingences motrices qu'à des manipulations des contingences sensorielles de la tâche. Par exemple, la différence croisé - non-croisé augmentait lorsque les participants devaient appuyer trois fois plutôt qu'une, et augmentait lorsqu'un changement de doigt était demandé après chaque réponse (Laroque, Achim, & Braun, 2001). Elle diminuait aussi lorsque les participants doivent répondre avec les bras croisés (Braun, Larocque et Achim, 2004). Iacoboni et Zaidel (1995) ont aussi testé l'impact d'une hausse de la complexité des stimuli et de la réponse motrice dans une tâche de Poffenberger et ont obtenu une différence croisé - non-croisé plus importante seulement dans la condition de motricité complexe chez des participants neurotypiques. L'effet le plus fort trouvé dans une méta-analyse exploratoire du paradigme de Poffenberger était une différence croisé - non-croisé plus grande pour des réponses avec l'index que pour des réponses avec le pouce (Braun, 1992), plutôt qu'un effet attribuable aux changements de la scène visuelle. Cependant, la même analyse suggérait tout de même que la manipulation de l'intensité et de l'excentricité des stimuli visuels pouvait influencer, de façon minime, la différence croisé - non-

croisé. L'impact détectable des manipulations motrices et l'impact négligeable des manipulations visuelles dans la majorité de ces études laissaient penser que le transfert d'une information prémotrice, et non le transfert d'une information visuelle, crée la différence croisé - non-croisé dans un cerveau neurotypique.

Parce que la tâche de Poffenberger indexe probablement un transfert d'information prémotrice, celle-ci n'était pas idéale pour étudier le transfert d'une information spécifiquement visuelle, et l'utilisation d'une méthode expérimentale différente devenait alors nécessaire. La tâche de Dimond a l'avantage d'exclure, par ses inférences, la possibilité que l'information transmise d'un hémisphère à l'autre soit de nature motrice ou prémotrice. De plus, les données électroencéphalographiques ont révélé plusieurs fois des corrélations entre l'avantage unilatéral ou bilatéral dans le paradigme de Dimond et le temps de transfert hémisphérique tel que mesuré par les potentiels évoqués dans le cortex occipital (Brown & Jeeves, 1993, Larson & Brown, 1997). En d'autres mots, plus la communication entre les hémisphères était efficace selon la mesure par potentiels évoqués, plus la coopération entre les hémisphères était efficace selon la mesure comportementale. Cela suggère que l'avantage unilatéral ou bilatéral, mesurable par la méthode de Dimond, a le potentiel de révéler des caractéristiques du transfert d'information visuelle par le corps calleux lors de certaines tâches de Dimond relativement simples.

1.1.5. Tâche de Dimond : transfert interhémisphérique ou traitement en parallèle?

Un obstacle de taille fait cependant en sorte qu'il est difficile de considérer la mesure de Dimond comme un estimé direct du temps de transfert interhémisphérique dans une forte proportion des études utilisant cette mesure. Contrairement à la mesure de Poffenberger qui a presque toujours une valeur positive lorsque mesurée avec un nombre suffisant d'essais, les réponses aux présentations bilatérales sont

fréquemment plus rapides que les réponses aux présentations unilatérales dans les tâches de Dimond. Cet avantage bilatéral ne peut alors être interprété comme un estimé de la latence du transfert entre les deux hémisphères, puisque cette latence serait alors négative.

Le résultat le plus cité et le plus reproduit à ce jour dans le paradigme de Dimond est un avantage unilatéral en termes de temps de réponse lors d'une tâche de comparaison de l'apparence physique de lettres, accompagné d'un avantage bilatéral lors d'une tâche de comparaison de l'identité sémantique de lettres présentées unilatéralement ou bilatéralement (Banich & Belger, 1990; Belger & Banich, 1992). L'avantage unilatéral de la tâche simple est interprété comme un indice du coût de transfert par le corps calleux. L'avantage bilatéral obtenu lors de la tâche complexe est attribué à l'utilisation d'une masse plus grande de matière grise plus tôt lors de la tâche, et à une parallélisation plus grande du traitement de l'information lorsqu'un stimulus pertinent apparaît dans chaque hémichamp visuel.

Banich a proposé une métaphore basée sur le travail en équipe qui est fort utile pour comprendre son modèle : la préparation d'un texte de quelques pages est plus courte si les étudiants forment des équipes, puisqu'il est utile de séparer la tâche en plusieurs parties et de combiner les parties à la fin : cela représente une parallélisation plus grande du traitement de l'information. Cependant, la préparation d'un texte de quelques lignes est plus courte si les étudiants travaillent seuls, puisque les discussions entourant la distribution de la tâche et la combinaison des multiples parties en un texte cohérent peuvent prendre beaucoup de temps et rendre ainsi le travail en équipe inefficace : cela représente un coût de transfert de l'information d'une unité de traitement à l'autre.

Cette interprétation a des implications importantes sur l'interprétation des résultats d'une manipulation des caractéristiques de la tâche de Dimond sur l'avantage unilatéral ou bilatéral. Pour pouvoir interpréter le résultat de cette manipulation sur la

mesure de Dimond comme un changement de l'efficacité du transfert d'information par le corps calleux, il faut pouvoir exclure l'interprétation basée sur un changement de l'efficacité du traitement de l'information dans les hémisphères.

Cependant, il est parfois possible d'attribuer un changement de l'avantage unilatéral ou bilatéral suite à une manipulation expérimentale au transfert calleux ou au traitement en parallèle. Par exemple, si un changement à la tâche fait augmenter les temps de réponse et rend le traitement des présentations bilatérales plus efficace, alors la latence additionnelle provient fort probablement du traitement à l'intérieur des hémisphères cérébraux. Or, si un changement à la tâche fait augmenter les temps de réponse et rend le traitement des présentations unilatérales plus efficace, alors il est fort probable que la latence additionnelle provienne d'une communication plus longue entre les hémisphères. De même, les effets d'une manipulation à la tâche inspirée par l'anatomie et la physiologie du corps calleux peuvent raisonnablement être interprétés comme des effets du transfert d'information passant par cette structure cérébrale.

1.1.6. Homotopie du corps calleux

Le corps calleux a comme particularité d'être composé en forte majorité de fibres homotopiques reliant une aire cérébrale à son aire homologue dans l'hémisphère opposé. Par exemple, deux études de tractographie de la matière blanche du cerveau ont démontré que les neurones corticaux ayant des projections calleuses forment la forte majorité de leurs synapses dans le lobe homologue de l'hémisphère opposé (Dougherty, Ben-Sachar, Bammer, Brewer, & Wandell, 2005; Hofer & Frahm, 2006). L'homotopie calleuse a aussi été détectée à l'intérieur des lobes occipitaux chez le chat (Segraves & Rosenquist, 1982) : une majorité des fibres calleuses reliaient des aires homologues du cortex visuel des deux hémisphères cérébraux. Ces connexions

homotopiques étaient aussi bidirectionnelles, ce qui permettait à chacun des deux hémisphères de transmettre des potentiels d'action vers l'autre hémisphère. Les méthodes histochimiques ont aussi révélé une symétrie des projections calleuses du lobe occipital chez l'humain (Clarke & Miklossy, 1990).

De plus, les premiers neurones corticaux possédant des projections calleuses susceptibles de transférer une information visuelle entre les deux hémisphères sont situés entre l'aire V1 et l'aire V2 (Clarke & Miklossy, 1990; Dougherty, Ben-Sachar, Bammer, Brewer, & Wandell, 2005) et servent probablement à assurer la fusion des deux parties du champ visuel. Lors de ces tâches, l'information visuelle qui parvient au cortex visuel primaire doit donc être traitée en partie dans le cortex visuel primaire de l'hémisphère qui reçoit l'information avant qu'un transfert d'information vers l'hémisphère opposé puisse survenir.

1.1.7. Corps calleux et transfert interhémisphérique de l'information visuelle

Puisque le cortex visuel a une organisation topographique, une prédiction découlant de l'homotopie des fibres du corps calleux propose que les neurones du système visuel traitant des parties du champ visuel symétriques par rapport au méridien communiquent plus facilement entre eux. Cette hypothèse s'appuie sur les données de Segraves & Rosenquist (1982), qui démontrent que les connexions calleuses sont plus nombreuses entre des neurones traitant des parties des hémichamps visuels symétriques par rapport au méridien vertical chez le chat. Si le même principe d'homotopie de la connectivité des neurones visuels s'applique à l'humain de façon précise, alors une tâche de comparaison de deux stimuli présentés à des emplacements symétriques et non-symétriques par rapport au méridien devrait permettre de relever cet effet de symétrie.

Trois tests de cette idée ont été réalisés précédemment. Desjardins & Braun (2006) ont obtenu des temps de réponse plus courts pour des stimuli orientés symétriquement par rapport au méridien vertical du champ visuel. Cependant, des paires de stimuli orientées horizontalement et verticalement étaient comparées, ce qui a fait en sorte que cette tâche ne permettait pas d'éliminer une interprétation basée sur un avantage en termes de temps de réponse pour les orientations de paires de stimuli horizontales. Desjardins, Braun, Achim, & Roberge (2009) ont cependant réussi à distinguer l'effet d'orientation et l'effet d'homotopie en présentant unilatéralement et bilatéralement des paires de stimuli (carrés et disques) à orientation horizontale et oblique, et ont révélé un avantage unilatéral plus grand pour les paires obliques que pour les paires horizontales qui a pu être attribué à l'homotopie du corps calleux.

Cet effet a de nouveau été obtenu lors d'une tâche de Dimond demandant une comparaison de l'identité physique de stimuli dont deux caractéristiques, la forme (carrés et disques) et la couleur (rouges et bleus) étaient manipulées (Braun & al., 2011). Cependant, l'effet attribué à l'homotopie calleuse était significativement plus fort lorsque les stimuli étaient des carrés, et était non-significatif lorsque seules les paires de disques étaient analysées. De plus, une étude subséquente (Braun, Achim, Roberge, & Gauvin, 2015) tentant de reproduire ces résultats tout en manipulant l'orientation de stimuli locaux en forme de lignes a révélé que des interactions importantes entre l'orientation des stimuli et l'orientation des paires de stimuli existaient, et pouvaient rendre moins fiable l'interprétation des effets de la symétrie par rapport au méridien sur les temps de réponse obtenus précédemment en tant qu'indicateurs d'un changement du temps de transfert interhémisphérique. Or, les trois études précédemment citées utilisaient au moins un stimulus dont l'orientation pouvait interagir avec les orientations de paires de stimuli.

Une vérification de l'effet de l'homotopie du corps calleux sur les temps de réponse contrôlant pour les concordances d'orientations est donc nécessaire pour pouvoir

éliminer le facteur confondant le plus susceptible d'avoir mené à une interprétation erronée des résultats précédents, et pour pouvoir affirmer de façon plus certaine que l'effet obtenu découle bien des conséquences de l'anatomie et de la physiologie du corps calleux.

1.2. Présentation de l'objectif et des éléments de la thèse

Le paradigme de Dimond peut vraisemblablement être utilisé pour étudier l'impact de modifications de diverses caractéristiques des stimuli visuels sur le coût de transfert interhémisphérique. Cependant, les conditions expérimentales modifiant ce coût dans les tâches de Dimond lors desquelles l'avantage unilatéral représente un coût de transfert demeurent peu connues. En effet, ce sont les manipulations influençant l'efficacité de la distribution du traitement de l'information dans deux hémisphères qui ont été le plus étudiées, l'effet de la manipulation du critère de décision visuel ou verbal étant le seul effet ayant été validé par de nombreuses reproductions de l'effet en laboratoire. Le chapitre II présente une méta-analyse exploratoire quantitative des caractéristiques des tâches de Dimond qui influencent ces deux phénomènes, soit le coût de transfert calleux et l'avantage du traitement en parallèle par deux hémisphères. Cette analyse a pour but de confirmer l'hypothèse de Banich au sujet de l'effet de la complexité du critère de décision, mais aussi d'élucider l'effet de facteurs expérimentaux ne faisant pas l'objet de modèles bien définis à ce jour, tels que la complexité des distracteurs et le fait de devoir répondre lorsque les deux stimuli sont identiques ou différents.

Plusieurs expérimentations précédentes réalisées avec le paradigme de Dimond visaient à démontrer un effet attribuable à l'homotopie des connexions calleuses reliant les aires du traitement visuel des deux hémisphères. Ces études démontraient de manière convaincante que le coût de transfert est plus petit lors de la comparaison

de paires horizontales que lors de la comparaison de paires obliques, et qu'il y avait donc un avantage lié à la symétrie des positions des stimuli par rapport au méridien vertical du champ visuel. Cependant, une interprétation alternative basée sur des concordances entre l'orientation des paires de stimuli et l'orientation des stimuli eux-mêmes demeurait disponible pour expliquer les résultats existants. Le chapitre III rapporte deux tâches de Dimond qui, pour la première fois, ont été conçues pour éliminer la possibilité que les effets d'homotopie calleuse précédemment rapportés pouvaient être attribuables à des interactions entre l'orientation des paires de stimuli et l'orientation des stimuli eux-mêmes.

Plusieurs études précédentes laissaient penser que le paradigme de Poffenberger indexe un transfert d'information prémotrice, alors que les tâches de comparaison de l'identité physique de stimuli dans la tâche de Dimond indexent plutôt un transfert d'information visuelle. Cependant, aucune expérience n'avait obtenu les mesures de Poffenberger et de Dimond en même temps tout en manipulant une caractéristique visuelle et une caractéristique motrice de la tâche. Le chapitre IV rapporte une telle série de tâches, qui avait pour but de tester l'hypothèse qu'une manipulation motrice n'influence que la mesure de Poffenberger, alors qu'une manipulation visuelle n'influence que la mesure de Dimond.

CHAPITRE II

DYNAMIQUES INTRA ET INTER-HÉMISPHÉRIQUES RÉVÉLÉES PAR LE
TEMPS DE RÉACTION DANS LE PARADIGME DE DIMOND :

UNE REVUE QUANTITATIVE DE LA LITTÉRATURE

Intra and inter hemispheric dynamics revealed by reaction time in the Dimond paradigm: A quantitative review of the literature

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Abstract

In stimulus matching tasks requiring discrimination of two unilaterally or bilaterally presented stimuli (Dimond paradigm), a well established *intrahemispheric processing bottleneck* model predicts that an increase in task difficulty as measured by reaction time should provide an advantage to bilateral stimulations. The purpose of the current investigation was to review the entire relevant literature on the Dimond paradigm and identify the experimental variables which reliably yield such effects. Forty nine experimental effects compatible with the “*intrahemispheric processing bottleneck*” model and 26 contrary effects were found. Manipulation of the complexity of the stimulus matching criterion significantly produced *intrahemispheric bottleneck effects*. This effect was also significantly greater when non-target stimuli required heavier processing. These two findings support the intrahemispheric bottleneck model: computationally complex tasks seem to overload a hemisphere’s processing capacity, an effect seen in the unilateral presentation conditions. However, manipulating the similarity of target stimuli produced contrary effects. Contrary effects were also obtained more readily when two physical matching tasks were compared. These two latter effects may best be explained as low level visual-perceptual limitations of interhemispheric transfer or integration.

2.1. Introduction

Experimental research using the visual half fields as the independent variable and reaction time (RT) as the dependent variable has been repeatedly exploited to study brain function. Hemispheric lateralization of cognitive functions has been extensively studied with the divided visual fields paradigm, separating the left visual field from the right visual field. Recognition tasks are most common in this paradigm. These tasks typically present one stimulus at a time in either visual field. Speed and accuracy of responses to stimuli presented in the left visual field are then compared to those obtained when stimuli are presented in the right visual field. The early processing of stimuli presented to one visual field occurs in the contralateral hemisphere. Therefore, left field advantages were thought to reveal right hemisphere specialization, and right field advantages were linked to left hemisphere specialization. With this approach, verbal stimuli were found to be processed faster or more accurately when presented to the right of a fixation cross while visuospatial material was processed faster or more accurately when presented to the left visual field (Durnford & Kimura, 1971). This result is consistent with left hemisphere specialization for language and right hemisphere specialization for visuospatial skills established by the anatomoclinical method.

However, the reliability of this experimental scheme has been questioned. For instance, RT and accuracy in a verbal recognition task are far from being able to replace the Wada procedure to determine whether language is lateralized in the left or right hemisphere of epileptic patients in pre-surgical tests (Channon, Schugens, Daum, & Polkey, 1990). The major problem with this approach is that in neurotypical participants, the cerebral commissures are extremely efficient in rapidly relaying

information, so that hemispheric specialization cannot be reliably identified (Ivry & Robertson, 1998). Research on lateralization of brain function using RT as the dependent variable has instead begun to rely on facilitation or inhibition of the brain activity of one hemisphere at a time through non-invasive cortical stimulation procedures such as TMS (Andres, Seron, & Olivier, 2005) and tDCS (Sparing, Dafotakis, Meister, Thirugnanasambandam, & Fink, 2008).

The interhemispheric commissures have also been studied with tachistoscopy. The earliest reliable experimental design used for this purpose was the Poffenberger paradigm (Poffenberger, 1912). In Poffenberger tasks, one stimulus is briefly presented to the left or to the right visual field. The participant must simply detect the stimulus and press a key with the left hand in half the trials, and with the right hand in the other half. There is no required recognition of the stimulus in the classical Poffenberger task, unlike in divided visual field tasks. If the same hemisphere processes the visual stimulus and the motor command for the response, interhemispheric transmission is not necessary. If one hemisphere receives the visual information and the contralateral hemisphere must execute the motor command, interhemispheric transmission is necessary. The difference between these two conditions therefore represents the interhemispheric transfer time. This experimental paradigm has yielded over a hundred research reports estimating interhemispheric transfer times in various contexts. The involvement of interhemispheric transfer generally adds about three milliseconds to RT (Braun, 1992), with very little variation. It has become pretty clear that what is relayed via the commissures is the final motor command. This result leaves few possibilities for novel experimental exploration taking into account more complex brain activity, such as the underlying hemispheric specialization or particularities of the interhemispheric commissures.

However, brain-inspired tachistoscopy is not dead by any means. Dimond (1969) introduced a tachistoscopy paradigm that in principle allows for simultaneous

inference testing of intra and interhemispheric dynamics underlying simple neural relay, but also attention and cognition. The Dimond paradigm continues to generate interest as indicated by continuing and numerous publications. Unlike divided visual field recognition tasks, Dimond tasks require comparison of two stimuli which are simultaneously presented unilaterally in one condition, and bilaterally in another. Pairs of stimuli presented in one visual field are initially processed only by the receiving hemisphere whereas pairs presented bilaterally initially impose processing of one target stimulus in each hemisphere. In unilateral presentations there is no requirement for interhemispheric communication of visual or cognitive information, but the burden of early stimulus processing falls entirely on one hemisphere. In contrast, bilateral presentation requires interhemispheric transfer of visual or cognitive information so that the target stimuli may be compared, but the burden of early stimulus processing is spread between the two hemispheres. Matching tasks are most often employed because they are an easy way to force interhemispheric transfer of information from one hemisphere to another. A comparison of the reaction time (RT) or error rate of the unilateral and bilateral conditions can reveal characteristics of the relations between the two hemispheres of the brain. Two classes of mechanisms potentially able to explain unilateral field advantages (UFA) and bilateral field advantages (BFA) in RT data come to mind. Limits of early processing of the single hemisphere may provide advantages to bilateral presentations, but limits of interhemispheric communication may provide advantages to unilateral presentations. Such brain dynamics need not be mutually incompatible.

Though manipulation of the size of the BFA through changes in experimental conditions had previously been reported, Banich & Belger (1990) were the first to obtain a significant UFA and a significant BFA in the same experiment, thereby popularizing a new research field centered on experimental manipulation not only of the size, but also of the direction of the effect. They obtained this first result by manipulating “computational complexity”, defined as the number of processing steps

required in order to do the task. This factor is a measure of task complexity. An easy version of their task required a response when two letter-shaped stimuli were physically exactly identical, while a more difficult version required a response when two stimuli represented the same letter, irrespective of capitalization. Visual identification and comparison was sufficient for the first task but at least one further step, the decoding of the visual stimulus as a linguistic symbol, was necessary for the second task. It is the complexity of the matching criterion which they manipulated. The easier physical matching task yielded a UFA while the more difficult letter-name matching task required more processing steps and accordingly yielded longer RT as well as a BFA. It is not the addition of a verbal component that was emphasized in the interpretation of this experiment. Rather, the modification of the match criterion was designed specifically so that a physical matching strategy would not be sufficient to accomplish the task.

The explanation of this effect given by Banich (1998) was that the necessary processing steps in computationally simple tasks are more efficiently accomplished by one hemisphere alone in order to avoid the cost of interhemispheric transfer. However, in more complex tasks one hemisphere cannot do the task efficiently by itself. The processing demands of the task overwhelm its processing capacity, creating an “intrahemispheric bottleneck”. Anything that the hemisphere cannot process now because it is too busy must be delayed. It then becomes advantageous to split the early processing steps between the two hemispheres and to take advantage of their parallel processing capabilities. In these more complex tasks, the cost of interhemispheric cooperation becomes minimal compared to the cost of the intrahemispheric processing bottleneck. Experimental effects supporting this model have frequently been reported in the literature (see our review below). However, effects contradicting this model have also been reported, albeit less frequently (see our review below). Theoretical explanations for the second category of findings have barely been considered.

While the effect of the complexity of the matching criterion on interhemispheric comparison is usually the effect of main interest in these studies, we note that it is not always the largest effect in terms of RT. Manipulations of the level of similarity between target stimuli, of the number of additional non-target stimuli, of the position of target stimuli and of the type of stimuli used are sometimes not statistically analyzed or otherwise overlooked even when they appear to have more important effects on RT, at first glance, than the experimental variable of traditional interest.

A tentative generalization of the model proposed by Banich to all studies within the Dimond paradigm might be possible. Mean RT of the experimental condition can be used to define, *a posteriori*, which of two conditions is easy and which is difficult. The rationale for the use of RT as a measure of task difficulty is that an individual whose performance on a task is faster than the others' would certainly be said to be more capable. Therefore RT seems to measure capacity, so long as accuracy rates are also maintained. If one change is introduced to a task and the average RT of a group of individuals rises, the explanation that the capacities of the group of participants have suddenly changed is not parsimonious. Rather, it is much more likely that the change in the task explains the result, and that higher capacity would be required to attain the same speed, i.e., the task has become more difficult.

A comparison between experiments where task complexity is explicitly manipulated and experiments where the manipulation is different thus becomes possible if task difficulty, operationalized by using RT, is used to define easy and hard conditions in all experiments. An intrahemispheric bottleneck effect is, under these conditions, defined as an increase in the size of the BFA (or a decrease in the size of the UFA) when difficulty (as measured by RT) increases.

One objection to the idea that the effect of difficulty as indexed by RT is equivalent to the effect of increases in task complexity (Belger & Banich, 1998) is that error rates are sometimes higher in the low complexity condition. The possible presence of

speed-accuracy tradeoffs may indeed cast doubt on this method of determining which of two experimental conditions is more difficult. However, significant coherence between error rates and RT across difficulty conditions is much more common (Belger & Banich, 1992; Kraft et al., 2005; Lavidor & Ellis, 2003; Weissman & Banich, 2000; Weissman, Banich, & Puente, 2000) than discordance, with only one example of the contrary (Belger & Banich, 1998). More importantly, in experiments in which task complexity was manipulated, the physical matching condition always yielded a lower global RT than the complex matching condition, with no exceptions. As a measure of difficulty RT therefore appears reliable, and intrahemispheric processing bottleneck effects should thus be obtained without explicitly manipulating task complexity.

Braun et al. (2011) found that unilateral presentations were significantly more advantageous, or bilateral presentations were less advantageous, in difficult conditions than in easy conditions. They obtained this result by manipulating the spatial location of target stimuli, not specifically task complexity, in a physical matching task. The results of these experiments can certainly not be explained by an overload of the single receiving hemisphere's capacity in the early stages of processing. These authors theorized that their finding can be explained by an interhemispheric transfer bottleneck associated with the callosal interhemispheric commissure, rather than an intrahemispheric processing bottleneck. They also hypothesized that physical matching tasks were more likely to yield these interhemispheric bottleneck effects, a prediction which appears to be consistent with the proposal by Banich that physical matching tasks yield UFAs because they do not overload a hemisphere's processing capacity.

The current quantitative review aims to determine whether the intrahemispheric bottleneck model applies to the Dimond paradigm as a whole or to

the subset of studies where task complexity is explicitly manipulated. Several other variations in the Dimond tasks were considered as well.

2.2. Methods

2.2.1. Selection criteria

Data sets relevant to the study of intrahemispheric bottleneck in neurotypical participants were gathered by an exhaustive review of the literature on interhemispheric dynamics in Dimond tasks. Articles published between the years 1969 and 2013 were sought with Google Scholar, PubMed and PsycArticles with the keywords "bilateral field advantage", "BFA" "unilateral field advantage", "UFA", "within hemisphere advantage", "across hemisphere advantage", "within field advantage", "across field advantage", as well as from reference lists of relevant articles and from lists of articles citing relevant articles. Search limits and Boolean operators were not used. Over 300 articles were screened based on their title and abstract. Of these, 124 were further assessed for eligibility based on their methodology and available data.

Only experiments realized with neurotypical volunteers were retained for the current review. Experiments had to respect the Dimond paradigm: There had to be a unilateral condition in which both stimuli were simultaneously presented in the same visual field, and a bilateral condition in which both stimuli were simultaneously presented in opposite visual fields. Central presentation of both stimuli does not ensure that one stimulus is presented to each hemisphere and that interhemispheric cooperation is necessary, thus it is not considered a bilateral presentation. Mean unilateral and bilateral RTs had to be available in an easy condition (short RTs) and a hard condition (long RTs).

The difference between the easy and hard difficulty conditions was the critical consideration. For the purposes of data selection and analysis, the “easy” condition was defined *a posteriori* as the one with shorter RT for both unilateral and bilateral trials, and the “hard” condition was defined as the one with longer RT for both unilateral and bilateral trials. If two conditions were present but could not be identified as “easy” and “hard”, the study was excluded from the database.

For the purpose of the current quantitative review, no trial was counted twice in the same database in order to preserve independence of the gathered data sets. More than one data set could be taken from the same article as long as no trial was counted twice. Data sets in which the RTs in easy and hard conditions came from the same participants were always privileged over data sets where the group of participants differed from one condition to another. This was done to minimize the impact of inter-individual variations in reaction time. When two groups were used, both were equivalent in education and age, so as to partially control confounding factors such as psychomotor speed.

The BFAs for the easy and the hard condition were calculated separately as “Unilateral RT minus Bilateral RT.” Positive values therefore indicated a longer RT for the unilateral condition, signifying that a BFA was obtained. Negative values corresponded to a UFA. Then, a “delta-balance” factor corresponding to the dependent variable was calculated as “Hard BFA minus Easy BFA”. Therefore, a positive value corresponds to a larger BFA in the difficult condition supportive of the intrahemispheric processing bottleneck model. The opposite result pattern, a negative value, corresponds to a lower BFA in the difficult condition and can be said to challenge the intrahemispheric processing bottleneck model. “delta-balance” represents the difference between the field advantages of the difficult and easy conditions, in milliseconds. Seventy five data sets respecting the above

inclusion/exclusion criteria, collected from 55 different source articles, were retained for statistical analysis.

The size of the bilateral field advantage relative to the global response time, not simply the size of the bilateral field advantage, was considered when selecting studies. A “delta-balance-a” adjusted factor was also created with “delta-balance” as the numerator and “Global RT” as the denominator. When selecting among multiple non-independent data sets of one study, inclusion in the database was determined by the largest “delta-balance-a.” While a selection based on the largest F-statistic could have been employed, such a criterion would have introduced a bias in the database towards effects of task complexity which have more often been subjected to statistical tests, even when these were not at first glance the largest effects available.

2.2.2. Independent variables

If mean RT of each condition can be considered a measure of difficulty, then the difference between these two mean RTs might also be considered a measure of the increase in task difficulty from the easy to the hard condition. As larger increases in difficulty might yield larger bottleneck effects, this “increase in difficulty” variable, measured in milliseconds, was included in the database. A square root transformation was used to make the distribution of this variable normal for purposes of statistical analysis. Global task difficulty of each experiment, represented by mean RT, was also used for statistical analyses.

The type of experimental manipulation between the easy and hard conditions varied across studies. Consequently, dichotomous variables were coded to express whether each of the three most common manipulations was present (0 = “not present”, 1 = “present”). For tasks using a manipulation of task complexity, the difficult condition necessitated additional processing steps compared to the easy condition. A

“manipulation of stimulus type” was also common. For instance, an easy condition using shapes as stimuli and a difficult condition using pictures as stimuli could be classified as a manipulation of stimulus type. Finally, in many data sets RTs were found to be shorter when both target stimuli were identical rather than non-identical in the absence of an explicit manipulation of task complexity, in what we have termed a “manipulation of stimulus similarity” (0 = similar or same, 1 = different). A typical example of such an effect comes from response choice tasks where RT is recorded for matching pairs and for non-matching pairs. Dichotomous variables were created for each of these three types of experimental manipulations. Other manipulations were also found, but they occurred in less than 10 data sets and were therefore given no further consideration.

A dichotomous “only physical matching” variable separated data sets where complex matching conditions were present (code: 0) from those limited to two physical matching conditions (code: 1). This factor permitted a test of the prediction that interhemispheric bottlenecks would be more readily obtainable with pairs of physical matching tasks. Complex matching conditions included all name-matching tasks, such as letter-name tasks, number-name matching tasks, and shape-name matching tasks, and required more processing steps following physical perception of stimuli before a matching pair could be found. A variable named “only complex matching” separated data sets where physical matching conditions were present (code: 0) from those with only complex matching conditions (code: 1).

A “verbal stimuli” dichotomous variable was also used to separate data sets in which stimuli were not language-related, such as shapes and pictures (code: 0), from those in which stimuli were language-related, such as letters, numbers and words (code: 1).

All experiments in the database required the presence of at least two stimuli for inter-stimulus comparison. A “non-target weight” factor with three possible values was created to code for the amount of processing required to identify target stimuli and

reject non-target stimuli (see figure 1), with the first value indicating a total absence of non-target stimuli, the second value indicating that non-target stimuli are not eligible targets and may be considered distractors, and the third value indicating that non-target stimuli are potential targets which could have been part of the target pair if a similar stimulus had been presented alongside it.

Non-target weight	Physical matching	Complex matching (Letter-name)
No non-targets (Coney, 1985)	A A	a A
Distractors (spatial cues) (Pollmann & al., 2003)	[A] c [A] b	[A] c b [a]
Distractors (non-eligible stimuli) (Marsolek & al., 2001)	A # A #	A # # a
Potential targets (Banich & Belger, 1990)	A C A	A C a

Figure 2.1. Match trials in different versions of the Dimond task. The “non-target weight” variable reflects the amount of processing required to distinguish target stimuli from non-target stimuli. In the absence of non-targets, all processing is target processing. When distractors are present, non-target stimuli must be recognized by the location of spatial cues (line 2) or by their non-eligibility as stimuli (line 3). Potential targets cannot be discarded as non-targets on the basis of recognition, and must be compared to other stimuli until a matching pair is found. Examples are taken from published letter-matching Dimond tasks with a physical matching and a complex (letter-name) matching condition.

Some tasks use a stimulus positioning pattern which is constant across trials, often by putting two stimuli on the left side and two on the right side. In these experiments, the number of stimuli presented to each hemisphere remained the same for every trial. Stimulus positioning patterns which are semi-constant are also common: In these

tasks, two stimuli are presented in one visual field and one stimulus is presented in the other visual field. Unlike constant patterns, semi-constant patterns do not always present the same number of stimuli to a hemisphere. However, the distribution of stimuli, often two stimuli in one field and one in the contralateral field, is the same for every trial. Finally, the stimulus positioning pattern can be uneven. This happens in tasks with 2 stimuli, for instance, where both stimuli are on the left or right in unilateral trials, but one stimulus appears in each visual field in bilateral trials. The perceptual load of each hemisphere is therefore different in unilateral and bilateral conditions. Concern about these uneven positional patterns is evoked to justify the addition of non-target stimuli. Consequently, we included “stimulus position pattern” as a variable in the database. The constant, semi-constant and uneven positioning patterns were coded as “0”, “1” and “2” for purposes of statistical analyses, respectively.

2.3. Results

2.3.1. Analyses on all data sets

Seventy five data sets met the inclusion/exclusion criteria outlined above, and were included in the database. Forty-nine of these data sets yielded positive “delta-balance” and were consistent with the intrahemispheric bottleneck model. However, the remaining 26 data sets yielded a negative “delta-balance”, challenging the wider formulation of the interhemispheric bottleneck model as an effect of task difficulty (see table 1).

Table 2.1. *Table of data sets selected for the current quantitative review.* Data sets are sorted from the largest intrahemispheric bottleneck effect to the largest contrary effect (as in figure 2). Variables retained for this table were those that were found by us to be significantly associated with delta-balance in the database of 75 data sets. The experiment column offers details on which data were used. The manipulation column describes the variable which was manipulated in order to obtain an easy and a hard condition. Global RT is the mean RT of all four conditions (easy-difficult; unilateral-bilateral) of each data set. “ Δ -difficulty” compares the mean RT of the easy condition with that of the difficult condition in order to obtain a measure of the difference in difficulty between both tasks. “Non-target weight” measures, on an ordinal scale, how much processing must be done during each trial before the additional stimuli present can be identified as non-targets. “0” indicates no additional stimuli, “Dis” indicates additional stimuli which can be identified as non-targets before comparison, and “PT” indicates potential targets which require comparison. “Only physical matching” separates experiments using two physical matching tasks (Y) from experiments using at least one complex matching condition, such as letter-name matching (N). Finally, “delta-balance” indicates the size and direction of the intrahemispheric bottleneck (or contrary) effect, with “**” indicating significant effects in the original article, “n.a.” signifying non-tested effects, and “n.s.” non-significant effects.

Article	Experiment	Manipulation	Global RT (ms)	Increase in difficulty (ms)	Non-target weight	Only physical matching	delta-balance
Koivisto & Revonsuo, 2003	Experiment 2	Complexity	1191	245	PT	N	158 n.a.
Liederman, Merola, & Martinez, 1985	Experiment 1	Amount of practice	919	87	0	N	144 n.a.
Banich & Belger, 1990	Experiment 1	Complexity	713	142	PT	N	108*

Belger & Banich, 1998		Complexity	675	148	PT	N	105 n.a.
Lavidor & Ellis, 2003	Experiment 1	Complexity	615	232	PT	N	105 n.s.
Weissman & Banich, 2000	Experiment 1	Complexity	472	108	PT	N	88*
Koivisto & Revonsuo, 2003	Experiment 1; unrelated stimuli	Stimulus category	1031	196	0	N	84 n.s.
Koivisto & Revonsuo, 2003	Experiment 1; identical stimuli	Stimulus category	708	103	0	N	83 n.a.
Koivisto, 2000	Experiment 2	Complexity	815	325	PT	N	82*
Marsolek, Nicholas, & Andresen, 2001	Experiment 2	Complexity	805	157	Dis	N	80*
Cherry, Adamson, Duclos, & Hellige, 2005		Complexity	690	136	PT	N	75*
Mikels & Reuter-Lorenz, 2004	Experiment 1	Complexity	557	123	Dis	N	75*

Weissman & Banich, 2000	Experiment 2	Complexity	533	123	PT	N	69*
Yoshizaki & Tsuji, 2000	Only "same" judgments	Complexity	634	90	Dis	N	68*
Patel & Hellige, 2007	Experiment 2	Stimulus category	873	42	PT	N	65*
Koivisto & Revonsuo, 2003	Experiment 2	Complexity	768	292	PT	N	64 n.a.
Reuter-Lorenz, Sstanczak, & Miller, 1999	Older adults	# of additional stimuli	649	131	PT	Y	62 n.a.
Butcher & Cavanagh, 2008	Stimulus category		661	176	PT	Y	62 n.a.
Liederman, Merola, & Martinez, 1985	Experiment 2	Amount of practice	997	77	0	N	58 n.a.
Lopez, Kosson, Weissman, & Banich, 2007	Congruence of two Control group characteristics		658	115	PT	N	55*
Zhang & Feng, 1999	Stimulus similarity		913	121	PT	N	54*
Belger & Banich, 1992	Complexity		812	115	PT	N	53*

Yoshizaki, Weissman, & Banich, 2007	Only "match" judgments	Stimulus position	565	116	Dis	N	52*
Compton & Mintzer, 2001	Amount of practice	581	143	PT	N	48*	
Cherbuin & Brinkman, 2005	Complexity	863	64	PT	N	48*	
Weissman & Banich, 1999	Congruence of two characteristics	452	111	Dis	N	47*	
Butcher & Cavanagh, 2012	Experiment 1	Stimulus category	681	74	PT	Y	46*
Coney, 1985	Experiment 1	Complexity	462	50	0	N	40*
Patel & Hellige, 2007	Experiment 1	Stimulus category	552	92	PT	Y	39*
Weissman & Banich, 1999	Experiment 3	Congruence of two characteristics	458	81	Dis	N	39*
Kraft, Müller, Hagendorf, Schira, Dick, Fendrich, & Brandt; 2005					Dis	Y	38*
Koivisto, 2000	Experiment 1	Stimulus position	826			N	38*
	Experiment 1	Complexity	653	161	0		

Coney, 1985	Experiment 2	Complexity	468	56	0	N	36*
Welcome & Chiarello, 2008	Complexity		741	64	Dis	N	36*
Jeeves, Ludwig, Moes, & Norman, 2001	Neurotypical control group	Stimulus category	644	185	0	Y	30 n.a.
Belger & Banich, 1998	Complexity		805	90	PT	N	29 n.a.
Yoshizaki, Sasaki, & Kato, 2008	Congruence of two characteristics		569	18	Dis	N	28 n.a.
Yoshizaki, Weissman, & Banich, 2007	"mismatch" judgments	Stimulus position	594	54	Dis	N	24 n.a.
Maertens & Pollmann, 2005	Complexity		701	84	Dis	N	21*
Reuter-Lorenz, Stanczak, & Miller, 1999	Younger adults	# of additional stimuli	525	60	PT	Y	18 n.a.
Ludwig, Jeeves, Norman, & DeWitt, 1993	Experiment 1	Stimulus similarity	871	81	0	N	18 n.s.

Ludwig, Jeeves, Norman, & DeWitt, 1993	Experiments 3-4 combined	# of additional stimuli	706	197	d	Manipulate	N	17*
Butcher & Cavanagh, 2012	Experiment 2	Stimulus category	444	32	Dis	Y	Y	17 n.s.
Ratinckx, Nuerk, van Dijck, & Willmes, 2006	Congruence of two characteristics		649	42	PT	N	N	17*
Ludwig & Jeeves, 1996 Rozenstein, Latzer, Stein, & Eviatar, 2011	Independent control group	Complexity	751	23	0	N	N	12 n.a.
Kraft, Pape, Hagendorf, Schmidt, Naito, & Brandt, 2007	Complexity	940	235	0	N	N	10 n.a.	
Yoshizaki, 2000	Experiment 1	Complexity	989	391	Dis	N	Y	5 n.s.
Braun, Collin, & Mailloux, 1997	Stimulus similarity	458	7	0	N	N	3 n.s.	
Moes, Jeeves, & Norman, 1996	Priming	792	19	0	N	-2	n.a.	

Davis & Schmit, 1973	Only "match"	judgments	Complexity	747	100	0	N	-4 n.s.
Koivisto & Revonsuo, 2003	Experiment 2	Semantic similarity	797	154	PT	N	-4 n.a.	
Leblanc-Sirois & Braun, in press	Grey circles, different	Stimulus position	442	10	0	Y	-4 n.s.	
Leblanc-Sirois & Braun, in press	Grey circles, same	Stimulus position	424	4	0	Y	-6*	
Desjardins, Braun, Achim, & Roberge, 2009	Stimulus position	391	6	0	Y	-7*		
Braun et al., 2011	Experiment 1	Stimulus category	391	13	0	Y	-9*	
Ludwig, Jeeves, Norman, & DeWitt, 1993	Experiment 2	<i>Stimulus similarity</i>	918	41	0	N	-11 n.a.	
Koivisto & Revonsuo, 2003	Experiment 1, semantically related stimuli	Stimulus category	938	245	0	N	-12 n.s.	
Weissman, Banich, & Puente, 2000	# of additional stimuli	749	278	Dis	N	-14 n.s.		

Jeeves & Lamb, 1986	<i>Stimulus similarity</i>	746	29	0	Y	-15 n.a.
Pollmann, Zaidel, & von Cramon, 2003	<i>Stimulus similarity</i>	660	58	Dis	N	-16*
Banich & Belger, 1990	Type of high-level task	705	31	PT	N	-16 n.a.
Brown & Jeeves, 1993	Only "mismatch" judgments	857	84	0	N	-19 n.a.
Kraft, Kehrer, Hagendorf, & Brandt, 2011	<i>Stimulus position</i>	851	71	Dis	Y	-25 n.s.
Compton, Feigenson, & Widick, 2005	<i>Stimulus category</i>	695	30	PT	Y	-26*
Brown, Jeeves, Burnison, & Dietrich, 1999	<i>Stimulus similarity</i>	859	69	0	N	-28 n.a.
Yoshizaki & Hatta, 2005	Only "mismatch" judgments	873	103	Dis	N	-33 n.s.

Brown & Jeeves, 1993	Only "match" judgements	<i>Stimulus similarity</i>	861	54	0	N	-36*
Mikels & Reuter-Lorenz, 2004	Experiment 2	Non-target characteristics	594	70	PT	Y	-38*
Yoshizaki, 2000	Experiment 2	Complexity	796	157	Dis	N	-42*
Norman, Jeeves, Milne, & Ludwig, 1992		<i>Stimulus similarity</i>	922	42	0	Y	-45 n.s.
Sereno & Kosslyn, 1991	Experiment 4	<i>Stimulus similarity</i>	930	87	0	Y	-70*
Sereno & Kosslyn, 1991	Experiment 1	<i>Stimulus similarity</i>	1091	61	0	Y	-96 n.s.
Yoshizaki & Hatta, 2005	Only "match" judgements	Amount of practice	866	91	Dis	N	-136*
Weissman, Banich, & Puente, 2000	# of additional stimuli		499	129	Dis	Y	-166*

In order to investigate differences between studies fitting the intrahemispheric bottleneck model and studies yielding contrary results, Kendall's Tau-b correlations between "delta-balance" as the criterion variable and predictor variables described in the previous section were used in order to determine which variables would be selected for use in a stepwise multiple regression. These included "global task difficulty", "difference in difficulty", "manipulation of stimulus type", "manipulation of task complexity", "manipulation of stimulus similarity", "only physical matching", "only complex matching", "verbal stimuli", "non-target weight", "stimulus position pattern", and "number of additional stimuli". Kendall's Tau-b correlations were used because many variables in the database were measured on an ordinal scale, and did not meet the postulates for Pearson correlation. The independent variables with a correlation of .2 or more with the dependent variable were then used in a stepwise multiple regression model. These were all significant, and included only "difference in difficulty" ($\text{Tau-b} = .288, p < .0005$), "manipulation of task complexity" ($\text{Tau-b} = .363, p < .0005$), "manipulation of stimulus similarity" ($\text{Tau-b} = -.341, p < .0005$), "only physical matching" ($\text{Tau-b} = -.291, p = .002$), and "non-target weight" ($\text{Tau-b} = .291, p = .001$). These variables were either normally distributed or dichotomous. The other independent variables did not correlate significantly with "delta-balance".

Multiple stepwise regression was used to obtain the best predictive model (adjusted $R^2 = .245, F_{(2,71)} = 8.894, p < .0005$). The model settled at three predictors: "manipulation of task complexity", "manipulation of stimulus similarity", and "only physical matching". The regression equation was created using standardized Z-scores for both the dependent and the independent variables: "delta-balance" = (.217 * "manipulation of task complexity") - (.274 * "manipulation of stimulus similarity") - (.251 * "only physical matching") + .003. The correlation between the predictor obtained through this equation and the "delta-balance" criterion was significant ($\text{Tau-b} = .433, p < .0005$).

The dichotomous “manipulation of task complexity” variable was the first predictor selected in the regression equation and it is positive, a result consistent with the intrahemispheric bottleneck model as formulated specifically by Banich (1998).

Twenty-three out of 25 data sets in which task complexity was manipulated show an intrahemispheric processing bottleneck effect (see figures 2 and 3), a result significantly different from chance according to a two-tailed binomial test ($p < .0001$). When the difficult condition is more computationally complex than the easy condition, larger intrahemispheric bottlenecks are obtained. In the group of data sets where task complexity was not manipulated, 26 out of 50 studies fit the intrahemispheric bottleneck model, a result no better than chance.

“Manipulation of stimulus similarity” was the second selected predictor, and it was negative. Unexpectedly, this predictor pushed experiments towards effects challenging the intrahemispheric bottleneck model. In 11 of the 12 studies where the manipulation is a change between “same” and “different”, the easy condition was the “same” condition. Nine out of these 11 studies presented an effect contradicting the intrahemispheric processing bottleneck model (see figures 2 and 3) with negative delta-balance values. The anomalous study (Braun, Collin, & Mailloux, 1997) also showed a larger advantage for unilateral presentations when participants had to react when both stimuli were the same, though this advantage was not significant. Still, ten out of 12 data sets yielding a smaller BFA for different stimuli is a result significantly different from chance in a two-tailed binomial test ($p = .035$). It suggests that matching two stimuli which are different may cause an increase in difficulty explainable by delays in interhemispheric transmission or coordination, not by increased processing times within each hemisphere.

“Only physical matching” was the third predictor retained in the stepwise multiple regression. This predictor remained significant even though the “manipulation of task complexity” predictor, with which it correlated significantly ($Tau-b = -.441$, p

<.0005), was selected in the regression. Only nine out of 21 experiments limited to physical matching supported the intrahemispheric bottleneck model while 12 experiments did not, a result no better than chance in a two-tailed binomial test ($p = .33$). Forty out of 54 experiments not limited to physical matching tasks respected the intrahemispheric bottleneck model ($p < .005$), with 14 contrary effects.

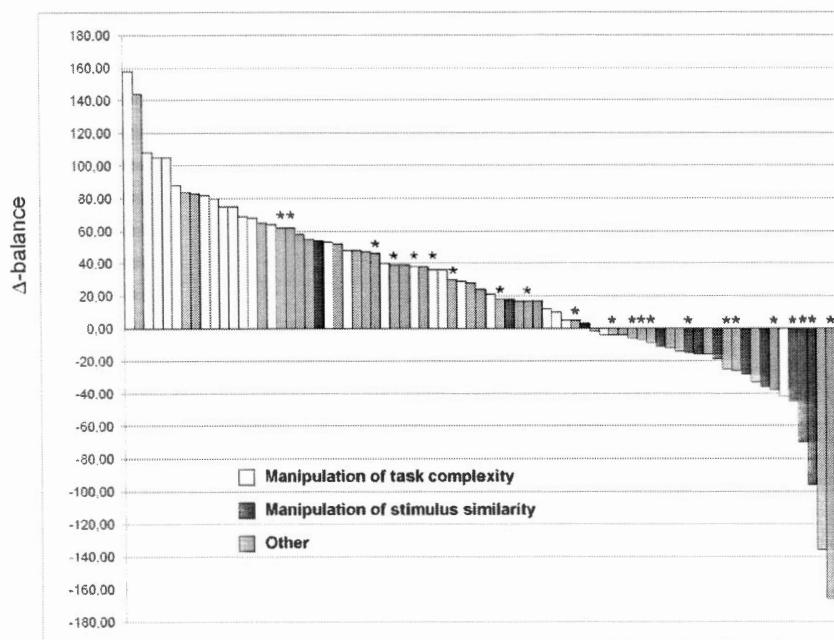


Figure 2.2. “*delta-balance*” and the three predictors. Each bar represents one of 75 data sets, and is shaded according to the type of manipulation. *delta-balance* values over zero indicate an intrahemispheric bottleneck effect. *delta-balance* values below zero indicate an interhemispheric bottleneck effect. Manipulation of task complexity tends to yield effects supporting the intrahemispheric bottleneck model, while manipulation of stimulus similarity tends to yield opposite effects. The asterisks (*) refer to the “complex matching condition” predictor, and indicate data sets where only physical matching tasks are used.

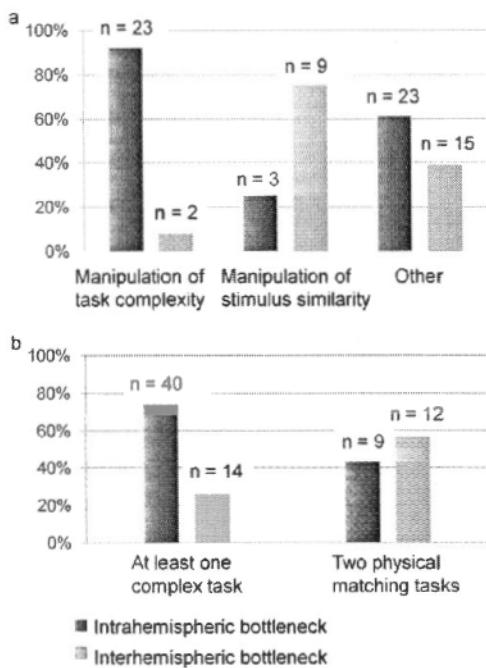


Figure 3. *Predictors of the intra and interhemispheric bottlenecks.* (a) Within-experiment manipulation of task complexity favors the intrahemispheric bottleneck effect, while manipulation of stimulus similarity favors the interhemispheric bottleneck. (b) Whole-experiment characteristics are also important. Complex tasks favor the intrahemispheric bottleneck while physical matching tasks non-significantly favor the interhemispheric bottleneck.

While these analyses help clarify why experiments yield intrahemispheric bottleneck or contrary effects, an understanding of what affects the size of each effect has yet to be reached. For this reason, further analyses were run separately on the 49 data sets supporting the intrahemispheric bottleneck effect and the 26 data sets yielding an inverted effect.

2.3.2. Effects supporting the intrahemispheric bottleneck model (49 data sets)

Statistical analyses were carried out with the data sets supporting the intrahemispheric bottleneck model in order to investigate whether some characteristics of the documented experiments led to larger effects. Tau-b correlations between the full set of independent variables and “delta-balance” were computed because many variables were distributed on an ordinal scale.

“Non-target weight” correlated significantly with “delta-balance” ($\text{Tau-b} = .281, p = .014$). Larger intrahemispheric bottleneck effects arose when the non-target weight was more important. This is also consistent with the intrahemispheric bottleneck model. Stimuli which require more processing steps in order to be identified as targets or non-targets are more likely to overload a single hemisphere’s cognitive and attentional resources.

2.3.3. Effects not supporting the intrahemispheric bottleneck model (26 data sets)

Statistical analyses were carried out with the data sets challenging the intrahemispheric bottleneck model in order to investigate whether some characteristics of the documented experiments led to larger effects. Tau-b correlations between the full set of independent variables and “delta-balance” were computed. In the set of interhemispheric bottleneck effects, there was a significant correlation between “global RT” and “delta-balance” ($\text{Tau-b} = -.288, p = .04$), more difficult tasks yielding larger effects.

2.3.4. Effects of differences in difficulty

In the 49 data sets supporting the intrahemispheric bottleneck model, “delta-balance” correlated significantly with “difference in difficulty” ($Tau-b = .351, p = .013$). Larger intrahemispheric bottleneck effects were therefore linked to larger differences in difficulty as indexed by RT. However, in the set of 26 contrary effects, there was also a significant correlation between “delta-balance” and “difference in difficulty” ($Tau-b = -.3, p = .032$). In this subset of the database, larger opposite effects were linked to larger differences in difficulty as indexed by RT. While these may appear to be contradictory results, another interpretation of this effect is that unlike task complexity, task difficulty influences the size of the intrahemispheric bottleneck or opposite effect, without influencing its direction. Indeed, “difference in difficulty” correlates best with the absolute value of “delta-balance” ($Tau-b = .348, p < .0005$).

2.4. Discussion

2.4.1. Limitations of the current study

Some limits of the current study stem from the screening process. For instance, articles not using the standard terminology associated with the Dimond paradigm may not have been identified. This review was also limited to published research. Publication bias therefore remains a concern. Selection of studies also caused some difficulties, notably because not all experiments in the Dimond paradigm aimed specifically to reveal the causes of the intrahemispheric and interhemispheric bottleneck effects. In many cases, the BFA or UFA of one study was the variable of main interest. In these cases, two experiments from the same article were sometimes combined into one data set as the easy and difficult conditions if both experiments were extremely similar and if the groups of participants for each study were

equivalent in age and level of education. However, inter-individual RT variability in these data sets remains incompletely controlled in the analyses carried out here. Moreover, individuals were not matched across data sets, further limiting the current study due to inter-individual variability.

The number of recorded “delta-balance” effects not tested for significance was also high. This can be explained by the fact that many articles were not originally written to answer the research question relevant to the present quantitative review, and that a bias in favor of specific models prompted researchers not to always test the “delta-balance” effects which were largest in terms of RT. Though weighting studies in function of their significance can often improve the quality of a quantitative review, not doing so was deemed necessary in order to counter this bias.

Some studies reporting significant “delta-balance” effects also had to be excluded from the current study when the size of “delta-balance” was unknown or when it was impossible to identify which of two conditions was easy and which was difficult. RT data were sometimes omitted in the written articles and instead only available in graphs. In these cases, data were extracted from the digital versions of the graphs if a pixel-analysis technique could be used to obtain relatively reliable (± 3 ms) data. If such a procedure could not be used and the data could not be obtained in another way, the study had to be excluded.

In a majority of the experiments reviewed here, control of many task characteristics relevant to the study of intra and interhemispheric bottleneck effects could be improved. Notably, in the most common experimental scheme (see figure 1) the inter-target distance is shorter for unilateral trials than for bilateral trials. Inter-target distance is known to affect RT in visual search tasks (Reddy, Van Rullen, & Koch, 2003). Response to horizontally aligned stimulus pairs in a physical matching task has previously been shown to occur faster than response to oblique stimulus pairs (Desjardins, Braun, Achim, & Roberge, 2009; Braun et al., 2011). However, the

obliqueness of the imaginary line linking the two target stimuli was also different in unilateral and bilateral trials in the most commonly used arrays. A small minority of studies balanced inter-stimulus distance and inter-stimulus obliqueness across all experimental conditions (Desjardins, Braun, Achim, & Roberge, 2009; Braun et al., 2011; Leblanc-Sirois & Braun, *in press*). Incomplete control of these variables can affect time spent on visual search differently in unilateral and bilateral trials, reducing the validity of “delta-balance” as a quantitative measure of unilateral or bilateral advantage.

Finally, though all selected data sets matched participants of the easy and hard conditions for age when two different groups were used and data obtained with non-neurotypical participants were excluded, we did not specifically use the age of participants as an exclusion criterion, nor did we control for this individual characteristic.

2.4.2. What creates the intrahemispheric bottleneck?

The most important significant predictor of the intrahemispheric bottleneck effect found in our analysis was manipulation of the complexity of the matching criterion. In other words, requiring additional processing steps such as verbal encoding created experimental conditions where unilateral presentations would overload a hemisphere’s processing capacity, yielding increases in the size of the BFA in difficult conditions, as expected. This result clearly supports the interpretation of the intrahemispheric processing bottleneck proposed by Banich (1998).

However, there is one data set opposing the complexity-dependent intrahemispheric bottleneck model (Yoshizaki, 2000) in which “delta-balance” reached significance. This experiment used Japanese characters representing syllables as stimuli. The easy condition demanded a comparison of character names, while the hard condition

demanded a comparison of the vowel associated with the two target characters. Extraction of the vowel from the character representing a syllable was necessary in the hard condition, but not in the easy condition. This constitutes an additional processing step. Yet, a BFA of 10 ms was obtained in the easy condition, and a BFA of 52 ms was obtained in the hard condition, yielding a -42 ms “delta-balance” and significantly contradicting the interhemispheric bottleneck model. However, vowel-identification may be subject to hemispheric specialization for language, and the last processing step of the complex condition may by necessity have to be accomplished serially for each stimulus in the left hemisphere even during bilateral trials, as opposed to character name identification which can be processed in parallel without loss of efficiency. The intrahemispheric bottleneck model cannot apply to the addition of processing steps which must be realized in one specific hemisphere because this type of processing is not spread out among hemispheres in bilateral trials.

In studies where an intrahemispheric bottleneck effect was present, the non-target weight of the additional stimuli also correlated with the size of the intrahemispheric bottleneck effect. One interpretation, consistent with the Banich model, is that non-target weight modifies the computational complexity of the task as a whole.

Additional stimuli can be responsible for no processing steps if absent, for very few processing steps if cues tell the participant where the target stimuli will appear prior to stimulus onset safely ignoring non-targets, for more processing steps if they are different in some way from target stimuli such as number signs in a letter matching task, and for yet more processing steps if they are potential targets which must be fully analyzed if they are to be distinguished from actual targets (see table 1).

Non-target weight was manipulated systematically in only one experiment (Ludwig, Norman, Jeeves, & DeWitt, 1993), modulating the intrahemispheric bottleneck effect as would be expected from our own meta-analytic observations. However, higher

levels of non-target weight in an experiment may yield larger intrahemispheric bottleneck effects because any manipulation of the complexity of a task is magnified by non-target weight. For instance, a change from a physical matching condition to a letter-naming matching condition in a task with additional letter stimuli will increase the number of processing steps required to identify targets. By contrast, if the two additional stimuli are number signs (#) or if there are no additional stimuli, then the processing steps associated with language will only be applied to the two target stimuli, and the increase in computational complexity for the task as a whole will be smaller.

One issue with additional stimuli which must be heavily processed before they can be dismissed as non-targets is that they force extensive processing in both hemispheres even in unilateral trials. Such stimuli must be processed as potential targets, just as the real targets are, for a large part of the task. Four experiments which use potential targets as additional stimuli and use an array of four stimuli where each hemisphere processes 2 stimuli are included in the database (Cherbuin & Brinkman, 2005; Butcher & Cavanagh, 2008; two experiments from Butcher & Cavanagh, 2012). The RTs from these four data sets' are consistent with the intrahemispheric bottleneck effect. However, an explanation through the intrahemispheric bottleneck model may be dubious in these cases because the early processing load of each hemisphere is equal in unilateral and bilateral conditions.

Weissman, Banich, & Puente (2000) compared arrays of three stimuli and arrays of four stimuli in a task using letters as stimuli and as potential targets. The arrays of three stimuli contained two stimuli in one visual field, with the remaining stimuli positioned in the opposite visual field. In contrast, the arrays of four stimuli were distributed equally between the visual fields. The shapes of the arrays used in this study are identical to those illustrated in figure 1. The arrays of four stimuli pushed the unilateral advantage or disadvantage towards a UFA, despite longer global RT

compared to the arrays of three stimuli. In the physical matching task, the difference between these array shapes was 183 ms, a very large effect for an experiment with a low (499 ms) global RT. Since raising the number of stimuli had previously yielded intrahemispheric bottleneck effects when the processing demands to both hemispheres remained asymmetric (Belger & Banich, 1998), the large contrary effect obtained by Weissman, Banich, & Puente (2000) might best be explained by the perceptual symmetry added in the second condition, and cannot be explained merely by the addition of stimuli. The processing strategies used under conditions of perceptual asymmetry between the hemispheres appear to be very different from those used when both hemispheres have the same amount of processing load. Intrahemispheric bottlenecks may best be studied in the absence of non-target stimuli, or with pre-trial cues showing the position of target stimuli.

2.4.3. What creates an interhemispheric bottleneck?

The main manipulation which influenced “delta-balance” towards an opposite effect in the current analysis was a manipulation in which one condition required the participant to match perceptually similar stimuli, while the other condition required the participant to match perceptually different stimuli. With only one non-significant exception, similarity matching was the easy condition. Effects compatible with the interhemispheric bottleneck model following a manipulation of stimulus similarity have reached significance on several occasions (Sereno & Kosslyn, 1991; Brown & Jeeves, 1993; Pollmann, Zaidel, & von Cramon, 2003).

When RT rises in tasks where stimulus similarity is manipulated, it is a larger UFA that most often follows, not a larger BFA as would be predicted by the intrahemispheric processing bottleneck model. The results obtained with manipulations of the similarity of target stimuli are more easily explainable in terms

of limitations of interhemispheric transfer, interhemispheric coordination, or interhemispheric integration of information. It is the interhemispheric commissure here which appears to be overloaded or otherwise slowed down when target stimuli are different (see figure 4).

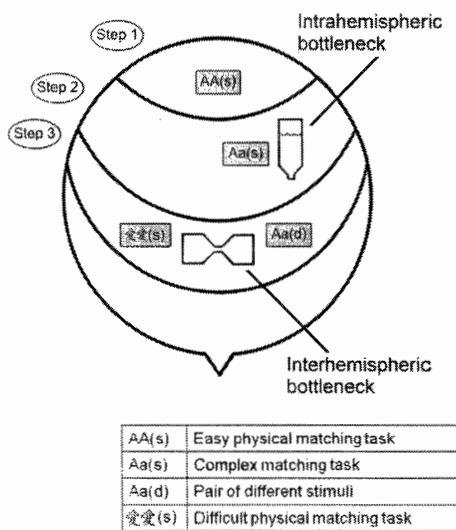


Figure 2.4. The intra and interhemispheric bottlenecks. In any Dimond task, it is expected that early visual processing will first occur in primary visual cortex (step 1). Then, one hemisphere may be overloaded in unilateral conditions (step 2), creating an intrahemispheric bottleneck. Finally, the obligation of sharing information with the contralateral hemisphere through the callosal commissure so that two stimuli can be matched may cause transfer delays attributable to an interhemispheric bottleneck (step 3). An easy perceptual identity matching condition, such as matching two “A” stimuli on the basis of shape, requires little processing, does not overload the hemispheres, and serves as the basic condition to which other conditions are compared in this figure. A complex non-physical matching condition, such as matching “A” and “a” on the basis of letter name, tends to overload the processing capacity of the hemisphere receiving visual information in unilateral conditions, creating an intrahemispheric bottleneck. A matching criterion which uses a pair of different target stimuli, requiring a response when “A” and “a” are different, tends to

create an interhemispheric bottleneck, as does a harder physical matching condition. (s) = same, (d) = different.

Bilateral callosal receptive fields tend to have the same selectivity for orientation on each side of the midline (Lepore & Guillemot, 1982), providing one physiological mechanism through which interhemispheric comparison of similar stimuli may occur faster than comparison of different stimuli. However, the group of 12 data sets which used a “same” and a “different” condition included only 4 experiments in which the matching was done on a purely visual basis. The other experiments manipulated stimulus similarity of targets while retaining a complex non-physical matching condition, such as letter-name matching. As an example, “AA” and “Aa” were both matching pairs in such tasks, but one is perceptually identical and the other is not. Physiological characteristics of visual callosal neurons may not be relevant if the information has already been encoded at a higher level before crossing the interhemispheric commissure. An explanation of the effect of manipulation of stimulus similarity based solely on the visual callosal system therefore appears insufficient, though these may instead provide a reason why studies using only physical matching conditions more often yield results supporting the interhemispheric bottleneck model. We do note, however, that the only large (“delta-balance” > 20 ms) counter-example found (Zhang & Feng, 1999) is also the only study where the stimuli of the “same” condition, Chinese characters, were not physically identical. Instead, they were perceptually very similar due to shared visual elements, whereas the “different” characters were not.

Similar results have been obtained with error rate data. Notably, the main purpose of the Hayes, Swallow, & Jiang (2010) study was to experimentally manipulate the level of similarity of target stimuli in a Dimond scheme. They expected to find reduced UFAs when the target stimuli were more different, based on the idea that very early perceptual grouping would be hindered by this manipulation and that perceptual

grouping would be more readily available when stimuli were presented unilaterally. Instead, they found that UFAs were larger when target stimuli were different, though they could not offer an explanation for this result.

Finally, it must also be noted that the purpose of the current quantitative review was not specifically to investigate the effect of manipulations of similarity of the target stimuli. The database of this quantitative review includes only 12 studies in which such a manipulation was used. Most of these effects were not statistically tested in the original studies in which the data appeared, and some effects of this type were left out of our database in favor of larger effects, due to the constraint of independence of data sets. The heterogeneity of the methods of experiments where levels of similarity are manipulated and the absence of a pre-existing model explaining this result adequately make this result difficult to interpret.

The third predictor of the interhemispheric bottleneck was the presence of two physical matching conditions. According to the prediction related to this variable, experiments realized with two physical matching conditions would reliably yield contrary effects. The results of the current review offer modest support to this prediction. As expected, it was easier to obtain interhemispheric bottleneck effects by comparing two physical matching conditions than when at least one complex condition was involved. However, with such tasks, interhemispheric bottleneck effects did not occur significantly more frequently than intrahemispheric bottleneck effects.

2.4.4. Future localization of intra and interhemispheric bottlenecks

A fMRI investigation of the intrahemispheric bottleneck effect was reported by Pollmann, Zaidel, & von Cramon (2003). They concluded that physiological evidence for the complexity-dependent intrahemispheric bottleneck was relatively weak,

though they did find increased activation in anterior areas when letter name, not letter shape, was the matching criterion. They proposed a different model based on brain imaging data, specifically a stronger activation in the ventral occipital cortex for unilateral trials of the difficult condition followed by a spread to the homologous brain area of the other hemisphere. Their interpretation of the intrahemispheric bottleneck effect is that in sufficiently difficult tasks, visual processing is realized bilaterally, regardless of presentation condition. In the bilateral condition, the distribution of information is efficient, as each half of the occipital cortex initially receives one target stimulus. In the unilateral condition, distribution is inefficient, as both target stimuli are first sent to the hemisphere contralateral to the presentation which must then share its visual information with the other hemisphere.

Intrahemispheric processing can then proceed in both hemispheres, in unilateral and in bilateral trials. Such a pattern of brain activity does not necessarily contradict the idea that there is an intrahemispheric bottleneck: it merely presents a process which can reduce the effects of the processing bottleneck and improve efficiency. Early interhemispheric sharing strategies may be used whenever possible because they are more efficient than letting one hemisphere's processing capacity be overloaded by task demands. The physical matching condition of the same study showed a UFA, indicating no important processing delays, and accordingly the pattern of spread of activity to the contralateral hemisphere was not present under this condition because the processing capacity of one hemisphere was sufficient for the task.

It is likely that under different conditions, an early interhemispheric information-sharing strategy cannot be used. In their experiment, Pollmann, Zaidel, & von Cramon (2003) used pre-stimulation cues identifying the locations of the two target stimuli. Therefore, processing non-targets became unnecessary because the correct location of true stimuli was known before the experimental trial began. The unilateral condition corresponded to a lack of involvement of one hemisphere immediately following stimulus presentation, because it could safely ignore the distractors being

presented to its contralateral visual field. This hemisphere's processing capacity was therefore available for processing of visual information coming from the other hemisphere through the interhemispheric commissure. This is not so when no pre-stimulation cues are used, because in this case non-target stimuli are not identified in advance. The participant is forced to pay attention to all stimuli, whether they are targets or non-targets. Yet, many intrahemispheric bottleneck effects have been documented using such tasks (see table 1). In these experiments, both hemispheres receive visual information from their associated visual fields, and must process it. In unilateral trials, the hemisphere which must process the non-targets is busy, and therefore not free to process a part of the contralateral hemisphere's load immediately.

In any case, the cerebral basis of the intrahemispheric bottleneck remains extremely vague and subject to alternative processing strategies which sidestep the issue, such as the task-sharing effect uncovered by Pollmann, Zaidel, & von Cramon (2003). In our opinion, this limitation may be surmounted by further investigation of contrary effects. If the results obtained by Banich and others can be explained by an intrahemispheric processing limitation of the hemispheres, these opposite results may be explainable through limits of interhemispheric transfer and integration of information, functions mediated by the interhemispheric commissure which could also be subject to bottleneck effects.

One advantage of pursuing hypotheses concerning these commissural limits is that the effects which support such hypotheses are more easily obtained if only simple perceptual matching tasks, such as physical matching tasks, are used. While the classical resource limitation effect uncovered by Banich & Belger (1990) requires higher-order cognitive functions, significant contrary effects have been found with the hard perceptual conditions yielding a global RT as low as 400 ms. This is promising in the long term for eventual physiological validation of theoretical

models. In such experiments, intrahemispheric processing relevant to RT is likely limited to visual areas, and unlikely to cause bottleneck effects due to the simplicity of the task. Manipulation of task difficulty is possible by controlling the degree of precision of visual information which must be transferred to the ipsilateral hemisphere for an accurate perceptual comparison between two target stimuli. We expect that matching two “A” stimuli creates a larger interhemispheric bottleneck when the only alternative to the stimulus is an “A” of a different font, rather than a different letter. The first case requires transfer of information to the ipsilateral hemisphere at a higher precision, and it should therefore overload the capacity of the corpus callosum and create an interhemispheric bottleneck effect.

The brain correlates of both bottleneck effects could be captured with high resolution event-related fMRI, using three matching conditions. First, an easy physical matching condition should yield a UFA. Second, if a harder physical matching condition were compared to the easy condition, a stronger UFA and an interhemispheric bottleneck effect could be expected. Stronger hemodynamic activation during bilateral trials at the border between visual areas V1 and V2 of both hemispheres, where cell bodies and dendrites of visual callosal neurons are located, would be expected to emerge commensurately to the amplitude of the UFA. Thirdly, a hard complex condition would be expected to produce a BFA and an intrahemispheric bottleneck effect. Stronger hemodynamic activation in visual cortex contralateral to the side of stimulus presentation during unilateral trials would be expected to be commensurate to the BFA.

CHAPITRE III

DYNAMIQUES INTERHÉMISPHÉRIQUES RÉVÉLÉES PAR LE TEMPS DE RÉPONSE DANS LE PARADIGME DE DIMOND

UNE INVESTIGATION EXPÉIMENTALE

Inter-hemispheric dynamics revealed by reaction time in the Dimond paradigm

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Running head : Callosal network dynamics and RT

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Abstract

The Dimond paradigm (DP) consists of tachistoscopically presenting two stimuli to be discriminated -either both stimuli in a single visual hemifield or one in each. The DP has been recently implemented by predecessors to index homotopy of the callosal fiber projection with reaction time (RT) as the dependent measure. Using simple perceptual discrimination tasks, it has been recently reported that the advantage of the unilateral stimulation condition significantly decreases with practice. This effect has been interpreted as being due to plasticity of the callosal network. Two experiments were designed to replicate these two little-known effects, namely callosal homotopy and callosal network plasticity. In addition, new evidence of another type of callosal network plasticity, termed “callosal network dispatching,” was sought by introducing to the DP double manipulation of orientations of stimulus-contours as well as of inter-stimulus arrays. Strong support for the callosal homotopy and callosal network plasticity effects was obtained. In addition, evidence for a “callosal network dispatcher” effect accrued.

3.1. Introduction

The Dimond paradigm

Dimond (1969) was the first to implement the idea that the extent of hemispheric resource sharing could be studied by comparing reaction times (RTs) of a discriminative judgment of two stimuli tachistoscopically simultaneously presented either both in a single visual hemifield or one in each visual hemifield. We term this method of investigating inter-hemispheric dynamics the “Dimond paradigm.” The experiments to be reported here make use exclusively of that paradigm.

Callosal homotopy

Axons of visual neurons traversing the corpus callosum (CC) project in a strongly homotopic manner to the other hemisphere, including in humans (Clarke & Miklossy, 1990; Dougherty, Ben-Sachar, Bammer, Brewer and Wandell, 2005). Thus, callosal neurons may be relatively limited to integration of stimuli which are symmetric relative to the vertical meridian (Herbert and Humphrey, 1996). Receptive fields of callosal neurons can extend at least as far as 16° from the meridian in monkey (Desimone, Moran, Schein and Mishkin, 1993) and in human (Dougherty et al, 2005; Rizzo and Robin, 1996). Fine grained single unit mapping with a retrograde degeneration technique (HRP) combined with single cell receptive field mapping has demonstrated that visual callosal axons are massively homotopic: their visual receptive fields are quite close to point-to-point on each side of the meridian in the cat (Segraves and Rosenquist, 1982). However, other authors conclude that there is a slight disparity (Houzel, Carvalho and Lent, 2002).

The “callosal homotopy” effect is revealed by RT in the Dimond paradigm

The callosal projection from both sides of the midsagittal plane is homotopic in three dimensions (depth, width, height). This concept of homotopy can be transposed from anatomical coordinates to the computer screen display. For example, suppose you are facing two computer screens perfectly stuck together side by side. Suppose you are fixating the cleavage between the two screens at midway. This makes the cleavage your vertical meridian. Then suppose the same symmetrical shape (a disc, a square, a diamond) is displayed in the middle of each computer screen. The pixels of each stimulus are then perfectly “homotopic” relative to the vertical meridian. However, suppose one stimulus is displayed northeast on the left screen and southwest in the other screen. You are still fixating the middle of the cleavage. The pixels of each stimulus are now “heterotopic” relative to the vertical meridian.

Commissures other than the corpus callosum are not believed to contribute the critical information required for such tasks in normal people (Brown, Jeeves, Dietrich and Burnison, 1999). Suppose that what must be relayed is a comparison running in both directions, from the left to the right hemisphere but also from the right to the left, simultaneously, at high speed. It is obvious that if the connection between the two hemispheres is limited to homotopic relay, but the two visual events to be relayed are not in homotopic relation, then some extra neural processing will be required. Stimuli located on both sides of the meridian but in heterotopic relation could engender a specific RT cost of inter-hemispheric integration because such visual information cannot be relayed directly or completely via the corpus callosum for comparison. Were the two stimuli to be in homotopic relation, then the interhemispheric integration could occur faster. It is important to understand that comparing any two stimuli can entail a modest RT cost if their inter-stimulus axis is oblique relative to the meridian, rather than, say horizontal, because cortical neurons in general, regardless of whether their receptive field is above fixation or below or to the right or left, or foveal or

peripheral, manifest a preference for horizontal integration over oblique integration. This effect has long been known to occur implicitly in the comparison of two stimuli as a result of their inter-stimulus axis (Li & Westheimer, 1979; Wenderoth, 1994). This general effect is termed the “oblique effect” (Berkley, Kitterle & Watkins, 1975). Thus, in the Dimond paradigm, to investigate a cost of specifically callosal limitation due to the homotopy of its fiber radiation, it is crucial to have a properly designed unilateral manipulation of obliqueness/horizontality of inter-stimulus axis as a baseline for detecting and isolating a putative homotopy effect. There must be an excedentary cost of heterotopy in the bilateral stimulation condition.

Using this line of reasoning, Desjardins and colleagues (2006) and Braun and colleagues (2011) tried to determine whether tachistoscopic visual stimulation and collection of RTs would reveal such an effect. They predicted that placing two stimuli to be discriminated in an oblique rather than a horizontal axis (relative to the meridian) on a computer screen (see figure 5 for an illustration) should present a cost in RT significantly greater in bilateral stimulation conditions (requiring inter-hemispheric integration) than in unilateral stimulation conditions (not requiring inter-hemispheric integration). They obtained precisely that pattern, significantly, in two distinct experiments (Desjardins and Braun, 2006; Braun et al., 2011, experiment 1). Stated more technically, the interaction between bilateral/unilateral stimulation and horizontal/oblique stimulus-pair location, relative to the meridian, was significant as predicted. More explicitly, a “homotopy effect” can be inferred if there is a greater cost of oblique stimulus-pair axes over horizontal stimulus-pair axes in the bilateral than in the unilateral stimulation condition. In both those experiments, the Dimond paradigm was implemented as a Go/No-go task. Significant demonstrations of the “callosal homotopy RT effect” were limited to conditions in which Go responses were to discrimination of stimulus shape (discs, squares).

A “callosal network plasticity effect” revealed by RT

The large field of research on the Dimond paradigm has become accustomed to an “*intra-hemispheric resource limitation effect*” first theorized and experimentally demonstrated by Banich and Belger (1990) and replicated several dozen times without much challenge from counter-results. The “*intra-hemispheric resource limitation effect*” is observed on tasks generating long RTs in the 600 to 900 ms range. When one of two subtasks is much more complex than the other, RTs become longer, and the balance of RT in unilateral and bilateral stimulation conditions moves toward a smaller UFA or even from a UFA to a BFA. For instance, short RTs accompanied by a UFA are observed when two stimuli must be matched on the basis of their physical identity, but long RTs accompanied by a BFA are observed when two letters must be matched on the basis of their name. Banich and Belger (1990) proposed that when a task is sufficiently complex a single hemisphere is overwhelmed by processing demands because it is solicited alone in the early stages of processing. A bottleneck ensues. However, if both hemispheres can participate in the early processing, in parallel, then that bottleneck is eschewed. Banich and Belger (1990) and nearly the totality of researchers having published on the Dimond paradigm seem to suppose that inter-hemispheric relay in the difficult condition entails an RT cost so negligible that it need not be mentioned nor controlled for. Accordingly, the experiments in question did not seek to perfectly balance out eccentricity of all stimuli, nor have they controlled for homotopy or analyzed practice effects in a single condition.

Braun et al (2011) found in their first experiment that practice on the task shortened RT in general and changed the balance of RTs in unilateral and bilateral field stimulation conditions in an unexpected direction (c.f., Banich & Belger, 1990, reviewed above), i.e., towards a smaller unilateral field advantage (UFA). The Braun et al (2011) finding, observed in a simpler perceptual matching task (RT was in the

300-500 ms range), is diametrically opposed to the “*intra-hemispheric resource limitation effect.*” With practice, the RT became shorter, but the unilateral/bilateral balance of RTs did not move toward a larger UFA as would be predicted by the “*intra-hemispheric resource limitation*” model. Instead, the balance moved toward a smaller UFA. A different brain mechanism has to be imagined to explain this effect.

Speed gains after practice are a result of adaptation to the task. Any adaptation to the task by the visual cortex which processes the stimuli, by the motor regions controlling the response, and by areas in between, would be captured in both unilateral trials and bilateral trials. However, an effect observed only on bilateral trials is more likely to capture an adaptation specific to the inter-hemispheric commissure. The result obtained by Braun et al (2011), greater adaptation in bilateral trials, therefore provisionally appears to be attributable to callosal network plasticity. This plasticity could be of several sorts. It could consist of slower adaptation of the commissural system than the intra-hemispheric network. Or the intra-hemispheric network could be quite fast and efficient but not plastic at all. The present report will address this issue.

A “callosal network dispatcher” effect revealed by RT

Braun et al (2011) reported a first experiment requiring a key press upon display of two identical stimuli (discs or squares). A second experiment was designed to still be a perceptual matching task, but to be as complex as possible. The purpose was to see whether, as would be predicted by Banich and Belger’s (1990) “*intra-hemispheric resource limitation model*” the balance of RT in unilateral versus bilateral stimulation conditions could be altered by task complexity. The rationale is that when a task gets very complex a single hemisphere becomes overtaxed at the early stage of visuoperceptual processing. An advantage then accrues from presenting half the

visual information to each hemisphere such that the whole visual brain can participate in the early visuoperceptual processing even though the two visual streams have to later be integrated via the corpus callosum. Accordingly, in Braun et al's (2011) two experiments, the unilateral/bilateral balance was expected to shift from a UFA in the simpler condition to a BFA in the more complex condition. The more complex task demands consisted of adding to the perceptual dimension of the task an attentional one: in addition to discrimination of shape the participant was required to discriminate colour (red vs blue) and the key press was required upon presentation of one identity (shape or colour) and one difference (shape or colour) thus adding an attentional constraint and an extra decision to the perceptual judgment. There was a significant UFA in their first experiment and a BFA in their second experiment, the interaction being highly significant, as predicted.

However, there were three problems with the Braun et al (2011) experiments. 1) The BFA in Experiment 2 was not statistically significant, 2) Their Experiment 2 could not distinguish the extent to which local/global orientational conflict caused the shift from a UFA to a BFA. In the Braun et al (2011) study, the square stimuli had oriented contours (horizontal and vertical). We term this aspect of orientation "local." In addition, in the Braun et al (2011) study, the orientations of the stimulus-pair arrays (or inter-stimulus axes) could be horizontal, oblique or vertical (the latter condition was not analyzed). We term this aspect of orientation "global." Braun et al (2011) compared horizontal and oblique inter-stimulus axes (global orientation) to investigate callosal homotopy but they used squares as stimuli and this stimulus comprises local orientation embedded in its contours. When the matching involved square-shaped stimuli the local and global orientations were discordant on some trials (oblique inter-stimulus axes), and on some trials they were concordant (horizontal inter-stimulus axes). See figure 5 for examples. The Braun et al (2011) study could not disentangle contributions of the two levels of orientation, local vs global, to the "callosal homotopy" effect. 3) Braun et al (2011) could not determine whether the

change in UFA/BFA balance of RT from their Experiment 1 to their Experiment 2 was due to task complexity coming from the change from a simple to a disjunctive perceptual decision or to a simpler task dimension consisting of discriminating identity vs difference of two shapes. Within the Dimond paradigm, comparison of two experiments differing only with respect to whether the key press is required upon display of identical versus different stimuli has been investigated by several predecessors. The impact has sometimes comprised a shift towards larger UFAs when different rather than identical stimuli are used (Sereno and Kosslyn, 1991; Brown and Jeeves, 1993; Pollmann, Zaidel, and von Cramon, 2003; Hayes, Swallow, and Jiang, 2010), but the opposite effect has also been observed (Zhang and Feng, 1999; Ludwig, Jeeves, Norman, and DeWitt, 1993). Apparently, the requirement of a key press upon display of identical versus differing stimuli is not the universal key to movement of the balance of RTs in unilateral versus bilateral stimulation conditions. What probably occurred in Braun et al (2011) is that discordance between local and global orientations is specifically the cause of the shift from a UFA to a BFA, not at all the requirement of judging sameness versus difference.

If this reasoning is correct, the corpus callosum could be construed to function as a dispatcher. This dispatcher would advantageously repartition perceptual streams involving conflict between local orientation (orientation of stimulus contours) and global orientation (orientation of the inter-stimulus array). In other words, the corpus callosum would be a “*dispatcher*” or “*parser*” with respect to various aspects of orientation in the visual field. Strong support for this idea would accrue from a finding of no shift in RT from unilateral versus bilateral display when stimuli consist exclusively of discs identical or different in luminance: a key press upon identity or upon difference would not affect the unilateral/bilateral balance. On the other hand, if all stimuli were oriented in a manner maximizing local-global conflict of orientations, a different pattern would be expected. If stimuli consisted of squares vs diamonds, then local (intra-stimulus) concordance/discordance of orientations would be

balanced over global horizontal vs oblique orientations (inter-stimulus axes) while at the same time being radicalized for concordance or discordance of local and global orientation. With such stimuli, a UFA would occur in an experiment requiring key press to two squares or two diamonds, but the pattern could switch over and become a strong BFA in an experiment requiring a key press to a square and a diamond because in that case, more conflict occurs between the task-specific local orientation and the task non-specific global orientation. Stimulus pair axis orientation would be expected to modulate that interaction.

Purposes of the present investigation

Two experiments reported here were designed to replicate and extend the main findings of Desjardins and Braun and colleagues (2006, 2009, 2011), namely 1) the “*callosal homotopy*” effect and 2) the “*callosal network plasticity*” effect, and 3) to test an entirely new mechanism of inter-hemispheric dynamics, the flag bearer of which would be the “*callosal network dispatcher*” effect.

In all three of the relevant experiments of Desjardins and Braun and colleagues (2006, 2011), the “*callosal homotopy*” effect was non significantly greater with the squares than the discs. In the case of the squares, the contours of the stimulus had a “cardinal” orientation (relative to the meridian). Since the central experimental strategy to generate the “*callosal homotopy*” effect is to manipulate inter-stimulus-orientation, independently of intra-stimulus orientation, the within-stimulus orientation of the squares could have introduced some perceptual complexity and unfortunately some imbalance into the design.

The squares on each side of a horizontally positioned pair appear in cardinally positioned quadrants (relative to the meridian), have a cardinally oriented inter-stimulus axis and have cardinally oriented borders. All of these orientation levels are concordant. However, if the stimulus pair axis is oblique relative to the meridian, then there is a mixture of cardinal and oblique orientations to integrate and this may involve some local heterotopy added on to the global heterotopy. Using two discs as stimuli differing or not in luminance would not involve any local heterotopy on the computer screen, only global heterotopy if their positioning is oblique. On the other hand, for local orientations to be balanced with global orientations and manipulated as well, diamonds should be displayed as frequently as squares.

Predictions

1) The “*callosal homotopy*” effect will reach significance. A cost will appear (longer RT) in the bilateral stimulation condition when inter-stimulus arrays are oblique. The appropriate interaction of *Unilateral/Bilateral Stimulation x Stimulus Pair Axis Orientation* will accrue. 2) The “*callosal network plasticity*” effect will reach significance. More precisely, RT will shorten with practice but it will shorten more in the bilateral stimulation condition than in the unilateral stimulation condition. The appropriate interaction of *Practice x Unilateral/Bilateral Stimulation* will accrue. 3) The “*callosal network dispatcher*” effect will reach significance. In the absence of any conflict between orientation of stimulus contours (local orientation) and inter-stimulus axis orientation (global orientation), the most robust UFA will accrue. However, in the condition where local and local/global orientations are all maximally conflicted, the most robust BFA will accrue. Unfortunately, this concept cannot be tested with the experiments presented here without embedding effects previously predicted. The most pertinent inference test of the “*callosal network dispatcher*” mechanism would be a significant interaction of *Unilateral/Bilateral Stimulation x*

Experiment (pale/dark discs vs squares/diamonds) x Inter-Stimulus Orientation x Same/Different stimuli.

3.2. Experiment 1

3.2.1 Methods

Participants

The first part of this experiment (see Procedure section) comprised 12 university students, six men and six women. The second part of this experiment (see Procedure section) also comprised 12 university students, six men and six women. In the cohort as a whole, years of education varied from 13 to 17 years. Ages varied from 19 to 26 years. In either of the two parts of the experiment, the men and women did not differ in age or education. All participants were right handed. All signed a certified consent form. Right hand dominance had to reach 90% on the items of the unpublished Collin and Braun scale of hand preference (unpublished document). This scale questions the respondent regarding 19 single-hand learned movements (writing, holding a racquet, hammering a nail, etc.). Candidates with a history of substance abuse, or psychiatric or neurological consultation were excluded. Abnormal vision, particularly of vergence, phoria, depth and acuity was verified with an Optec Vision Tester (Stereo Optical Co, Inc) and motivated rejection if a problem occurred. A routine was implemented to detect excessive error rates in practice trials and throughout each experiment. Candidates were informed beforehand that they would be paid 10 \$CAN and excused at this stage if their error rate (omissions, commissions) reached chance in any block of trials using one hand (see the Procedure section for further details).

Remaining participants completed the experiment and received the full stipend (25 \$CAN).

Stimuli

Stimuli were displayed for 60 ms. The possible locations of the stimulus pairs are illustrated in Figure 1. Inter-stimulus distance (median-to-median) was 5.25 cm (3.85°). Stimulus pair eccentricity (mid-distance of the stimuli relative to fixation cross) was 6.4 cm (4.7°), such that the blind spot was avoided and the stimulus field kept within the sensitivity range of callosally fed visual neurons, which does not extend much beyond 7° . Stimulus pairs were randomly presented to the participant in four array sets (two unilateral and two bilateral; see figure 1). Each of these stimulus arrays was equidistant from fixation.

The chin rest was set at 57 cm from the computer screen. The participant viewed the stimuli by peering into a black tube which prevented reflections on the screen from ambient lighting in the laboratory. The distal end of the tube formed a circle hiding the contour of the video monitor so as to remove these visual references to the horizontal and the vertical. Participants were required to fixate the fixation cross throughout the experiment. Probability of occurrence of stimuli in the various locations was balanced. Because there was no bias in the probability of any stimulatory direction, control of fixation (with EOG, pupillometry or otherwise) was not necessary. See figure 1 for all the possible locations of the stimuli.

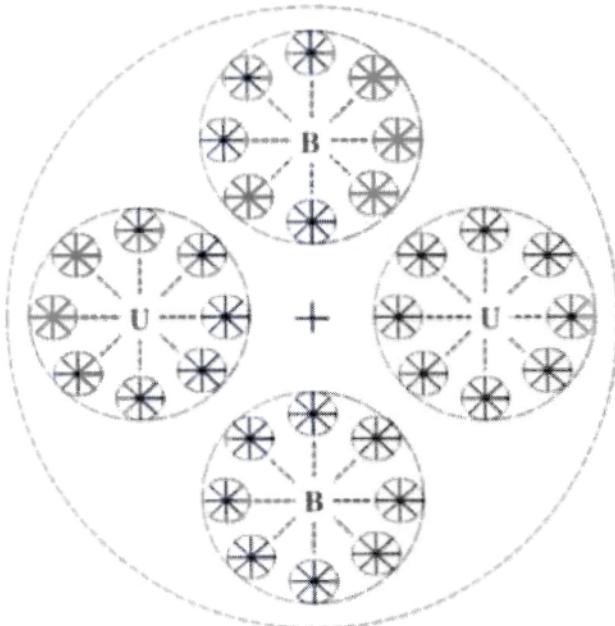


Figure 3.1. Schematic representation of the stimulus pair locations in the experiment. The larger dashed circle delimits the zone seen by the participant, enclosed in a flat-black (non reflecting) viewing tube. Stimuli consisted of grey discs (not depicted) at opposite positions within one of the medium dashed circles. The dashed straight lines represent the inter-stimulus axes, the orientations of which are the *Stimulus-Pair Axis Orientation* factor. The smallest dashed circles define the outer boundaries of the individual stimuli. The participant fixated the central cross hairs throughout the experiment. All 16 Go pairs (4 quadrants x 4 stimulus pair axis orientation) were equiprobable. All 16 NoGo pairs were also equiprobable, but represented only 20% of all stimuli. Distance from fixation was the same for the center of each stimulus pair. B= conditions of bilateral stimulation. U = conditions of unilateral stimulation. RTs to vertical stimulus pairs were excluded from statistical analysis, because those in the B condition do not clearly qualify as either within or between fields.

In Experiment 1, instead of discs and squares, the stimuli were grey discs, exactly the same dimension as the disc stimuli used in Desjardins and Braun and colleagues (2006, 2009, 2011). The stimuli were two grey discs on a lighter grey background

(RGB value: 198,198,198) (1.18 mcd/m²). The grey discs could differ in darkness: their RGB values were (128,128,128) and (66,66,66), respectively (.72 mcd/m² and .40 mcd/m² respectively). These discs were exactly of the same dimension and appeared in the same locations as the “discs” of Desjardins and Braun (2006) and Braun and colleagues (2011). The centers of the four quadrants were located an equal distance (6.75 cm) from the fixation cross. Stimulus dimension was 1.2 cm in diameter. Inter-stimulus distance (external margins) was 5.8 cm. Stimulus pair eccentricity (mid-distance of the stimuli relative to fixation cross) was 6.4 cm (7 °). All stimuli had the same number of pixels (1225 in 800 x 600 screen resolution).

Procedure

For both parts of the experiment, all aspects of the tasks remained the same as Braun et al (2011). For the first group (the Go was to discs of identical luminance. The experiment was identical for the second group except that Go was required upon display of discs of different rather than identical shades of grey. All the experiments were implemented on a Pentium-II PC with E-Prime version 1 software. The monitor was a Panasonic colour CRT monitor (model DX-T7535). A fixation cross at center screen was displayed at all times except during error feedback and changes of responding hand.

Both sub-experiments were in the go/no-go format, with 80% of trials formatted as go and 20% as no-go. The required response was a press of the space bar with the index finger. Missed Go trials (omission errors) were automatically replaced. One NoGo stimulus was inserted at a random position (1 to 5) within each consecutive set of five trials. Thus as few as zero and as many as eight trials could separate two NoGo trials. Had the participants known this, they could have correctly anticipated a NoGo

condition on only one out of every 25 NoGo trials (i.e., after 8 consecutive Go stimuli which occurred only when a NoGo position 5 followed a NoGo position 1).

Trials were grouped into eight blocks each comprising 400 correct Go trials selected randomly with probability inversely reflecting their previous occurrences in the session. Rest was offered as required between blocks. The hand required to respond in consecutive blocks followed an AB, BA, BA, AB sequence, with starting hand counterbalanced across participants. A response shorter than 125 ms was coded as an anticipation error and a message YOU RESPONDED TOO QUICKLY was displayed for 500 ms. A response after 750 ms was coded as an omission error and a message YOU RESPONDED TOO SLOWLY was displayed for 500 ms. A response to a NoGo stimulation was coded as a commission error and the message YOU WERE REQUIRED NOT TO RESPOND was displayed for 500 ms. After a correct response (or 750 ms in the case of NoGo stimulation), delay until the next stimulation varied from 350 to 2000 ms according to a logarithmic ramp favouring short response-to-stimulus intervals (average : 750 ms). Before experimentation, each participant got a 40 trial practice run.

Statistical design for reaction times

This experiment comprised a single dependent variable of interest, namely RT (intra-participant and within sub-condition means). Preliminary analyses indicated that gender did not modulate any effect, so the gender factor was dropped from the design. The experimental design as a whole repeated itself four times and practice was thus implemented as these four levels. In the unilateral stimulation conditions there was no effect of *Visual Field*, nor was there an interaction between *Visual Field* and *Stimulus-Pair Axis Orientation* (see Magnusson, Landro & Johnsen., 1985, for similar results), thus simplifying inferences about callosal dynamics, as there was no

reason to suspect that either hemisphere could not do the task as well as the other (Magnussen et al., 1985). The Northern and Southern quadrants did not differ significantly, so that factor was not considered further. Vertically arranged stimulus pairs were excluded from analysis because they are neither unilateral nor bilateral when presented on the midline: their presence was necessary in order to distribute attention in a balanced manner in oblique and cardinal directions considering that the research hypotheses relied on effects of that sort.

The most important within-participant factor distinguished Inter Field (bilateral stimulation) versus Intra Field (unilateral stimulation) and that factor was named *Bilateral/Unilateral Stimulation* (opposing bilateral to unilateral pairs of stimuli). The next most important within factor was the *Stimulus-Pair Axis Orientation* factor (comprising three levels, an oblique relation relative to the meridian like a forward or backward slash versus a horizontal relation). Whenever this factor was involved in an effect, only the quadratic trend was to be reported (representing the two obliques vs the horizontal orientation). The two levels of greyness of the discs, named *Stimulus Type*, were meaningful only in Experiment 1. Finally, there was one experiment requiring a Go to identical discs and one experiment requiring a Go to different discs. This between factor was named *Go to Similar/Different Stimuli*. All effects involving *Bilateral/Unilateral Stimulation* will be reported. No other effects will be reported except main effectss involved in interactions containing *Bilateral/Unilateral Stimulation*.

3.2.2. Results

Errors

The rate of errors of anticipation was 0.01 %. The rate of errors of omission was .32 % of go trials. The rate of errors of commission was 14.3 % of no-go trials. Neither errors of omission nor of commission held any significant simple or interactive relation to *Bilateral/Unilateral Stimulation*.

Reaction times

The RTs used for analysis were within-participant and within-condition means. With the usually normal RT distribution clipped at each end by the anticipation error rule (< 125 ms) and the omission error rule (> 750 ms), this is a better metric than the median.

Effects pertaining to the Experiment as a whole

We first report tests of the three hypotheses based on analysis of variance of sub-experiments 1 and 2 combined. Effects involving the *Bilateral/Unilateral Stimulation* included its own main effects ($F_{(1,22)} = 7.23$, $p = .013$, unilateral = 418 ms, bilateral = 422 ms). The interaction between *Bilateral/Unilateral Stimulation* and *Stimulus Pair Axis Orientation* was significant (quadratic trend: $F_{(1,22)} = 12.579$, $p = .002$). See the next sections for decomposition and illustration. No other interaction directly relevant to the three research hypotheses reached significance. Exceptionally, because the third hypothesis predicts non significance in this experiment of the interaction between *Bilateral/Unilateral Stimulation* and *Go to Same versus Different Stimuli*, the inference test is reported: ($F_{(1,22)} = .014$, $p = .906$).

Effects pertaining only to key presses to “identical” stimuli

We next report analysis of variance of the data from the condition involving key presses to identical stimuli only. The main effects of *Bilateral/Unilateral Stimulation* was significant ($F_{(1,11)} = 6.501$, $p = .032$, unilateral = 417 ms, bilateral = 421 ms). The main effects of *Stimulus Pair Axis Orientation* was significant (quadratic trend = $F_{(1,11)} = 4.416$, $p = .006$, horizontal = 417 ms, oblique = 420 ms). The interaction between *Bilateral/Unilateral Stimulation* and *Stimulus Pair Axis Orientation* was significant (quadratic trend $F_{(1,11)} = 9.603$, $p = .010$). The horizontal condition produced shorter RTs than the oblique and that difference was greater in the bilateral than unilateral condition with the overall callosal homotopy effect being of 7.563 ms. See figure 3 (left panel). The *Practice* effect fell close to significance ($F_{(1,11)} = 4.759$, $p = .052$), showing an 11 ms advantage in the second half of the experiment. The interaction between *Practice* and *Bilateral/Unilateral Stimulation* reached significance ($F_{(1,11)} = 16.64$, $p = .002$). A non significant 10 ms practice effect in the unilateral condition ($F_{(1,11)} = 2.813$, $p = .122$) and a significant 14 ms practice effect ($F_{(1,11)} = 7.210$, $p = .021$) in the bilateral condition were found. See figure 4 (left panel).

Effects pertaining only to key presses to “differing” stimuli

Analysis of variance of the key presses to stimuli of different luminance yielded no significant effects involving *Bilateral/Unilateral Stimulation*.

3.2.3. Discussion of experiment 1

This set of findings replicates and extends the main results of Experiments 1 and 2 of Braun et al (2011). With key press to identical stimuli, the “*callosal homotopy*” effect and “*callosal network plasticity*” effect are both of the same nature as the analogous

experiment 1 of Braun et al (2011) and are significant. This demonstrates that both these putative mechanisms of inter-hemispheric dynamics, “*callosal homotopy*” and “*callosal network plasticity*” are supported by the relevant effects with stimuli having no intrinsic orientation. Thus, it is really the inter-stimulus axis, as would be expected from homotopy of the callosal radiation, not uncontrolled “oblique effect” properties of callosal vs non callosal neuronal receptive fields, that generates the effect. Finally, as predicted from the proposed “*callosal network dispatcher*” mechanism, the balance of RTs in unilateral and bilateral conditions was unaffected by whether the key press was required to identical versus differing stimuli.

3.3. Experiment 2

Whereas in Experiment 1, the stimuli were without intrinsic orientation, in the next experiment the plan was to use stimuli with nothing but intrinsic orientation, while systematically manipulating it. It was also decided to investigate key press to identical stimuli and to different stimuli in the same experimental session, i.e., within subjects. A number of other design changes were made to improve the experiment, reduce error rates, and control artifacts.

3.3.1. Methods

Participants

Participants were selected using the same inclusion/exclusion criteria as for the previous experiment. The participants were eight female and eight male university

students. Years of education varied from 12 to 19 years. Ages varied from 21 to 31 years. The men and women did not differ in age or education.

Stimuli

The stimuli included a square as in Desjardins and Braun and colleagues (2006, 2009, 2011), but changes were made to the characteristics of this stimulus. Unlike in previous experiments, the square was not fully filled with colour. Only its border, 6 pixels thick, was yellow (255,255,0, 1.9 mcd/m²) on a dark blue (0,0,128, .065 mcd/m²) background. The length of its sides was 35 pixels. Perhaps most importantly, the array of stimulus emplacements on the screen was doubled: until this experiment, participants had been stimulated in four quadrants, but these were all cardinal (east, west, north, south), so we stimulated equally and topographically identically in the intermediary zones (southwest, southeast, northwest, northeast) to assure that a cardinal attentional bias would not be entrained. See figure 2. The second stimulus was the same square rotated 45 degrees, i.e. a diamond. Thus, inter-stimulus orientations could be cardinal or oblique, and intra-stimulus boundaries could also be cardinal or oblique (relative to the meridian). We were interested of course in determining whether local and global stimulus orientations would interact and we decided to assure that all aspects of stimulus orientation would be balanced for cardinality and obliqueness. As a consequence, the crosshair fixation stimulus was replaced by a circle 15 pixels in width because crosshairs, however small, could project attention cardinally.

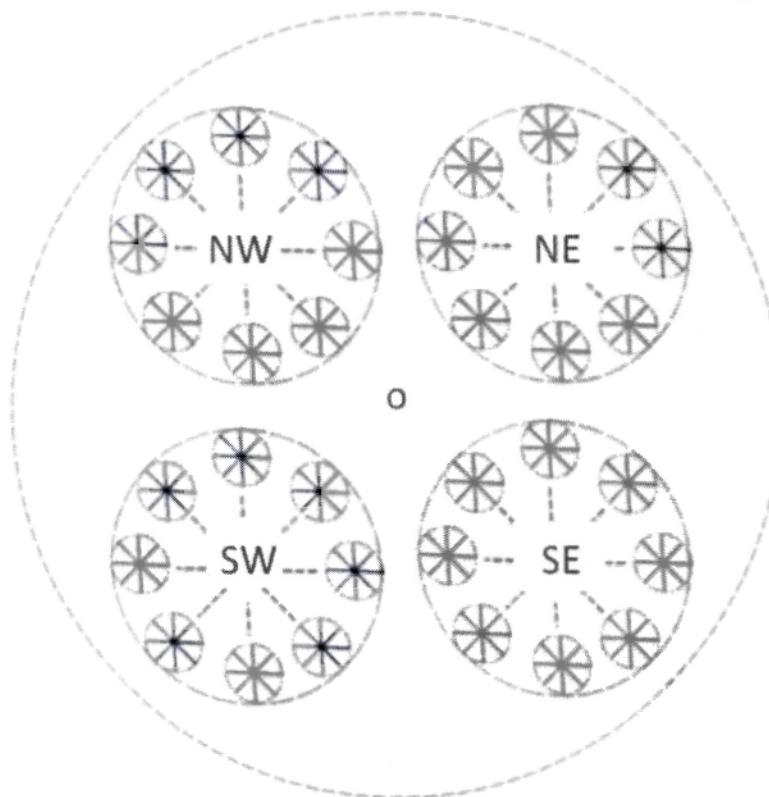


Figure 3.2. Schematic representation of half the stimulus pair locations in the experiment. The other locations are depicted in figure 1. Stimuli consisted of squares and/or diamonds (not depicted) at opposite positions within one of the medium dashed circles. All 32 Go pairs (8 quadrants x 4 stimulus pair axis orientations) were equiprobable. All 32 NoGo pairs were also equiprobable, but represented only 33% of all stimuli. Distance from fixation was the same for the center of each stimulus pair. NE, NW, SE and SW = northeast, northwest, southeast and southwest stimulus fields. The stimulus locations depicted here as well as all vertical stimulus pair axes were excluded from statistical analysis: they were used only to distribute attention evenly throughout the visual field during the experiment.

Thus the entire experiment was balanced for cardinality and obliqueness of orientations in every possible respect (recall that the viewing perimeter, through a tube, was circular). In this experiment there were 1536 trials altogether presented in

two complete replications of the entire design, equally balanced for the two matching criteria (same and different), the two hands, the eight quadrants, the four inter-stimulus orientations, and the two stimuli (square and diamond). The duration of display of the stimulus was augmented by 40 ms, to 100 ms. The response-to-stimulus onset interval was augmented by 500 ms. These two changes had to be introduced to reduce error rates. All other aspects of the experiment were identical to Experiment 1.

Procedure

The instructions and procedure were similar to the previous experiment except that 8 blocks of 192 trials were presented in which the proportion of Go and No go trials was changed from 80/20 to 66/33 to reduce the rate of errors of commission. Each block required the participant to respond either to identical stimuli or to different stimuli. All other aspects of the procedure were identical to Experiment 1.

Statistical design for reaction times

The dependent variable of interest is RT (within-participant, within sub-condition means). Gender was dropped from the design for the same reason as previously. The experimental design as a whole repeated itself two times and *Practice* was thus implemented as these two levels. In the unilateral stimulation conditions there was no effect of *Visual Field*, nor was there an interaction between *Visual Field* and *Stimulus-Pair Axis Orientation*, thus simplifying inferences about callosal dynamics, as there was no reason to suspect that either hemisphere could not do the task as well as the other. The Northern and Southern quadrants did not differ significantly, so that factor was not considered further. The data from northeast, northwest, southeast,

southwest quadrants was irrelevant to this report and will henceforth be ignored: their purpose was for experimentally controlled balancing of attention only. Vertical stimulus pair axes were also ignored for the same reason. The other factors in analyses of variance were the same as in the previous sections except that the factor distinguishing key press to identical versus different stimuli now becomes a within-participants factor. All relevant effects involving *Bilateral/Unilateral Stimulation* will be reported. No other effects will be reported except main effectss involved in interactions containing *Bilateral/Unilateral Stimulation*. The *Positional Equality* confound factor was also tested as described in experiment 1.

3.3.2. Results

Errors

Anticipation, omission and commission error rates were respectively .01 %, 2.1 % of Go trials and 27.7 % of No-go trials. Neither errors of omission nor of commission held any significant simple or interactive relation to *Bilateral/Unilateral Stimulation*.

Reaction times

With the usually normal RT distribution clipped at each end by the anticipation error rule (< 125 ms) and the omission error rule (> 900 ms), this is a better metric than the median.

Effects pertaining to the experiment as a whole

We first report the relevant results of analysis of variance of the entire experiment. The main effects of *Bilateral/Unilateral Stimulation* was not significant. Overall, the *Practice* effect consisted of shorter RT in the second half of the experiment (RT = 488 ms) than in the first (RT = 497 ms) but the effect was not significant. However, The interaction of *Practice* with *Bilateral/Unilateral Stimulation* was significant ($F_{(1,15)} = 8.568, p = .010$). A non significant 5 ms practice effect in the unilateral condition ($F_{(1,11)} = 0.853, p = .363$) and a significant 13 ms practice effect ($F_{(1,11)} = 8.001, p = .008$) in the bilateral condition were found. See figure 4 (right panel). The interaction between *Bilateral/ Unilateral Stimulation* and *Go to Same/Different Stimuli* was significant ($F_{(1,15)} = 34.552, p < .0005$). A UFA of 4 ms was obtained when the required key press was to identical stimuli, but a BFA of 14 ms was obtained in the condition in which a key press was required upon display of two different stimuli. See figure 5 (right panel). It is noteworthy that this occurred despite the absence of a main effects of *Go to Same/Different stimuli*: the “different” condition yielded RTs a mere half millisecond longer on average than the “same” condition. This interaction will be described and illustrated in more detail in the next paragraphs. The only other effect of interest involving *Bilateral/Unilateral Stimulation* was the three-way interaction between *Bilateral/Unilateral Stimulation*, *Stimulus Pair Axis Orientation* and *Go to Same/Different Stimuli*.

Effects pertaining to key presses to “identical” stimuli

We now report results of analysis of variance of half the experiment, those pertaining only to key presses to display of identical stimuli. Note that these trials do not represent the chronological half of the experiment. The main effects of *Bilateral/Unilateral Stimulation* consisted of the unilateral field advantage or UFA mentioned in the preceding paragraph ($F_{(1,15)} = 29.175, p < .0005$). The interaction between *Bilateral/Unilateral Stimulation* and *Stimulus Pair Axis Orientation* was

significant (quadratic trend: $F_{(1,15)} = 6.904$, $p = .019$), comprising a homotopy effect of 10 ms. See figure 3 (right panel).

Effects pertaining to key presses to “differing” stimuli

Finally, the other half of the experiment, involving only key presses to display stimuli with different orientations (squares vs diamonds) yielded the following result. Only the main effects of *Bilateral/Unilateral Stimulation* reached significance ($F_{(1,15)} = 22.799$, $p < .0005$) and the effect consisted of a 14 ms BFA.

3.3.3. Discussion of experiment 2

These results support the first two putative mechanisms and attenuant hypotheses proposed in the introduction, namely the “*callosal homotopy*” and “*callosal network plasticity*” mechanisms. When a key press was required upon display of identical stimuli, the homotopy effect reached a significant 9 ms. In the experiment as a whole, with practice, RTs shortened and the balance of unilateral/bilateral conditions significantly flipped from a significant UFA to a significant BFA.

It was thought that previous experiments yielding a significant homotopy effect (Desjardins et al, 2006, 2009, Braun et al, 2011) could have been biased toward cardinality (via the fixation cross and/or the cardinal emplacement of quadrants in which stimulus pairs were placed) somehow exaggerating the so called “*callosal homotopy*” effect by a few milliseconds. It turns out that this would not likely be the case. At any rate, we are now assured that in an experimental environment entirely

controlled and balanced for local (stimulus-contour) and global (inter-stimulus array) orientation, the homotopy effect still reaches significance.

The third putative mechanism, predicting a “*callosal network dispatching*” effect is particularly well supported here by Experiment 2. The evidence accrues from the extraordinarily significant dissociation between *Bilateral/Unilateral Stimulation* and *Go to Same/Different Stimuli* and also, more specifically, the modestly significant three-way interaction between *Bilateral/Unilateral Stimulation*, *Stimulus Pair Axis Orientation* and *Go to Same/Different Stimuli*. Inspection of the means suggests to us that it is not the callosal system that is stumped by complexities of perceptual analysis, it is the hemisphere receiving alone the ensemble of visual information. In figure 5 the two extreme RTs are in the unilateral stimulation condition, shortest when a stimulus pair is presented on a horizontal axis and the key press is to identical stimuli (472 ms), longest when the stimulus pair is on an oblique axis and the key press is to different stimuli (506 ms). The difference between these two conditions is 34 ms. It appears that a single hemisphere is particularly well equipped to handle perceptual analysis in the absence of conflict between two intra-stimulus orientations, and in the absence of conflict between local intra-stimulus orientation and global stimulus pair axis orientation. Conversely, it appears that a single hemisphere is particularly poorly equipped to handle perceptual analysis when conflict arises between two local intra-stimulus orientations, and when conflict arises between intra-stimulus orientation and stimulus pair axis orientation, particularly when these two conflicts are combined. In short, it appears that the callosal system helps to optimally distribute attention to orientation from local and global fields in the early stages of visual processing in a “shape” discrimination task.

3.4. Experiments 1 and 2 combined

As explained in the introduction, the ultimate and most relevant test of the third proposed mechanism, the “*callosal network dispatcher*”, would be to show that a significant BFA accrues when local/global orientations are most discordant and a significant UFA accrues when there is no local orientation at all. To test this particular inference, the data had to be reformatted so as to allow comparison of Experiments 1 and 2. The within-participants effect of *Go to Same/Different Stimuli* thereby has to be processed as a between-participants factor, making our inference tests slightly more conservative. The effect of greatest interest is the interaction between *Experiment 1/2* and *Bilateral/Unilateral Stimulation* and *Go to Same/Different Stimuli*.

3.4.1 Results

The interaction between *Experiment 1/2* and *Bilateral/Unilateral Stimulation* and *Go to Same/Different Stimuli* was significant ($F_{(1,52)} = 29.037$. $p < .0005$). See figure 5. However, the interaction between *Experiment 1/2* and *Bilateral/Unilateral Stimulation*, *Go to Same/Different Stimuli* and *Stimulus Pair Axis Orientation* was not significant. This omnibus test covers a lot of ground, probably too much. What is perhaps more important is that the pattern predicted in the Predictions section for the callosal network dispatcher effect was obtained if one considers only the specific terms of the prediction made. Recall that in Experiment 1, in the Go to same stimuli condition, the UFA was significant ($F_{(1,11)} = 6.501$, $p = .032$, unilateral = 417 ms, bilateral = 421 ms). Recall also that in experiment 2, in the Go to different stimuli

condition involving local discordance of orientation in addition to local/global discordance of orientation, the BFA was significant ($F_{(1,15)} = 22,799$, $p < .0005$, and the effect consisted of a 14 ms BFA). See figure 5.

The « callosal homotopy » effect

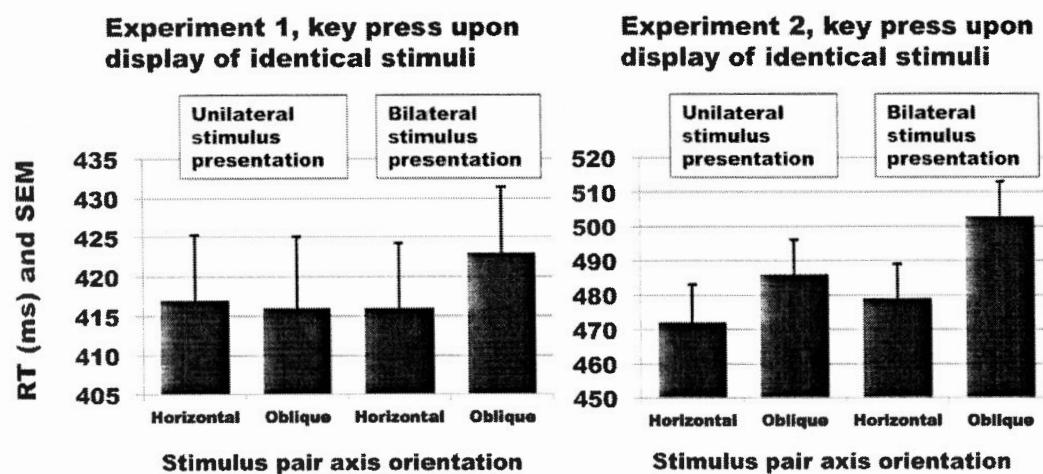


Figure 3.3. These histograms provide details of the significant “*callosal homotopy*” effects obtained in Experiments 1 (on the left) and 2 (on the right). The “*callosal homotopy*” effect consists of a greater cost of oblique stimulus pair axis orientation in bilateral than in unilateral stimulation conditions. The most salient cost is in the bilateral stimulation condition when the stimulus pair axis is oblique relative to the meridian, suggesting that the system driving the effect is commissural.

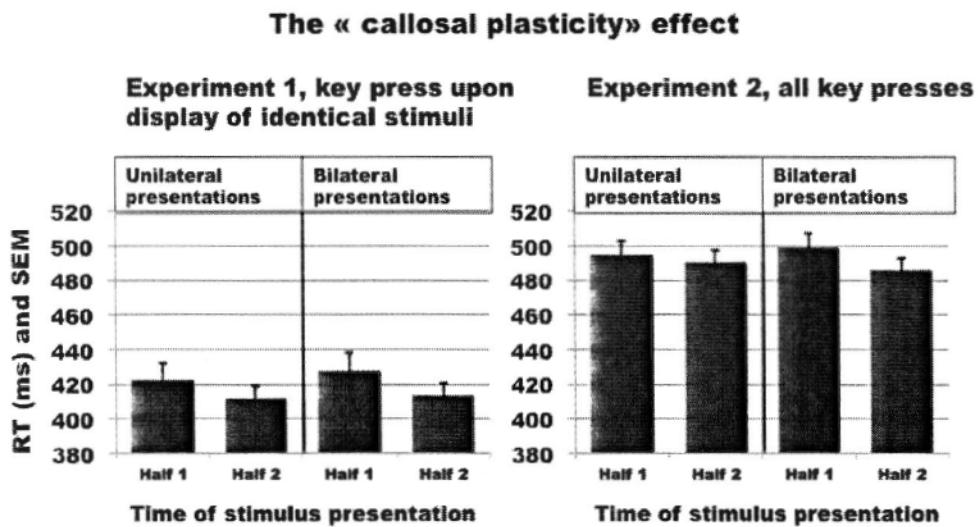


Figure 3.4. This figure illustrates the “*callosal plasticity*” effect. In both Experiment 1 (left figure) and Experiment 2 (right figure), the *Bilateral/Unilateral Stimulation x Practice* effect is significant, showing a stronger effect of practice for bilateral presentations than for unilateral presentations. The difference can be attributed to the capacity of the inter-hemispheric commissure to adapt to the task. Note that the *Bilateral/Unilateral Stimulation x Practice* effect is short of significance in conditions not illustrated here.

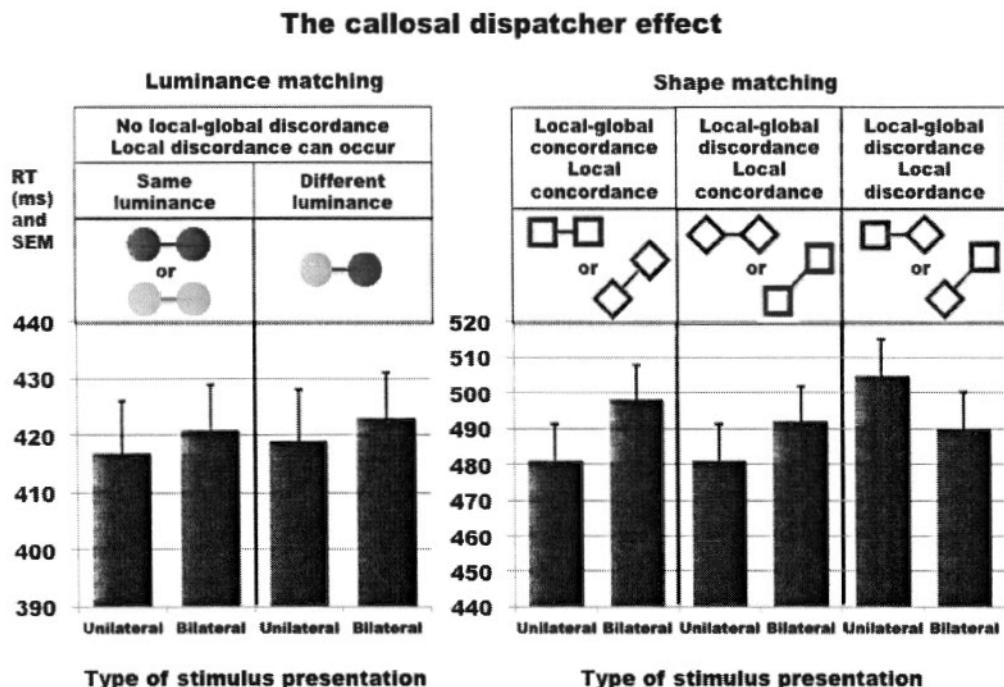


Figure 3.5. The same unilateral field advantage (UFA) is observed in Experiment 1 (left side of the figure), whether the participant is responding to identical stimuli or different stimuli (discs of differing luminance). However, in Experiment 2, a significant UFA is observed when the participant is responding to identical stimuli (two squares or two diamonds), but a significant bilateral field advantage (BFA) is observed when the participant is responding to different stimuli (a diamond and a square). The shortest and longest RTs are observed in unilateral stimulation conditions suggesting that a single hemisphere is readily able to integrate stimuli of concordant orientation, but has great difficulty integrating stimuli of discordant orientation. Stimuli without oriented contours (discs) or with cardinal (square) or oblique (diamond) contours are illustrated as are cardinal and oblique inter-stimulus axes (which are depicted here as full lines between stimuli). The words “obliqueness” and “cardinality” are used in this report only in reference to the meridian. Local-global concordances and discordances are also illustrated. The illustrative examples at the top of the figure are not exhaustive. The RT data in the lower portion of the figure are not limited to the examples illustrated.

3.4.2. General discussion

For this investigation three proposed mechanisms of inter-hemispheric dynamics were subjected to precisely predefined inference tests. The first has been termed the “*callosal homotopy*” mechanism by Desjardins and colleagues (2006) and was supported by the appropriate interaction of *Bilateral/Unilateral Stimulation* and *Stimulus Pair Axis Orientation*, significant as predicted, in both experiments. This demonstrates that the idea of this mechanism is supported with stimuli having no intrinsic orientation (Experiment 1) as well as with full balancing of any kind of orientation of the fixation stimulus, the target stimuli, the stimulus fields or quadrants (Experiment 2).

The second putative mechanism was termed “*callosal network plasticity*”, and it was supported by an appropriate interaction between *Practice* and *Bilateral/Unilateral Stimulation*, significant in both experiments. This demonstrates that our idea of this putative mechanism is supported with stimuli having no intrinsic orientation (Experiment 1) as well as with full balancing of any kind of orientation of the fixation stimulus, the target stimuli, the stimulus fields or quadrants (Experiment 2). This effect is opposite to the common effect observed on cognitive tasks formatted in the Dimond paradigm wherein a UFA on simple perceptual matching task becomes a smaller UFA or a BFA on a complex cognitive task involving learned abstract symbols. In both experiments reported here, the more practiced condition yielded slightly shorter RTs (weakly significantly or even non significantly so). Nothing here but the simplest of perceptual matching is ever required of the participant. It may still appear surprising that the initial significant UFA gets significantly weaker in experiment 1, and even turns into a significant BFA with *Practice* in experiment 2. Inspection of figure 4 reveals that it is basically in the bilateral stimulation conditions

that the extremes of RT are found. This suggests to us that a large part of the adaptation captured in these tasks can be attributed to the corpus callosum.

The third proposed mechanism, the “*callosal network dispatcher*”, is supported by the complete absence of the interaction between *Bilateral/Unilateral Stimulation* and *Go to Same/Different Stimuli* in Experiment 1 contrasted with the extraordinarily significant dissociation of *Bilateral/Unilateral Stimulation* and *Go to Same/Different Stimuli* in Experiment 2 and also the modestly significant three-way interaction between *Bilateral/Unilateral Stimulation*, *Stimulus Pair Axis Orientation* and *Go to Same/Different Stimuli* in Experiment 2. Most importantly, the idea of that mechanism is supported by the highly significant interaction between *Experiment (1/2)*, *Bilateral/Unilateral Stimulation* and *Go to Same/Different Stimuli*. However, the limit of the “*callosal network dispatcher*” concept is reached with the absence of the expected significant four-way interaction: *Experiment (1/2)*, *Bilateral/Unilateral Stimulation* and *Go to Same/Different Stimuli x Inter-Stimulus Orientation*. We interpret these effects, all significant except this one, as follows: the “*callosal homotopy*” effect is still dominant in the shape discrimination task when there is no local orientation conflict. However, the “*callosal homotopy*” effect is overrun by the “*callosal network dispatcher*” effect when all possible orientation conflicts are combined (see figure 5).

We propose that some of the callosal network partitioning seems to consist of parsing signals that stump primary visual cortex when an attempt is made by the latter within a single hemisphere to integrate divergent local and global orientations. Because the callosal network is unconnected to primary visual cortex but is most densely connected to tertiary visual cortex (Maunsell and Van Essen, 1987), the CC is in a privileged position to disentangle complex perceptual effects which can disturb visual processing in primary visual cortex. We assume that this disturbance, in conditions of unilateral stimulation, must consist of back propagation from tertiary visual cortex

back into primary visual cortex, back propagation which arrives there unpartitioned. More generally, we intuit that all the mechanisms underlying the three classes of effects reported here are neuronal network effects, not effects of single cell adaptation.

A skeptical reader might doubt whether RT drawn from perceptual discrimination tasks such as these is simple enough and stable enough to measure inter-hemispheric dynamics of any sort. Some reassurance ought to accrue from the fact that in this investigation the crossed-uncrossed difference (CUD) in RT, also known as inter-hemispheric transfer time (ITT) was in the range expected in simple reaction time experiments. The CUD was 2.6 ms and the *Field x Hand* interaction was significant ($t = 3.082$, $p = .003$).

CHAPITRE IV

EFFETS DE L'ORIENTATION DE LA PAIRE DE STIMULI ET DU
CHANGEMENT DE MAINS SUR LES ESTIMÉS DU TEMPS DE TRANSFERT
INTERHÉMISPHÉRIQUES BASÉS SUR DES TEMPS DE RÉPONSE

Effects of stimulus pair orientation and hand switching on reaction time estimates of
interhemispheric transfer

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interhemispheric transfer time; callosal homotopy.

Running head : Diverging RT indexes of interhemispheric transfer

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Abstract

Two behavioral estimates of interhemispheric transfer time, the crossed-uncrossed difference (CUD) and the unilateral field advantage (UFA), are thought to respectively index transfer of premotor and visual information across the corpus callosum in neurotypical participants. However, no attempt to manipulate visual and motor contingencies in a set of tasks while measuring the CUD and the UFA has yet been reported. In two go/no-go comparison experiments, stimulus pair orientations were manipulated. The hand of response changed after each correct response in the second, but not the first experiment. No correlation was found between the CUD and the UFA, supporting the hypothesis that these two measures index different types of information transfer across hemispheres. An effect of manipulation of stimulus pair orientation on UFAs was attributed to the homotopy of callosal fibers transferring visual information, while an effect of hand switching on CUDs was attributed mostly to spatial compatibility.

4.1. Introduction

The Poffenberger paradigm was invented to estimate the time required for the critical transfer of information from one hemisphere to the other. Poffenberger (1912) presented visual stimuli in the left and right halves of the visual field, and required a motor response by the left or right hand. Visual information from the left visual field is processed in the right hemisphere, whereas visual information from the right visual field is processed in the left hemisphere. Likewise, motor responses from the left hand are controlled by the right hemisphere, and motor responses from the right hand

are controlled by the left hemisphere. If the side of the visual field and the side of the hand are discordant (crossed trial), both hemispheres are involved in the task.

Interhemispheric transfer of information is then necessary for the production of the motor response. If the side of the visual field and the side of the motor response are concordant (uncrossed trial), only one brain hemisphere's processing capacity is required during the task, and interhemispheric transfer of information is not strictly necessary. Poffenberger inferred that the crossed-uncrossed difference (CUD) in reaction time (RT) represented an estimate of interhemispheric transfer time (IHTT).

Dimond (1969) created another tachistoscopic method for the study of interhemispheric dynamics. He presented pairs of visual stimuli which had to be compared. On bilateral trials, one stimulus was positioned within each visual hemifield, and a transfer of visual or cognitive information was necessary to decide whether the stimulus pair formed a matching pair. On unilateral trials, both stimuli were positioned within the same visual hemifield, and no such transfer of information was necessary for the stimuli to be compared. A subtraction of RTs from unilateral and bilateral trials for correct responses was thought to yield an estimate of the efficiency of interhemispheric communication.

There are important differences between effects found in the Poffenberger and Dimond paradigms which follow logically from their respective structures. For instance, Poffenberger's interhemispheric inference does not specify the type of information, visual or premotor, which is transferred across hemispheres, and thus usually considers only simple RT. In contrast, Dimond's interhemispheric inference does not consider the possibility of a transfer of premotor information. Dimond tasks are typically go/no-go tasks. To determine whether a motor response must be made, the two stimuli must first be compared. The information that is transferred during bilateral trials must be information that allows for such a comparison, such as visual or cognitive information.

Poffenberger first proposed that the CUD was an estimate of IHTT. As expected from this inference, mean CUD for the population has been positive in all Poffenberger tasks reported in two separate meta-analyses, reflecting faster performance when interhemispheric communication is not strictly necessary (Marzi et al. 1991; Braun 1992). Moreover, CUDs are extremely long in callosotomised patients, clearly implicating the corpus callosum as a structure necessary for interhemispheric communication in Poffenberger's paradigm (Savazzi et al. 2007).

Dimond's measure cannot be interpreted as a simple estimate of IHTT. RTs of bilateral trials are often shorter than RTs of unilateral trials (Banich and Belger 1990; Belger and Banich 1992; Leblanc-Sirois and Braun 2014), reflecting an advantage linked to cooperation between both hemispheres in these tasks rather than a cost of interhemispheric relay. Dimond's so-called measure of interhemispheric dynamics must be interpreted as a combination of two sources of delay (Leblanc-Sirois and Braun 2014), one linked to interhemispheric transfer and one linked to processing delays within the hemispheres. A modest correlation between Poffenberger's and Dimond's measures, however, would still be expected if both CUD and the bilateral-unilateral difference partly reflected interhemispheric transfer of visual information.

Attempts to obtain correlations between different measures thought to be influenced by IHTT have been made, and have included visual evoked potential (VEP) estimates of IHTT. The onset of stimulus display in visual tasks creates a pattern of electrical activity in the visual cortex of the hemisphere contralateral to stimulus presentation. An echo of this pattern of activity with reduced amplitude also occurs in the hemisphere ipsilateral to presentation (Lines et al. 1984; Rugg et al. 1985; Saron and Davidson 1989), approximately 3 ms later when measured in central electrodes and 10 to 20 milliseconds later when measured over the occipital cortex. This echo is absent in patients whose corpus callosum has been surgically sectioned (Brown et al.

1999), reflecting the important role of the corpus callosum for the generation of VEP-IHTT.

Two studies (Saron and Davidson 1989; Friedrich et al. 2017) have attempted to document correlations between CUD and VEP-IHTT, but failed to obtain significant effects. Electric activity measured at frontal, not posterior, electrode sites has also been shown to better predict CUD (Thut et al. 1999), supporting the hypothesis that CUD reflects the latency of transfer of premotor information, not visual information. In contrast, VEP-IHTT measured at posterior electrodes were correlated with Dimond's measure in two separate studies (Brown and Jeeves 1993; Larson and Brown 1997), supporting the view that the transfer of visual information, not premotor information, is important in simple versions of the Dimond task.

Previous attempts to manipulate Poffenberger's CUD by modifying visual characteristics of Poffenberger tasks have generally not been successful. A meta-analysis comparing CUD between tasks with different characteristics (Braun 1992) did find that larger distances between the stimuli and the vertical meridian and decreased luminance yielded longer CUDs. However, most relevant studies failed to obtain a significant effect of stimulus eccentricity or luminance on CUDs (Berlucchi et al. 1971, 1977; Milner and Lines 1982; Lines et al. 1984; Clarke and Zaidel 1989). Moreover, the strongest effect documented by Braun's (1992) meta-analysis was a shorter CUD when the thumb, rather than the index, was used for responses. The same meta-analysis found no effect of stimulus size on CUD.

However, manipulation of motor demands within the Poffenberger task has yielded significant results within single studies. Braun et al. (2004) found that CUDs were halved in a simple reaction time task when arms were crossed, though Berlucchi et al. (1977) found no such effect in a similar task and Anzola et al. (1977) obtained this effect only in a choice reaction time task, not in a simple reaction time task. Larocque et al. (2001) found that CUDs in a simple reaction time task were longer when a

sequence of three keypresses was necessary rather than just one keypress, and were also longer when the finger of response alternated between the index and the middle finger. In a test exploring both motor and visual task manipulations, (Iacoboni and Zaidel 1995) obtained an effect of response complexity on CUD in the absence of an effect of stimulus complexity.

Unlike Poffenberger's measure, Dimond's measure has shown sensitivity to manipulation of visual elements of the task. In particular, when the invisible line separating two stimuli of a pair was oblique relative to the horizon, a larger unilateral field advantage (UFA) was obtained than when it was horizontal, in four separate experiments (Desjardins et al. 2009; Braun et al. 2011, 2015; Leblanc-Sirois and Braun 2015). This effect was attributed to the homotopy of callosal connections, perpendicular to the falx, which more often link areas of visual cortex that process parts of the visual field that are symmetric across the vertical meridian.

Poffenberger's and Dimond's measures of interhemispheric dynamics have previously been obtained in the same task, and attempts to explore the relation between the two have been made. In a Dimond task with bilateral presentations, unilateral left field presentations, and unilateral right field presentations, Braun et al. (1997) previously reported significant correlations between Poffenberger's and Dimond's "measures". However, Poffenberger's measure in a "go on same" condition requiring identical stimuli correlated with Dimond's measure in a "go on different" condition requiring non-identical stimuli, and vice-versa. Moreover, the significant correlations were between different dependent variables: no correlation was reported between these two RT measures within one experimental condition. To the best of our knowledge, this result has not been replicated, and no attempt to experimentally separate Dimond's and Poffenberger's measures within the same set of tasks has yet been made.

Purpose of the current experiments

The current set of experiments aimed to study differences between two measures of interhemispheric transfer of information, Dimond's measure and Poffenberger's CUD, during visual go/no-go tasks. More precisely, the experiments aimed to demonstrate that Dimond's measure primarily indexes interhemispheric transfer of visual information, while Poffenberger's CUD primarily indexes transfer of premotor information. For this purpose, one visual element was manipulated within each of two experiments, and a difference between the motor demands separated both experiments.

4.2. Experiment 1

4.2.1. Methods

Task

Twelve right handed participants (6 male, 6 female) aged 18 to 30 were recruited among university students. Handedness was tested with the Collin and Braun questionnaire (unpublished), a checklist of 19 questions about the preferred hand for actions such as cutting bread, holding a racquet, and writing. Participants had no history of neurological or psychiatric problems, and were tested for adequate vision with an Optec Vision Tester (Stereo Optical Co., Inc), with a focus on acuity and correct tonic vergence, prior to the experiment.

The go/no-go Dimond task was programmed in ePrime version 1.1 software. Participants viewed the computer screen display through a flat black 57 cm long tube

preventing reflections and properly shaping the stimulus field as a circle (see Fig 1). Stimuli were dark (rgb: 66, 66, 66) and medium (rgb: 128, 128, 128) grey disks displayed on a light grey (rgb: 198, 195, 198) background. Stimuli were presented in pairs. For 80% percent of all trials, both stimuli of a pair were identical. This high frequency of go trials was chosen in order to maximize the number of trials for which RT was available. For 20% of all trials, they were different. Stimulus pairs were presented in one of four quadrants positioned above, below, to the left, or to the right of the center-screen fixation point. An equal number of stimulus pairs were presented in each of the four quadrants. The center of each quadrant was positioned 6.4 cm away from the fixation cross. Stimulus pairs were separated by an invisible horizontal, or vertical, oblique slash, or oblique backslash line. An equal number of stimulus pairs were presented in each of the four stimulus pair orientations. The distance between two stimuli of a pair was kept constant at 5.25 cm.

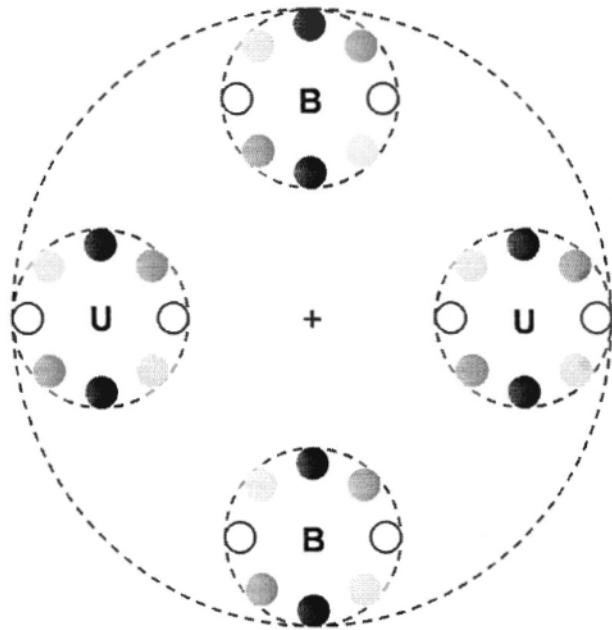


Fig 4.1. Possible stimulus pair positions in experiments 1 and 2. U = Unilateral presentations. B = Bilateral presentations. For each trial, two stimuli were presented simultaneously within one quadrant, in one of four pair orientations located to the left, right, top or bottom of the central fixation cross (+). Dotted lines were not visible for the participants. Black, white, and grey disks illustrate the possible location of stimulus pairs, and do not represent the stimuli used during the study. Black and white disk pairs represent cardinal pair orientations, only white disk pairs represent horizontal pair orientations, and both types of grey disk pairs represent oblique pair orientations.

Participants had to fixate the fixation cross (+) and press the space bar on the keyboard when two stimuli presented simultaneously in peripheral vision were identical. A minimum of 2560 trials per participant, distributed between 8 trial runs separated by short breaks, was used. Response hand did not change during a trial run.

An AB BA BA AB counterbalancing was used for response hand. One half of the participant group began with the left hand, while the other half began with the right hand.

Each trial began with a fixation point displayed between 350 and 2000 ms, according to a logarithmic ramp favoring shorter durations. A pair of stimuli was then displayed for 60 ms. The fixation remained on screen during stimulus display. Following stimulus onset, participants had 750 ms to respond. After 750 ms or after a response was registered, the fixation remained on screen for 500 ms if the response or non-response was correct. If a commission error (responding on a no-go trial) was registered, a “wrong response” error message was instead displayed for 500 ms. If an omission error (failure to respond on a go trial) was registered, a “too long” error message was displayed for 500 ms.

Analyses of unilateral-bilateral differences for this task have previously been reported only for RT (Leblanc-Sirois and Braun 2015). RT results are reported again here in order to allow a comparison with Experiment 2 during which motor demands are different. Accounts of both experiments are here accompanied by new analyses of error rates and focus on different measures. Analyses of left-right hand and visual field interactions in RT and error rates for this task have not previously been reported in the scientific literature.

Statistical methods

Two separate series of analyses of variance were respectively meant to test the significance of Dimond’s and Poffenberger’s measures. The first series of analyses of variance was meant to investigate effects of unilateral and bilateral stimulus pair presentations, and included 4 factors of interest. A 4-level *block* factor contrasted the four pairs of trial runs in temporal order and provided a measure of practice or fatigue

effects. A 2-level *response hand* factor contrasted left-handed and right-handed responses. A 2-level *bilateral vs unilateral* factor contrasted pairs of stimuli presented on different sides of the midline of the visual field against stimulus pairs presented wholly within either the left or right visual field. Finally, a 3-level *pair orientation* factor contrasted pairs of stimuli separated by an invisible line in the shape of a slash, horizontal line, or backslash. Because vertical pairs are likely processed in both brain hemispheres at once during bilateral presentations (Bourne 2006) due to the individual stimuli being on the vertical meridian, they were not used during this analysis. Their inclusion in the task served to distribute attention equally to cardinal and oblique orientations. Because the callosal homotopy hypothesis predicts that horizontal pair orientations should yield a smaller UFA than both oblique pair orientations, the quadratic trend was reported for “pair orientation” and all its interactions. RT was the dependent variable of main interest, but secondary analyses of variance were also run with the rate of commission and omission errors as dependent variables. Only effects of *bilateral vs unilateral*, *pair orientation*, and their interactions with other factors were of interest for the present report.

The second series of analyses of variance was meant to obtain a significance measure for Poffenberger’s CUD, and also included 4 factors of interest. There were a 4 level *block* factor, a 2 level *response hand* factor and a 2 level *visual field* factor, contrasting the left and right visual fields. For this analysis, data from stimulus presentations in the top and bottom quadrant were not used. Finally, a 2 level *pair orientation* factor was used, distinguishing both oblique from both cardinal orientations. The *response hand * visual field* interaction was of primary interest, because it was an index of Poffenberger’s CUD: Stimulus pairs presented to the left of fixation are expected to yield shorter RTs for left hand responses, and stimulus pairs presented to the right of fixation are expected to yield shorter RTs for right hand responses. The dependent variables were RT as in the previous series of analyses. To

avoid repetition, only effects of *hand* and *visual field* and their interactions with other variables were reported.

4.2.2. Results

Dimond analyses

Mean RT of all trials of Experiment 1 included in the Dimond analysis was 419 ms.

An effect of *bilateral vs unilateral* presentation was found ($F_{(1,11)} = 6.03$, $p = .032$), with longer RTs for bilateral presentations than unilateral presentations. An effect of *pair orientation* was also found (quadratic trend: $F_{(1,11)} = 11.18$, $p = .007$, partial $\eta^2 = .465$), with horizontal pair RTs being shorter than RTs for pairs of stimuli positioned in oblique orientations. A significant interaction between *bilateral vs unilateral* and *pair orientation* was obtained (quadratic trend: $F_{(1,11)} = 9.58$, $p = .01$), with a non-significant 1 ms BFA for horizontal presentations and a significant ($F_{(1,11)} = 12.15$, $p = .005$) 7 ms UFA for oblique orientations. The only other interaction involving the two factors of main interest was an interaction between *block* and *bilateral vs unilateral* ($F_{(1,11)} = 4.11$, $p = .041$), with a larger UFA at the beginning of the task which became shorter as time on task accrued (linear trend: $F_{(1,11)} = 6.39$, $p = .028$). UFAs of 6 ms, 8 ms, 0 ms, and 2 ms were obtained during the four blocks. This linear trend has previously been interpreted as an effect potentially attributable to callosal plasticity in the same dataset (Leblanc-Sirois & Braun, 2015).

Mean commission and omission error rates were 26% and 2%, respectively. With commission error rate as the dependent variable, only the *bilateral vs unilateral* effect was significant ($F_{(1,11)} = 8.88, p = .013$), revealing more errors for bilateral than unilateral presentations. With omission error rate as the dependent variable, the *bilateral vs unilateral* effect was again significant ($F_{(1,11)} = 8.69, p = .013$), revealing more omission errors for bilateral over unilateral presentations. There was an effect of *pair orientation* (quadratic trend: $F_{(1,11)} = 15.22, p = .002$). Fewer errors of omission were made following horizontal pair presentations than following oblique pair presentations. A significant *bilateral vs unilateral * pair orientation* interaction was also obtained (quadratic trend: $F_{(1,11)} = 12.20, p = .005$). Decomposing this effect yielded no significant bilateral or unilateral field advantage for horizontal pair presentations, but yielded a significant UFA ($F_{(1,11)} = 11.53, p = .007$) for oblique presentations. Mean RTs and error rates for bilateral and unilateral presentations, and for horizontal and oblique pair orientations of Experiment 1, are available in Table 1.

Poffenberger analyses

With RT of Experiment 1 as the dependent variable, there were no significant *response hand* ($F_{(1,11)} = 1.22, p = .29$) or *visual field* ($F_{(1,11)} = 1.96, p = .19$) effects. However, a significant *response hand * visual field* interaction was found ($F_{(1,11)} = 27.4, p < .0005$). A CUD of 5 ms was recorded. No other interactions were significant.

For commission errors, no effects of *response hand* ($F_{(1,11)} = 0.66, p = .43$) or *visual field* ($F_{(1,11)} = 2.19, p = .16$) were found, but there was a significant interaction between the two ($F_{(1,11)} = 6.01, p = .032$), yielding fewer commission errors for crossed presentations than for uncrossed presentations. The only other significant interaction involving a factor of primary interest was a significant *block * visual*

field interaction ($F_{(1,11)} = 3.8$, $p = .039$), with a higher proportion of commission errors occurring for right visual field stimuli as time on task accrued. No *response hand* or *visual field* effects or interactions were found in omission error rates.

The correlation between RT measures of CUD and UFA was calculated, and was found to be non-significant ($r = -.023$, $p = .94$). The correlation between RT CUD and the length of the UFA difference between horizontal and oblique presentations was also non-significant ($r = -.153$, $p = .64$). Mean RTs and error rates for crossed and uncrossed presentations in Experiment 1 are available in Table 1.

4.3. Experiment 2

In simple reaction time tasks, the complexity of the motor response has been shown to influence a measure of interhemispheric transfer time, the CUD (Braun et al. 2004; Iacoboni and Zaidel 1995). In particular, CUDs lengthened significantly when participants had to alternate between the left and right hands within a block, after each correct response. Experiment 2 was an attempt to investigate whether the effects of callosal homotopy remained significant when participants have to alternate between hands after each correct go trial. This second experiment was also made as similar as possible to Experiment 1 in order to allow a comparison between conditions with and without hand switch after each correct go trial.

4.3.1. Methods

Twelve right handed participants (6 male, 6 female) aged 18 to 30 were recruited among university students. Participants had no history of neurological or psychiatric problems, and were tested for adequate vision prior to the experiment.

The experimental procedure was similar to the task of Experiment 1, but response hand varied within trial runs rather than between trial runs. Participants were told to switch response hands after each correct response to a go trial. The left index finger on the “Z” key was used for left hand responses. The right index finger on the “2” key on the numeric pad was used for right hand responses. These two keys were chosen for their left and right position and for their equidistance to the edge of the keyboard. To facilitate responses, a keyboard on which the keys surrounding the “Z” and the “2” were absent was used during the experiment.

To help participants respond with the correct hand, the fixation cross on each trial had to be replaced by a bracket (“>” or “<”) pointing to the side of the response hand for the current trial. To draw attention to the change of hands, a fixation blink in between trials was created by decreasing the duration of the blank display with fixation (or error message during failed trials) from 500 ms to 400 ms, and by adding a blank display without fixation for 100 ms afterwards, separating the end of each trial from the beginning of the next trial.

Commission and omission errors were followed by feedback to the participant as in the previous task. “Incorrect hand” errors on go trials were also recorded and indicated to the participant by a “wrong hand” error message. As with omission errors, incorrect hand responses were not counted as correct, and trials yielding incorrect hand responses were replaced within each trial run. Statistical methods were identical to those of Experiment 1, with the addition of analyses of variance on incorrect hand error rates.

4.3.2. Results

Dimond analyses

Mean RT of Experiment 2 for all data included in the Dimond analysis was 429 ms. With RT data, there were no significant main effectss of *bilateral vs unilateral* ($F_{(1,11)} = 1.98$, $p = .187$) and *pair orientation* (quadratic trend: $F_{(1,11)} = 0.002$, $p = .963$, partial $\eta^2 = .435$). However, there was a significant interaction between *bilateral vs unilateral* and *pair orientation* (quadratic trend: $F_{(1,11)} = 8.46$, $p = .014$) in the expected direction: there was a non-significant 4 ms BFA for horizontal pair orientations ($F = 1.29$, $p = .28$) and a significant 4 ms UFA ($F_{(1,11)} = 11.34$, $p = .006$) for oblique pair orientations.

Mean commission error rate was 28%. With commission errors, there was a significant effect of *bilateral vs unilateral* ($F_{(1,11)} = 5.46$, $p = .039$), with higher rate of commission errors for bilateral than for unilateral trials. This result constituted a significant UFA obtained with commission errors. A trend towards a *bilateral vs unilateral * pair orientation* interaction was also detected (quadratic trend: $F_{(1,11)} = 4.78$, $p = .051$) in a direction concordant with RT data, with a non-significant BFA for horizontal pair orientations and a non-significant UFA for oblique pair orientations. Mean omission error rate was 2.4%, with no significant effects or interactions involving *bilateral vs unilateral* or *pair orientation*. Mean “incorrect hand” error rate was 1.1%. With “incorrect hand” error data, there was a significant effect of *bilateral vs unilateral* ($F_{(1,11)} = 22.21$, $p = .001$), showing more hand side errors for unilateral over bilateral presentations. However, there was no interaction between *bilateral vs unilateral* and *pair orientation* (quadratic trend: $F_{(1,11)} = 0.46$, $p =$

.51). Mean RTs and error rates for bilateral and unilateral presentations, and for horizontal and oblique pair orientations of Experiment 2, are available in Table 1.

Poffenberger analyses

With RT data of Experiment 2, there was a significant effect of *response hand* ($F_{(1,11)} = 5.97$, $p = .033$), with shorter RT for the right over the left hand. A significant effect of *visual field* was also obtained ($F_{(1,11)} = 9.88$, $p = .009$), with an advantage of the left visual field over the right visual field. There was a significant interaction between *response hand* and *visual field* ($F_{(1,11)} = 25.5$, $p < .0005$), yielding a CUD of 25 ms.

With commission error data, there were no effects of *response hand* ($F_{(1,11)} = 2.17$, $p = .169$) or *visual field* ($F_{(1,11)} = 3.4$, $p = .092$), but an interaction between the two was found ($F_{(1,11)} = 5.95$, $p = .033$), indicating more commission errors for uncrossed over crossed presentations. The direction of this inverse CUD was opposite to that of the CUD obtained in RT data. With omission error data, there were no effects of *response hand* ($F_{(1,11)} = 0.004$, $p = .95$) or *visual field* ($F_{(1,11)} = 0.92$, $p = .359$), but there was a significant interaction between the two ($F_{(1,11)} = 13.51$, $p = .004$), indicating fewer omission errors for uncrossed over crossed presentations, an effect in the same direction as RT data. With incorrect hand error rates as the dependent variable, there were no effects of *response hand* ($F_{(1,11)} = 0.004$, $p = .95$) or *visual field* ($F_{(1,11)} = 0.32$, $p = .585$), but there was a significant interaction between the two ($F_{(1,11)} = 24.72$, $p < .0005$), indicating fewer “incorrect hand” errors for uncrossed presentations than for crossed presentations, indicating better performance on uncrossed trials as with RT and omission errors.

The correlation between RT measures of CUD and UFA was calculated, and was found to be non-significant ($r = .17$, $p = .60$). The correlation between RT CUD and the length of the UFA difference between horizontal and oblique presentations was

also non-significant ($r = .22$, $p = .49$). Mean RTs and error rates for crossed and uncrossed presentations in Experiment 2 are available in Table 1.

Table 4.1. Mean values for mean RTs, commission error rates (% CE), omission error rates (% OE) and incorrect hand error rates (% IHE) in Experiments 1 and 2.

	No hand switch within block			Hand switch within block			
	RT (ms)	% CE	% OE	RT (ms)	% CE	% OE	% IHE
Horizontal/Bilateral	416	29.8	1.1	428	30.4	2.2	0.9
Horizontal/Unilateral	417	23.3	1.4	431	25.0	2.6	1.5
Oblique/Bilateral	423	29.2	3.0	432	27.7	2.6	0.9
Oblique/Unilateral	416	23.2	1.6	427	29.1	2.2	1.3
Uncrossed	414	25.3	1.4	415	28.0	1.6	0.6
Crossed	419	21.4	1.5	440	23.2	3.1	2.4

4.4. Both experiments combined

As previously stated, the principal purpose of the two experiments was to test the hypothesis that manipulating the visual characteristics of a Dimond task would modify the UFA or BFA without influencing Poffenberger's CUD, while manipulating the motor contingencies would change Poffenberger's CUD without altering the UFA or BFA. For this purpose, the same statistical analyses realized in the two experiments separately were run again on the data from the two experiments combined. A two level *experiment* between subjects factor, contrasting the first experiment during which response hand changed between trial runs and the second experiment during which response hand changed within trial runs, was added to the analyses of variance. Only effects of *experiment* and its interactions will be of interest for the next section of the present report.

4.4.1. Results

Dimond analyses

With RT as the dependent variable, the main effect of *experiment* on RT was non-significant ($F_{(1,22)} = 0.69$, $p = .42$). There was no interaction between *experiment* and *bilateral vs unilateral* ($F_{(1,22)} = 0.71$, $p = .407$) and no triple interaction between *experiment*, *bilateral vs unilateral*, and *pair orientation* (quadratic trend: $F_{(1,22)} < .01$, $p = .95$). There were no other significant interactions with *experiment* in RT data. *Experiment* had no significant effect and did not significantly interact with other factors in commission error rates or omission error rates.

Poffenberger analyses

With RT as the dependent variable, there was no interaction between *response hand* and *experiment* ($F_{(1,22)} = 3.06$, $p = .09$) and no interaction between *visual field* and *experiment* ($F_{(1,22)} = 0.76$, $p = .39$). However, a significant triple interaction between *response hand*, *visual field*, and *experiment* was obtained ($F_{(1,22)} = 15.55$, $p = .001$, partial $\eta^2 = .414$), showing a larger CUD when response hand varied within blocks. No other significant interactions involving *experiment* were found in RT data.

With commission error rate, no significant interactions involving *experiment* were found as the dependent variable. However, with omission error rate as the dependent variable, there was a significant triple interaction between *response hand*, *visual field*, and *experiment* ($F_{(1,22)} = 10.05$, $p = .004$). As with RT data, the CUD in omission errors was larger when response hand varied within blocks rather than between blocks. The partial correlation, controlling for *experiment*, between RT-CUD and RT-UFA remained non-significant ($r = .097$, $p = .66$).

4.4.2. General discussion

Unilateral field advantage influenced by stimulus orientation

In both experiments reported here, UFA was longer for oblique than for horizontal orientations. This effect of stimulus orientation on the UFA, a measure thought to reflect the latency of interhemispheric transfer of non-motor information, was interpreted as consequence of the homotopy of callosal fibers transporting visual information. The current experiments constitute two successful replications of this previously obtained effect (Desjardins et al. 2009; Braun et al. 2011, 2015) in similar tasks, and show that this effect resists manipulation of motor demands of the task.

Several researchers (Zaidel 1983; Brown et al. 1998) have previously argued that accuracy should also be lower when interhemispheric transfer of information is necessary, as a result of signal degradation attributable to the limited number of callosal connections and the longer distances between communicating neurons located in opposing hemispheres. Lower error rates in oblique rather than horizontal bilateral presentations relative to their respective unilateral control presentations had yet to be found. Both the significant homotopy effect obtained with omission errors in Experiment 1 and the trend towards a homotopy effect in Experiment 2 suggest a larger reduction in precision when bilaterally presented stimuli are not symmetric across the vertical meridian.

Spatial compatibility influences Poffenberger's CUD in go/no-go tasks

Poffenberger's CUD was also significant in both experiments, despite the relative complexity of the current task relative to simple reaction time or go/no-go tasks traditionally used to estimate interhemispheric transfer time. Its mean value fell very

close to the usual 2 to 4 ms estimates of CUD obtained with simple reaction time and simple go/no-go tasks (Marzi et al. 1991; Braun 1992), so long as response hand was kept constant during each trial run. However, when response hand alternated within each trial run, a very large mean CUD of 25 ms was obtained. This CUD value falls outside the normal range for behavioral estimates of IHTT, and even falls outside the longer 10 to 20 ms range for estimates of VEP-IHTT (Saron and Davidson 1989).

Two explanations based on directed visual attention versus spatial compatibility were considered for these large CUDs in Experiment 2. An attentional explanation proposes that participants' visual attention deviates towards the side of the visual field ipsilateral to the hand required for the next response, perhaps because of the hint towards the hand of response given at the site of the fixation (Hommel et al. 2001). The higher rate of commission and incorrect hand errors for uncrossed trials were consistent with this explanation. However, the attentional explanation also predicted that omission errors would be more frequent in uncrossed trials, but the opposite result was obtained. This result corresponds to a response bias towards the side of response, not to higher accuracy towards the side of response.

The spatial compatibility explanation instead proposes that participants more often evaluated trials as matches if the sides of the stimulus pairs and of the response were spatially concordant. The spatial compatibility explanation is consistent with the direction of CUDs obtained for RTs and all three error types of Experiment 2. The spatial compatibility effect occurred even though similarities between both stimuli, not spatial concordance, separated go from no-go trials. Spatial compatibility effects occurred even though no correlation between hand side and stimulus pair side existed.

The CUD has previously been shown to be in part determined by interhemispheric transfer time and in part by spatial compatibility effects (Braun et al. 2004) which are also callosally mediated (Di Stefano et al. 1992; Aglioti et al. 1996). Because the CUDs of Experiment 2 are extremely long, a very large part of the increase in CUD

resulting from the more complex motor condition is likely attributable to spatial compatibility. Longer delays attributable to spatial incompatibility in Experiment 2 may result from the need to actively process stimulus location and response location on each trial, whereas in Experiment 1 response location remains fixed and does not need to be determined on every trial.

Dimond's measure and Poffenberger's CUD represent different types of interhemispheric transfer

The logic of Dimond's inference regarding interhemispheric dynamics excludes premotor information. Accordingly, neither Dimond's "measure" nor the homotopy effect were affected by changes in the task's motor demands. Additionally, two arguments emerging from data collected during the two experiments strongly suggest that a transfer of heavily cognitively processed information can be excluded as well. Stated otherwise, the interhemispheric transfer indexed in the current perceptual matching task is almost certainly a transfer of visual information. First, a short UFA was found in Experiment 1, while a non-significant UFA was found in Experiment 2, with no significant difference between these two results (See Fig 2). Secondly, short UFAs in Dimond tasks have previously been associated with transfer of visual information, while transfer of information that has been verbally encoded normally yield relatively large and significant BFAs (Banich and Belger 1990; Belger and Banich 1992), usually longer than 20 ms. A recent meta-analysis of Dimond tasks showed that to be the case in 23 out of 25 experiments (Leblanc-Sirois and Braun 2014). Moreover, the bilateral-unilateral differences were affected by a manipulation of stimulus pair orientation, in both experiments. Information pertaining to stimulus location obviously does not require verbal encoding. Indeed, such a robust UFA as obtained in both current experiments would be expected only if stimuli were not verbally encoded before information is transferred across the corpus callosum.

Moreover, data collected from both experiments confirm that Poffenberger's CUD was not tied to the transfer of visual information. In both experiments, a manipulation of the visual scene known to affect the latency of the transfer of visual information did not modify CUDs significantly (See Fig 2). Data instead confirmed a link between Poffenberger's CUD and the transfer of premotor information, because a manipulation of motor demands of the task yielded a change in the length of CUDs. However, it is probable that a large part of this CUD difference between both experiments can be accounted for by spatial compatibility. The current set of experiments did not precisely determine to which extent the CUD difference represented a change in IHTT.

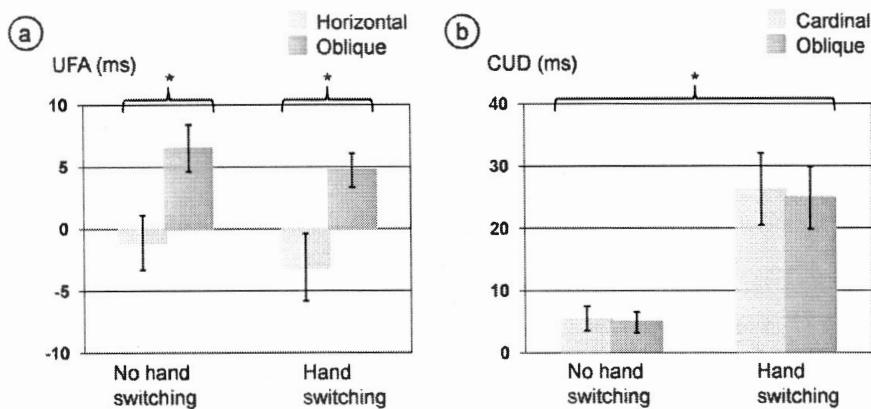


Fig 4.2. Manipulation of visual and motor conditions yields differences in Dimond's and Poffenberger's measures, respectively. a) UFAs are larger for oblique stimulus pair presentations than for horizontal stimulus pair presentations, irrespective of motor demands. b) CUDs are longer when participants must switch hands within trial runs than when response hand is fixed within a trial run, irrespective of stimulus pair orientation. Error bars represent standard error of the mean. * = statistically significant.

A correlation between UFA and CUD measures obtained for each participant was also expected if the transfer of visual information accounted for both measures. The non-significance of this correlation in both experiments also provided an argument for the idea that different types of information transfer across hemispheres influence Dimond's and Poffenberger's measures.

In conclusion, results obtained in both experiments indicate that Dimond's measure of interhemispheric dynamics and Poffenberger's CUD do not index the same type of interhemispheric transfer of information. The balance between unilateral and bilateral presentations was found to be sensitive to a manipulation of stimulus pair orientation, but not to the addition of frequent changes in response hand. The difference between crossed and uncrossed trials was instead sensitive to a manipulation of motor demands, but was not sensitive to a change in stimulus pair orientation.

CHAPITRE V

DISCUSSION GÉNÉRALE

5.1. Discussion liée à la méta-analyse du chapitre II

5.1.1. Effet de la complexité de la tâche sur les dynamiques interhémisphériques

Malgré l'abondance d'études ayant tenté de préciser l'impact de caractéristiques des tâches visuelles sur la coopération entre deux hémisphères cérébraux dans le paradigme de Dimond, aucune méta-analyse de cette littérature scientifique n'avait été produite à ce jour. Deux modèles explicatifs du déroulement de cette tâche avaient été publiés : Banich et Belger (Banich & Belger, 1990; Belger & Banich, 1992) proposaient qu'à mesure que le traitement de stimuli visuels devenait plus complexe, un traitement en parallèle par deux hémisphères devenait de plus en plus avantageux. Ainsi, elles obtenaient des temps de réponse plus longs et un avantage bilatéral plus grand lorsqu'une tâche demandant une comparaison physique de deux lettres était transformée en tâche demandant une comparaison de l'identité verbale des lettres, ce qui constituait une hausse de la complexité du traitement. Elles expliquaient cet effet en proposant l'idée que le recrutement des deux hémisphères cérébraux devient plus avantageux à mesure qu'une tâche devient plus complexe. Une métaphore décrivant bien cette idée est celle d'un goulot d'étranglement qui limite la quantité d'information pouvant être traitée en même temps, et qui s'élargit lorsque les deux hémisphères participent au traitement.

En contradiction apparente avec ce modèle, Braun et collègues (Desjardins, Braun, Achim, & Roberge, 2009; Braun & al., 2011) manipulaient l'endroit où les paires de stimuli étaient présentées lors de tâches demandant de comparer physiquement deux stimuli, connues pour produire un avantage unilatéral (Banich & Belger, 1990). Ils obtenaient alors un résultat dans la direction inverse de l'effet prédit par le modèle de Banich et Belger, soit un avantage unilatéral plus grand lorsque les temps de réponse étaient plus longs. Ils proposaient que cet effet résulte d'un allongement de la latence liée au transfert interhémisphérique d'information.

Afin d'étudier l'impact de manipulations expérimentales sur les deux composantes de l'avantage unilatéral ou bilatéral, soit l'avantage lié à la parallélisation du traitement de l'information et le coût du transfert calleux, la méta-analyse exploratoire du chapitre II a recensé toutes les combinaisons d'expériences lors desquelles un changement du temps de réponse était accompagné d'un changement de l'avantage unilatéral ou bilatéral. Cette procédure a tout d'abord permis de révéler que des modifications aux deux composantes étaient fréquemment retrouvées dans la littérature scientifique, et qu'une interprétation prudente de l'avantage unilatéral ou bilatéral en tant que combinaison de changements aux deux composantes devenait alors nécessaire. La possibilité de quantifier séparément les changements aux deux composantes à l'intérieur d'un ensemble de données demeure cependant limitée, puisqu'il est très difficile de départager leurs effets.

Dans le but d'étudier les changements de la latence d'une seule composante de l'avantage unilatéral ou bilatéral, il demeure possible de limiter le changement de la latence de l'autre composante en utilisant des manipulations expérimentales peu susceptibles d'influencer celle-ci. Pour isoler la composante liée à la parallélisation du traitement de l'information, la méta-analyse du chapitre II a identifié deux caractéristiques des tâches visuelles susceptibles de rendre la coopération entre les deux hémisphères cérébraux plus avantageuse. Selon les résultats obtenus, l'implication des deux hémisphères était plus avantageuse lorsqu'un traitement verbal des stimuli visuels était nécessaire. De plus, l'implication des deux hémisphères était plus avantageuse lorsque des distracteurs étaient présents dans la scène visuelle, ceux-ci devant aussi être traités. Ces deux résultats confirmaient l'hypothèse de Banich, selon laquelle l'avantage de l'utilisation des deux hémisphères lors du traitement de l'information est plus grand lorsque ce traitement est plus complexe.

5.1.2. Effets des caractéristiques visuelles de la tâche

À l'opposé, dans le but de mieux isoler la composante liée au transfert interhémisphérique lors de recherches subséquentes, deux caractéristiques des tâches visuelles susceptibles de faciliter l'observation de changements de la latence de la composante de l'avantage unilatéral ou bilatéral liée au transfert interhémisphérique ont été trouvées. Lorsque deux tâches demandaient une comparaison de l'identité physique des stimuli, le temps de réponse global le plus long annonçait le plus souvent un coût de transfert, et non un avantage lié à la coopération interhémisphérique. Finalement, la comparaison de deux stimuli différents entraînait un transfert interhémisphérique plus long que la comparaison de deux stimuli identiques. Cependant, un résultat nul et un résultat contraire à l'effet de similarité des stimuli ont été obtenus au chapitre III. Ces sont discutés à la section 5.2.4.

Il demeure vrai que les deux caractéristiques influençant la transmission interhémisphérique selon la méta-analyse sont des caractéristiques visuelles de la tâche. Ces résultats suggèrent que les tâches les plus susceptibles de révéler des changements à la composante liée au transfert interhémisphérique sont des tâches simples, sans distracteurs, ne demandant qu'une comparaison physique entre deux stimuli visuels présentés de façon simultanée.

5.2. Discussion liée au chapitre III

5.2.1. Effet attribué à l'homotopie calleuse

Le corps calleux est formé en majorité de fibres homotopiques reliant des aires homologues dans les hémisphères gauche et droit du cortex cérébral (Dougherty, Ben-Sachar, Bammer, Brewer, & Wandell, 2005; Hofer & Frahm, 2006). Cette

symétrie des fibres du corps calleux a aussi été liée au processus de fusion méridionale du champ visuel (Clarke, 2003), suggérant une spécialisation du corps calleux pour un transfert d'information visuelle symétrique par rapport au méridien vertical.

Quatre expériences précédentes (Desjardins, Braun, Achim, & Roberge, 2009; Braun & al., 2011; Braun, Achim, Roberge, & Gauvin, 2015) ont tenté de vérifier si cette spécialisation du corps calleux pour ce type de symétrie fait en sorte que le transfert interhémisphérique d'information visuelle est plus rapide pour des stimuli positionnés de façon symétrique plutôt qu'asymétrique par rapport au méridien vertical. La méthode de Dimond a donc été utilisée pour isoler la latence liée aux dynamiques interhémisphériques des autres sources de latence. Lors de trois expériences sur quatre, les analyses statistiques révélaient un UFA significativement plus grand pour des paires de stimuli disposées à l'horizontale que pour des paires de stimuli disposées en oblique. Cet effet avait été attribué à l'homotopie du corps calleux.

Cependant, une explication alternative proposait que l'effet attribué à l'homotopie résulte plutôt d'interactions entre l'orientation locale des stimuli utilisés et l'orientation plus globale des paires de stimuli. En effet, l'effet attribué à l'homotopie n'était significatif que pour des paires de carrés, et non pour des paires de disques, lors d'une des trois études (Braun & al., 2011). De plus, des interactions entre l'orientation locale des stimuli et l'orientation de la position des paires de stimuli étaient décelées dans la troisième étude (Braun, Achim, Roberge, & Gauvin, 2015). En tout, une démonstration convaincante de l'effet d'homotopie dans le paradigme de Dimond n'avait donc pas été produite.

Un des objectifs des deux expériences présentées au chapitre III était de clarifier l'interprétation de l'effet d'orientation des paires de stimuli sur l'UFA. Deux approches différentes ont été adoptées : Lors de la première expérience, les orientations locales des stimuli ont été éliminées par l'utilisation de stimuli en forme

de disques. Lors de la seconde expérience, les orientations locales des stimuli, l'orientation de la ligne invisible séparant les deux stimuli d'une paire, et l'orientation du point central de cette ligne par rapport à la fixation ont toutes été contrôlées. L'effet d'homotopie était significatif à la première expérience lorsque des stimuli identiques étaient utilisés, mais il n'atteignait pas le seuil de signification dans les trois autres conditions. De plus, l'effet d'homotopie calleuse a de nouveau été démontré avec des stimuli en forme de disque lors d'une tâche avec alternance de mains lors de la seconde expérience du chapitre IV.

Une série d'analyses statistiques additionnelles sur les données rassemblées de 60 participants à partir des tâches avec stimuli en forme de disques réalisées au cours du projet de recherche, dont font partie deux tâches n'ayant pas fait l'objet d'un article scientifique (voir appendice A, section 6.1.) a révélé que globalement, l'avantage pour les présentations unilatérales était plus grand lorsque les paires de stimuli étaient disposées en oblique plutôt qu'à l'horizontale. La part de la latence attribuable au transfert interhémisphérique était entre 2 et 6 millisecondes plus courte lorsque deux stimuli visuels devant être comparés étaient disposés de manière symétrique par rapport au méridien vertical du champ visuel. L'hypothèse selon laquelle cet effet pouvait être expliqué uniquement par des effets de concordances d'orientations lors d'expériences précédentes a donc été rejetée.

5.2.2. Interprétation des tests additionnels de l'hypothèse d'homotopie calleuse

Une autre hypothèse alternative expliquant l'effet dit d'homotopie calleuse proposait que cet effet apparaissait à cause d'une différence entre les paires horizontales bilatérales et unilatérales dans l'excentricité des deux stimuli formant chaque paire. En effet, les paires horizontales bilatérales contenaient deux stimuli à équidistance de la fixation, tandis que les paires horizontales unilatérales contenaient un stimulus

rapproché et un stimulus éloigné. L'orientation de la paire et la distance de chaque stimulus par rapport à la fixation ne pouvaient pas être contrôlés simultanément. Le choix de contrôler pour l'orientation plutôt que pour la distance de chaque stimulus par rapport à la fixation lors des analyses statistiques présentées au cours des chapitres III et IV a été fait en raison de l'influence importante qu'a l'orientation dans la perception visuelle (Appelle, 1972; Furmanski & Engel, 2000), et en particulier dans la détection de la symétrie (Corballis, Miller, & Morgan, 1971; Wenderoth, 1994; Herbert & Humphrey, 1996; Wagemans, 1997; Saarinen & Levi, 2000).

Cependant, un test de l'homotopie utilisant les paires unilatérales verticales plutôt qu'horizontales et réalisé sur l'ensemble des données avec stimuli non-orientés (voir appendice A, section 6.2.) a été réalisé, et le résultat s'est avéré non-significatif. Toutefois, il était alors difficile d'identifier si ce nouveau résultat non-significatif était attribuable à la fausseté de l'hypothèse d'homotopie calleuse ou à des différences dans la latence de la perception de paires horizontales et verticales.

Un second test de l'hypothèse liée à l'excentricité a donc été réalisé à l'aide des stimuli des quadrants obliques de l'expérience 2 du chapitre III (voir appendice A, section 6.3.). Ces données permettaient une comparaison entre des paires obliques à excentricité égale et inégale des deux stimuli par rapport à la fixation, et les résultats ne pouvaient être confondus par l'orientation. Ce test a permis d'obtenir un résultat significatif dans la direction contraire de l'idée que la différence d'excentricité aurait pu créer un effet d'homotopie factice. En effet, un tel effet aurait pu survenir si l'égalité des excentricités des deux stimuli par rapport à une fixation faisait diminuer les temps de réponse, ou si la latence des temps de réponse dépendait de l'excentricité du stimulus le plus éloigné. Or, les temps de réponse suivaient plutôt l'excentricité du stimulus le plus rapproché, ce qui suggérait que les différences d'excentricité auraient plutôt pu produire un effet d'homotopie inversé. L'hypothèse d'un effet d'homotopie réel résiste donc face à l'hypothèse alternative d'un effet factice lié aux excentricités.

5.2.3. Effet attribué à la plasticité calleuse

Un effet attribué à la plasticité calleuse a été relevé lors des deux expériences du chapitre III. En effet, dans les deux cas, les avantages unilatéraux diminuaient à mesure que le temps passé à réaliser la tâche augmentait. Cependant, une vérification de la significativité de cet effet a plus récemment été réalisé sur un ensemble de données tirées de toutes les expériences de la thèse, et aucun effet de pratique n'a été trouvé (voir appendice A, section 6.4.). Dans ces circonstances, il n'est plus nécessaire de postuler un quelconque mécanisme de plasticité calleuse pour expliquer les résultats obtenus.

5.2.4. Effet de similarité des stimuli ou de « dispatcher » calleux

Une proposition du chapitre III suggérait que le corps calleux joue un rôle important dans la gestion des concordances et des discordances d'orientation. Cette hypothèse du « dispatcher » calleux proposait que le corps calleux contribue à la facilitation de l'analyse de la scène visuelle lorsque des discordances entre des niveaux local et global sont présentes.

L'effet obtenu était cependant mieux décrit comme un avantage unilatéral obtenu lorsque les stimuli sont orientés similairement, mais un avantage bilatéral obtenu lorsque les stimuli sont orientés différemment. Une discordance locale-globale n'entraînait en effet pas de changement dans l'avantage unilatéral. Un changement dans la concordance locale (orientation des stimuli visuels) expliquait plutôt les résultats. Cependant, le fait qu'un avantage plus large pour les paires différentes n'existe que pour les stimuli orientés (carrés et losanges) et pas pour les disques a été interprété comme un signe que l'effet obtenu était spécifique aux orientations et n'était pas causé par la similarité et la différence des stimuli visuels utilisés, ce qui rejoignait l'idée du « dispatcher » calleux.

Le passage d'un avantage unilatéral lorsque les carrés sont orientés de façon similaire à un avantage bilatéral lorsque l'orientation locale des stimuli diffère est aussi contraire à un effet obtenu dans la méta-analyse du chapitre II. En effet, 10 des 12 tâches répertoriées manipulant la similarité des stimuli lors de cette étude obtenaient un effet contraire, soit un avantage unilatéral plus grand avec des stimuli différents. Ces effets sont difficilement réconciliables, mais pourraient résulter soit de la complexité de la recherche visuelle de l'expérience 2 du chapitre III, soit d'un effet spécifique aux orientations dont le mécanisme nécessite plusieurs clarifications.

De plus, cet effet a initialement été attribué à un changement de la latence du transfert interhémisphérique plutôt qu'à un changement dans la latence du traitement intrahémisphérique. En grande partie, cette attribution se justifiait par le fait que les temps de réponse des essais bilatéraux étaient un petit peu plus bas dans la condition avec stimuli différents qu'avec stimuli identiques, malgré le résultat inverse significatif pour les paires unilatérales. Ce profil se distingue des effets de traitement intrahémisphérique connus, qui génèrent habituellement de fortes hausses des temps de réponse unilatéraux et bilatéraux. Cependant, il demeure possible que le traitement bilatéral soit maximalement efficace dans les deux versions de la tâche et n'entraîne pas de délai additionnel dans la condition avec stimuli différents, malgré l'augmentation d'une latence de traitement. Cette hypothèse est aussi concordante avec le fait que la tâche de comparaison des orientations était plus difficile que la tâche de comparaison de luminance, comme en témoignent les temps de réponse plus élevés. Cette difficulté additionnelle résultait probablement de l'inclusion de quadrants orientés obliquement par rapport à la fixation dans l'expérience 2 du chapitre III. Bref, un flou considérable règne sur l'interprétation de l'avantage bilatéral obtenu seulement lorsqu'une comparaison entre un carré orienté de façon cardinale et un carré orienté en oblique devait être réalisée.

5.3. Discussion liée au chapitre IV

Pour qu'un hémisphère cérébral puisse produire une réponse motrice à un stimulus visuel présenté à l'autre hémisphère, un transfert d'information soit visuelle ou prémotrice doit être effectué. Plusieurs chercheurs ont tenté d'identifier le type d'information transféré à l'aide de corrélats cérébraux. Cependant, des preuves de l'existence d'un transfert d'information visuelle par la partie postérieure du corps calleux (Saron & Davidson, 1989) et d'un transfert d'information motrice par la partie antérieure du corps calleux (Thut & al., 1999) ont été obtenues par des méthodes électroencéphalographiques. Les études réalisées avec des patients atteints d'agénésie congénitale du corps calleux et les patients ayant subi une callosotomie ont aussi révélé que des patients callosotomisés antérieurs (Iacoboni, Fried, & Zaidel, 1994; Berlucchi, Aglioti, Marzi, & Tassinari, 1995) et postérieurs (Berlucchi, Aglioti, Marzi, & Tassinari, 1995) étaient capables de répondre avec la main contralatérale au champ visuel dans lequel un stimulus visuel était présenté, presqu'aussi rapidement que des participants neurotypiques.

Chez le participant neurotypique, il semble donc y avoir une course entre au moins deux opérations de traitement visuomoteur utilisées simultanément lorsqu'un stimulus visuel apparaît dans un hémichamp et demande une réponse de la main opposée (Clarke & Zaidel, 1989). Une de ces séries inclut un transfert d'information visuelle par le corps calleux postérieur, tandis qu'une autre inclut un transfert d'information prémotrice par le corps calleux antérieur. Cependant, un tel modèle de course entre diverses séries de processus demeure compatible avec l'idée, maintes fois proposée, que la voie impliquant un transfert d'information prémotrice est en général plus rapide (Berlucchi, Heron, Hyman, Rizzolatti, & Umiltà, 1971; Thut & al., 1999; Iacoboni & Zaidel, 2004).

Les expériences décrites au chapitre IV ont aussi fait pencher la balance en faveur d'un lien entre la méthode de Poffenberger et un transfert d'information prémotrice.

Lors de cette série d'expériences, une manipulation de la scène visuelle et une manipulation des contingences motrices étaient utilisés. Ainsi, les paires de stimuli étaient disposées à l'horizontale ou en oblique. De même, certains participants devaient toujours répondre avec la même main lors de chaque série d'essais alors que d'autres devaient alterner la main de réponse après chaque réponse correcte.

Les analyses statistiques ont révélé que la différence croisé - non-croisé n'était affectée que par la modification des contingences motrices de la tâche, et non par les variations de la scène visuelle, contrairement à l'avantage unilatéral qui fluctuait avec les changements visuels mais pas avec la manipulation motrice. De plus, l'absence d'une corrélation entre la différence croisé - non-croisé et l'avantage unilatéral ou l'effet d'homotopie suggérait que la nature de l'information transférée n'est pas identique dans les paradigmes de Dimond et de Poffenberger. Puisque les tâches simples du paradigme de Dimond indexent vraisemblablement un transfert d'information visuelle, ces résultats étaient interprétés comme un argument en faveur de l'idée selon laquelle la différence croisé -non-croisé représente une latence liée au transfert d'information non-visuelle, et donc prémotrice.

Une limite importante à l'interprétation de la mesure de Poffenberger dans la tâche de go/no-go était mise en évidence par les résultats du chapitre IV. Il était connu que pour les tâches plus complexes que le temps de réaction simple, la différence croisé - non-croisé reflétait une combinaison du temps de transfert interhémisphérique et d'effets de compatibilité spatiale (Zaidel & Iacoboni, 2003), quoique certains chercheurs ont suggéré que cette critique s'appliquait aussi aux tâches les plus simples (Hommel, 1996; Braun, Larocque, & Achim, 2004). Il demeurait alors possible que le changement de la différence croisé - non-croisé suite à une manipulation des contingences motrices de la tâche n'était attribuable qu'à des effets de compatibilité spatiale n'étant pas spécifiquement moteurs.

5.4. Utilité des mesures des dynamiques interhémisphériques en recherche clinique

Les tests de Poffenberger et de Dimond ne sont probablement pas appropriés pour une utilisation clinique hors des cas d'anomalie claire touchant le corps calleux, en raison de la variabilité des temps de réponse, de la durée relativement courte des effets recherchés en temps de réponse, de la fiabilité test-retest moindre des tests comportementaux des dynamiques interhémisphériques, et du nombre d'essais important nécessaire afin d'obtenir des résultats fiables pour un seul participant.

Cependant, une utilisation de ces tests en recherche clinique dans le but de révéler des anomalies de la communication entre les deux hémisphères a été jugée utile par de nombreuses équipes de recherche. Ainsi, des anomalies liées aux dynamiques interhémisphériques ont été révélées par les tâches de Poffenberger et de Dimond dans plusieurs pathologies, dont la schizophrénie (Mohr, Pulvermüller, Cohen, & Rochstroh, 2000; Florio, Fossella, Maravita, Miniussi, & Marzi, 2002), la dyslexie (Markee, Brown, Moore, & Theberge, 1996), les troubles alimentaires (Rozenstein, Latzer, Stein, & Eviatar, 2011), le trouble du déficit de l'attention avec hyperactivité (Mohamed, Börger, Geuze, & van der Meere, 2015), et la phénylcétonurie (Gourovitch, Craft, Dowton, Ambros, & Sparta, 1994; Banich, Passarotti, White, Nortz, & Steiner, 2010).

La tâche de Poffenberger est le plus souvent utilisée pour révéler que le transfert interhémisphérique est plus rapide dans une des deux directions dans certains groupes de patients (Banich, Passarotti, White, Nortz, & Steiner, 2010; Florio, Fossella, Maravita, Miniussi, & Marzi, 2010). Ces résultats sont interprétés comme un signe d'anomalies plus saillantes dans l'hémisphère duquel émergent les fibres calleuses transportant plus lentement l'information. Cependant, il demeure difficile d'affirmer si cette asymétrie concerne un transfert d'information prémotrice ou visuelle dans les pathologies concernées en raison des multiples voies de traitement possibles pour l'intégration visuomotrice.

En contrepartie, la méthode de Dimond est le plus souvent utilisée pour étudier la coopération entre les hémisphères à l'aide de l'avantage bilatéral dans des tâches complexes demandant par exemple une comparaison de l'identité de certains graphèmes (Mohr, Pulvermüller, Cohen, & Rochstroh, 2000; Banich, Passarotti, White, Nortz, & Steiner, 2010; Mohamed, Börger, Geuze, & van der Meere, 2015) ou une comparaison entre deux expressions faciales (Rozenstein, Latzer, Stein, & Eviatar, 2011). Dans les groupes cliniques étudiés, un avantage bilatéral absent est alors interprété comme un signe de difficultés de communication entre les deux hémisphères cérébraux. Le déficit observé lors de ces tâches est probablement attribuable à une anomalie d'un transfert survenant relativement tardivement, afin de maximiser le temps lors duquel un traitement en parallèle par les deux hémisphères cérébraux est possible (Banich & Belger, 1990; Belger & Banich, 1992).

5.5. Conclusion

Les résultats des trois chapitres centraux de la présente thèse au sujet de versions plus simples de la tâche de Dimond qui ne demandent qu'une comparaison des éléments visuels de deux stimuli suggèrent que ces tâches indexent un transfert d'information visuelle. De plus, la latence associée à ce transfert d'information peut être manipulée de manière concordante avec les connaissances disponibles sur l'anatomie du corps calleux. Les recherches présentes représentent donc un premier pas vers l'utilisation de tâches de Dimond simples et de l'avantage unilatéral pour étudier les anomalies du transfert interhémisphérique de l'information visuelle dans diverses pathologies, un avantage unilatéral plus grand étant interprétable en tant que signe d'un transfert moins efficace de l'information d'un hémisphère à l'autre.

APPENDICE A

ANALYSES ADDITIONNELLES

6.1. Tests statistiques sur expériences rassemblées avec stimuli en forme de disque

L'effet attribuable à l'homotopie calleuse dans les tâches visuelles du paradigme de Dimond est un avantage unilatéral plus court lorsque les paires de stimuli sont orientées à l'horizontale plutôt qu'en oblique, les paires horizontales en présentation bilatérale étant symétrique par rapport au méridien vertical tandis que les paires obliques ne le sont pas. Cet effet avait été documenté auparavant dans la littérature scientifique (Desjardins, Braun, Achim, & Roberge, 2009; Braun & al., 2011), mais pouvait être attribué à l'orientation des stimuli (Braun, Achim, Roberge, & Gauvin, 2015).

Une confirmation qu'un avantage unilatéral était présent était tout d'abord recherchée, dans le but de démontrer que la latence liée à la parallélisation du traitement d'information était basse. Afin de confirmer que l'avantage unilatéral est plus court lorsque les paires de stimuli visuels sont disposées à l'horizontale plutôt qu'en oblique en présence de stimuli non-orientés, les expériences utilisant des stimuli en forme de disques réalisées lors du projet de recherche ont été rassemblées pour des tests statistiques. De plus, la possibilité que l'effet d'homotopie et l'avantage unilatéral nécessitent une symétrie en miroir impliquant les caractéristiques visuelles des stimuli utilisés, et non seulement leur position, a été explorée.

6.1.1. Choix des données et méthode statistique

La différence entre l'avantage unilatéral pour les orientations de paire horizontales et obliques a été calculée pour les données de 60 participants répartis dans 5 conditions expérimentales (voir chapitre III pour un compte rendu complet de la méthode). Seule l'identité des stimuli et le critère de décision différaient entre les quatre premières conditions. Dans la première condition, les participants devaient répondre lorsque deux disques gris avaient la même luminance. Dans la seconde condition, les

participants devaient répondre lorsque deux disques gris avaient une luminance différente. Ces deux conditions expérimentales ont été rapportées au chapitre III. Dans la troisième condition, les participants devaient répondre lorsque deux disques de la même couleur (bleu ou rouge) étaient identiques. Dans la quatrième condition, les participants devaient répondre lorsque deux disques de couleur étaient différents. Ces deux dernières conditions n'ont pas fait l'objet d'une publication scientifique. Dans la cinquième condition, la détection de deux disques gris de teintes identiques entraînait de nouveau une réponse. Contrairement aux quatre premières conditions, la main de réponse alternait aussi après chaque réponse correcte (voir chapitre IV pour un compte rendu complet de la méthode).

Pour tester l'avantage unilatéral dans l'ensemble des données, un test d'intercept a été réalisé sur la variable dépendante, soit la taille de l'avantage unilatéral, sans variable indépendante. Pour tester l'effet d'homotopie dans l'ensemble des données, un second test d'intercept a été réalisé avec la taille de l'effet d'homotopie (soit la différence entre les avantages unilatéraux pour les orientations de paires horizontales et obliques) comme variable dépendante.

Pour tester la possibilité que l'effet d'homotopie nécessite des stimuli identiques et/ou symétriques, deux analyses de variance à un facteur, soit *pareil vs différent*, ont été réalisées sur les données des quatre premières conditions. Le facteur utilisé représentait la différence entre les essais avec réponse à des stimuli identiques et les essais avec réponse à des stimuli différents. Tous les stimuli identiques étaient aussi symétriques par rapport à un axe de symétrie, cet axe étant vertical pour les paires horizontales et oblique pour les paires obliques.

6.1.2. Résultat et discussion

L'avantage unilatéral était significatif dans l'ensemble des données ($F_{(1,59)} = 7,72, p = ,007$), et avait une longueur de 2,2 millisecondes (intervalle de confiance à 95% : 0,6 – 3,7 ms). La tâche de Dimond utilisée était donc adéquate pour l'étude de la composante de l'avantage unilatéral ou bilatéral liée au transfert interhémisphérique.

La différence entre les avantages unilatéraux pour les orientations de paires horizontales et obliques, attribuable à l'homotopie du corps calleux, était significativement différente de zéro ($F_{(1,59)} = 13,08, p = ,001$). L'avantage unilatéral avait une longueur de 4,4 millisecondes (intervalle de confiance à 95% : 1,9 - 6,8 ms) plus court pour les paires de stimuli orientées à l'horizontale qu'en oblique. La direction de l'effet était compatible avec l'hypothèse de l'homotopie calleuse. Comme les stimuli étaient des disques, l'orientation locale des stimuli n'a pas influencé l'effet obtenu.

Aucun effet significatif de *pareil vs différent* n'a été observé dans l'avantage unilatéral ($F_{(1,47)} = 0,003, p=,960$) ni dans l'effet d'homotopie ($F_{(1,47)} = 0.22, p=.643$) lors de tests séparés sur ces deux valeurs. Ce résultat ne permettait donc pas d'affirmer un rôle du corps calleux en tant que détecteur de symétrie ou de similarité.

6.2. Test statistique de l'effet d'homotopie avec paires unilatérales verticales

Le choix de comparer des présentations bilatérales avec paires horizontales de stimuli à des présentations unilatérales avec paires horizontales de stimuli tout au long de la thèse doctorale avait pour but de contrôler l'orientation des paires de stimuli, mais créait alors une inégalité entre les présentations unilatérales et bilatérales correspondantes. En effet, lors des présentations bilatérales horizontales, les deux stimuli étaient disposés à des distances égales du point de fixation, alors que lors des

présentations unilatérales, un stimulus visuel était plus excentrique que l'autre. Il n'était possible de contrôler qu'un seul de ces facteurs confondants potentiels à la fois. Cependant, il aurait aussi été possible de contrôler pour l'équidistance des deux stimuli par rapport à la fixation, plutôt que pour l'orientation de la paire. Afin de tester à nouveau l'hypothèse de l'homotopie calleuse présentée au chapitre III, le test statistique suivant propose un tel exercice.

6.2.1. Choix des données et méthode statistique

Le test statistique suivant est réalisé sur l'ensemble des données provenant des conditions utilisant des stimuli sans orientation locale, soit des cercles gris ou de couleur. Les données des 60 participants de la section précédente ont donc été incluses.

La méthode statistique utilisée était une analyse de variance qui incluaient les facteurs *temps* à 4 niveaux, *main*, *bilatuni*, et *orientation de paires* (trois niveaux pour les orientations oblique, verticale unilatérale/horizontale bilatérale, oblique inversée, dans cet ordre).

6.2.2. Résultat et discussion

L'interaction d'intérêt principal, *bilatuni * orientation de paires*, n'était pas significative ($F_{(2,55)}=0,31$, $p=.733$). Le test statistique présent n'offre donc pas un nouveau soutien à l'explication du résultat du chapitre III en termes d'homotopie calleuse. Au contraire, une explication alternative du même effet par des différences bilatérales-unilatérales dans la distance entre chacun des deux stimuli et le point de fixation est possible.

Cependant, cette explication alternative se base sur un test ne contrôlant pas un des facteurs connus pour avoir un impact important sur les temps de réponse dans des tâches de comparaison visuelle, soit l'orientation des paires de stimuli devant être comparés. Par exemple, un large avantage pour la détection de symétrie lorsqu'un axe vertical est utilisé plutôt qu'un axe horizontal est trouvé dans multiples études (voir Wagemans, 1997, pour une revue de la littérature). De plus, la puissance de cette explication alternative dépend du modèle de recherche visuelle qui est adopté. Trois hypothèses possibles sont mises à l'épreuve dans la prochaine section.

6.3. Tests liés à la recherche visuelle dans la tâche utilisée

Quoiqu'on sache qu'une excentricité plus grande d'un stimulus visuel fait augmenter le temps de réponse (Berlucchi, Heron, Hyman, Rizzolatti, & Umiltà, 1972) lorsqu'une seule cible doit être détectée ou jugée, l'effet de l'excentricité de deux stimuli dans une tâche de comparaison visuelle sont beaucoup moins bien documentés. Quatre modèles de l'effet d'excentricité des stimuli sont plausibles dans la tâche de Dimond utilisée à répétition lors de la présente thèse. Le premier propose que plus l'excentricité du stimulus le plus excentrique est grande, plus les temps de réponse sont élevés. Le second propose que plus l'excentricité du stimulus le plus près de la fixation est petite, plus les temps de réponse sont bas. Le troisième propose un raccourcissement des temps de réponse lorsque les deux stimuli comparés sont équidistants de la fixation, tandis que le quatrième propose un rallongement des temps de réponse dans cette situation.

L'enjeu lié à l'excentricité des stimuli étant une explication alternative de l'effet d'homotopie, il importe de préciser les prédictions de chacun des trois hypothèses quant à l'interaction *bilatuni * orientations de paires* lorsqu'une paire horizontale est utilisée pour les analyses dans tous les quadrants. L'hypothèse du rallongement du

temps de réponse lié à l'excentricité du stimulus le plus distant prédit que la paire horizontale unilatérale aura un temps de réponse plus long que la paire horizontale bilatérale, ce qui pourrait créer un effet d'homotopie factice. De même, l'hypothèse de l'avantage lié à l'équidistance des deux stimuli par rapport à la fixation prédirait aussi un temps de réponse plus long pour la paire horizontale unilatérale que pour la paire horizontale bilatérale, ce qui risque aussi de créer un effet d'homotopie factice. Au contraire, si les temps de réponse raccourcissent lorsque le stimulus le moins excentrique se rapproche, ou que le temps de réponse est plus long lorsque les deux stimuli sont équidistants de la fixation, alors un temps de réponse plus court pour la paire horizontale bilatérale par rapport à la paire horizontale unilatérale peut être prédit. Ce résultat possible va dans le sens contraire de l'homotopie, qui ne peut alors être expliquée par des effets d'excentricité. La thèse ci-présente contient des données adéquates pour un test des trois modèles ci-dessus.

6.3.1. Choix des données et méthode statistique

Les données des paires orientées en oblique à l'intérieur des quadrants obliques de la tâche 2 du chapitre III permettent un test adéquat des modèles de la recherche visuelle de deux stimuli devant être comparés. En effet, celles-ci contiennent un nombre égal de réponses réussies à des paires de stimuli équidistants à la fixation et de paires de stimuli dont l'un est plus excentrique et l'autre moins excentrique que les stimuli des paires équidistantes. La distance du stimulus le plus rapproché de la ligne médiane est identique pour les deux types de paires, et il en est de même pour les stimuli les plus distants, ce qui permet un contrôle pour les effets potentiels liés au transfert interhémisphérique. Finalement, comme toutes les paires analysées sont disposées en oblique, les différences observées ne sont pas dues à l'orientation horizontale ou verticale des paires. Les paires en question proviennent de 16 participants et totalisent 2048 essais.

Deux temps de réponse moyens, soit un pour les paires de stimuli à excentricité égale et une pour les paires de stimuli à excentricité inégale, ont été calculés pour chaque participant. Une analyse de variance a ensuite été réalisée pour contraster les temps de réponse des paires de stimuli à excentricité égale et les paires de stimuli à excentricité inégale.

6.3.2. Résultats et discussion

La différence entre les temps de réponse des paires de stimuli à excentricité égale (502 ms) et les paires de stimuli à excentricité inégale (492 ms) était significative ($F_{(1,15)}=13,99$, $p=.002$). Ce résultat est compatible avec l'hypothèse selon laquelle une distance plus courte entre la fixation et le stimulus le moins excentrique favorise des temps de réponse plus bas. Ce résultat n'est pas compatible avec l'hypothèse selon laquelle une équidistance des deux stimuli avec la fixation favorise des temps de réponse plus bas, ni avec l'hypothèse selon laquelle l'excentricité du stimulus le plus excentrique corrèle positivement avec le temps de réponse.

Les résultats correspondent aussi à l'idée que la position du stimulus le moins excentrique fournit une information quant à la position du stimulus le plus excentrique pendant la tâche de comparaison utilisée, et qu'il y a donc un apprentissage des positions possibles des paires pendant la tâche.

Finalement, ce résultat a des répercussions sur l'interprétation de l'interaction *bilatuni * orientation de paires* dans les analyses de Dimond. En effet, comme le seul modèle de la recherche visuelle compatible avec l'analyse des paires orientées en oblique à l'intérieur des quadrants obliques est celui qui ne peut pas entraîner l'interaction *bilatuni * orientation de paires* obtenu, le résultat présent renforce de manière importante l'explication de cette interaction basée sur des caractéristiques anatomiques du corps calleux.

6.4. Effet de plasticité calleuse testé sur un grand ensemble de données

Un test statistique de l'effet de pratique trouvé au chapitre III sur toutes les données collectées était aussi possible. Afin de s'assurer de la fiabilité des résultats obtenus, et dans le but de préciser l'interprétation des résultats, ce test a été réalisé.

6.4.1. Choix des données et méthode statistique

L'ensemble des résultats de 92 participants provenant de 7 conditions différentes, soit les quatre conditions rapportées au chapitre III (cercles gris pâles et foncés identiques et différents, carrés/losanges identiques et différents), les deux études avec cercles de couleur mentionnées ci-dessus et n'ayant pas fait l'objet d'articles scientifiques, et l'expérience additionnelle avec alternance de mains rapportée au chapitre IV.

Une analyse de variance a été faite avec les facteurs suivants : *moitié*, séparant la moitié 1 et la moitié 2 de la tâche, *bilatuni*, séparant les présentations bilatérales et unilatérales, *orientation des paires*, séparant les présentations obliques, horizontales, et obliques inversées, et *main*, séparant les réponses de la main gauche et droite. La variable *condition*, séparant les 7 conditions mentionnées ci-dessus, était aussi incluse dans l'analyse. Seuls les résultats de l'interaction entre *moitié* et *bilatuni* et la triple interaction avec *orientation de paires* étaient rapportées lors de ce test spécifique de l'effet de plasticité calleuse postulé au chapitre III.

6.4.2. Résultat et discussion

Ni l'interaction entre *moitié* et *bilatuni* ($F_{(1,85)}=0,42$, $p=.52$), ni la triple interaction avec *orientation de paires* ($F_{(2,85)}=0,21$, $p=.81$) n'étaient significatives. Dans les

circonstances, il n'est pas nécessaire de postuler un mécanisme de plasticité calleuse pour expliquer les résultats obtenus au chapitre III.

6.5. Corrélation entre les mesures de Dimond et de Poffenberger

Le chapitre IV proposait une corrélation nulle entre l'avantage unilatéral et la différence croisé - non-croisé, deux estimés du temps de transfert interhémisphérique découlant d'inférences différentes et indexant, selon le modèle présenté, respectivement un transfert d'information visuelle et un transfert d'information prémotrice. Pour vérifier que la corrélation n'était pas nulle à cause du nombre restreint de participants aux expériences du chapitre IV, cette corrélation a de nouveau été calculée à partir des données de tous les participants.

6.5.1. Choix des données et méthode statistique

L'ensemble des résultats de 76 participants provenant de 7 conditions différentes, soit les quatre conditions rapportées au chapitre III (cercles gris pâles et foncés identiques et différents, carrés/losanges identiques et différents), les deux études avec cercles de couleur mentionnées ci-dessus et n'ayant pas fait l'objet d'articles scientifiques, et l'expérience additionnelle avec alternance de mains rapportée au chapitre IV.

Une corrélation partielle contrôlant pour l'influence des diverses conditions a été calculée à partir des deux variables d'intérêt principal, soit la longueur de l'avantage unilatéral et la longueur de la différence croisé - non-croisé.

6.5.2. Résultat et discussion

Il n'y avait pas de corrélation entre l'avantage unilatéral et la différence croisé - non-croisé ($r_{(73)} = -.047$, $p=.687$). Ce résultat est compatible avec l'idée que l'avantage unilatéral et la différence croisé non-croisé indexent des types de transfert différent. Des analyses supplémentaires sur chacune des expériences séparées ne montrent aussi pas de corrélation significative. Le nuage de points de la figure 6.1. de la prochaine page permet cependant de constater que les mesures utilisées ont une fiabilité moindre pour évaluer le temps de transfert participant par participant, plusieurs d'entre eux obtenant par exemple une différence croisé - non-croisé négative en raison des erreurs de mesure. Pour cette raison, la sensibilité à différentes manipulations, et non la corrélation non-significative ci-dessus, forme l'argument le plus fort du chapitre IV en soutien à une séparation du type d'information transféré selon l'estimé utilisé.

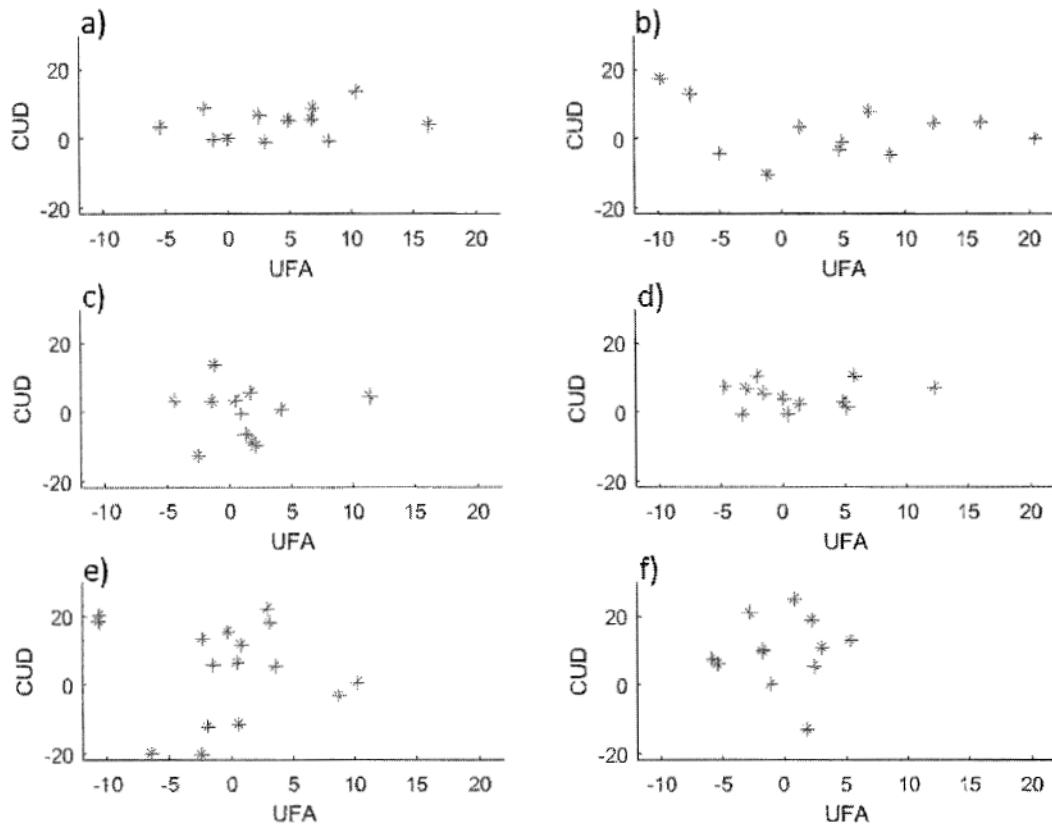


Figure 6.1. Avantage unilatéral (UFA) et différence croisé - non-croisé (CUD) pour les études de comparaison de luminance avec réponse aux stimuli identiques (a) et différents (b) du chapitre III, les études de comparaison des couleurs avec réponse aux stimuli identiques (c) et différents (d) qui n'ont pas fait l'objet d'un chapitre de la thèse, l'étude avec alternance de mains du chapitre IV (e), et l'étude de discrimination des orientations du chapitre III (f). Les moyennes pour cette dernière étude ont été calculées en combinant les conditions avec réponse aux stimuli identiques et différents.

APPENDICE B

ADDENDA ET PRÉCISIONS

7.1. Addendum au chapitre II

Les degrés de liberté du modèle de régression en page 41 devraient être (3,71) et non (2,71), puisque trois prédicteurs sont présents.

Les avantages bilatéraux rapportés à la page 49 pour l'étude de Yoshizaki (2000) étaient inversés : un avantage bilatéral de 52 ms pour la condition facile et de 10 ms pour la condition difficile auraient dû être rapportés. Le delta-balance de -42 millisecondes, crucial aux analyses statistiques subséquentes, était rapporté correctement.

7.2. Addendum au chapitre III

Les taux d'erreur justes dans l'étude rapportée au chapitre III sont de 27,7% pour les erreurs de commission, 2,1% pour les erreurs d'omission, et de 0,1% pour les erreurs d'anticipation.

L'analyse de l'interaction main * champ rapportée à la dernière phrase du chapitre III aurait dû être rédigée ainsi afin d'y inclure les degrés de liberté : $F_{(1,27)}=3.082$, $p=.003$.

7.3. Addendum au chapitre IV

Premièrement, l'analyse de l'interaction entre *Bloc* et *bilatuni* à la page 105 aurait dû être rapportée avec des degrés de liberté de (3,33).

Le choix d'une interprétation fondée sur un effet de compatibilité spatiale plutôt que sur un effet de déplacement attentionnel pour l'immense CUD trouvé à l'étude 2

mérite une explication clarifiée, que voici : Si l'attention est dirigée vers le côté de la réponse motrice, alors la prédition d'un taux plus bas d'erreurs d'omission et de commission pour les présentations non-croisées peut être faite, car on attend une précision plus élevée du côté où l'attention est dirigée, qui correspond ici au côté de la réponse demandée.

Si une tendance à effectuer une réponse motrice lorsque la main de réponse et le stimulus visuel sont situés du même côté existe, alors la prédition d'un taux d'erreurs d'omission plus bas et d'un taux d'erreurs de commission plus élevé pour les essais non-croisés peut être faite, car plus de réponses (correctes et erronées) seront alors enregistrées dans cette condition. Cette explication a été surnommée « effet de compatibilité spatiale », car une telle compatibilité entraîne plus souvent une réponse motrice.

Les statistiques cruciales pour distinguer ces deux conditions sont donc les interactions main * champ pour les taux d'erreur de commission et d'omission. Il y avait une interaction main * champ pour les erreurs de commission, montrant plus d'erreurs de commission pour les essais non-croisés. Il y avait une interaction main * champ pour les erreurs d'omission, montrant moins d'erreurs de commission pour les essais non-croisés. Ce profil correspond donc à un biais favorisant les réponses motrices lorsque le côté de la main de réponse et le côté de stimulation visuelle correspondent, tel que décrit au paragraphe précédent.

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