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Interactions multimodales visuelles et tactiles dans l'espace

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RÉSUMÉ

L’intégration de stimulations provenant de modalités sensorielles différentes nous offre des avantages perceptifs tels qu’une meilleure discrimination et une accélération des temps de réponse (TR) face aux évènements environnementaux. Cette thèse a investigué les effets de la position spatiale de stimulations visuelles et tactiles sur le gain de redondance (GR), qui correspond à une réduction du temps de réaction lorsque deux stimulations sont présentées simultanément plutôt qu’isolément.

La première étude a comparé le GR lorsque les mêmes stimulations visuotactiles sont présentées dans une tâche de détection et une tâche de discrimination spatiale. Les stimulations étaient présentées unilatéralement dans le même hémichamp ou bilatéralement dans les hémichamps opposés. Dans la tâche de détection, les participants devaient répondre à toutes les stimulations, peu importe leur localisation. Les résultats de cette tâche démontrent que les stimulations unilatérales et bilatérales produisent un GR et une violation du modèle de course indissociables. Dans la tâche de discrimination spatiale où les participants devaient répondre seulement aux stimulations présentées dans l’hémichamp droit, les TR aux stimulations bilatérales étaient moins rapides. Nous n’avons pas observé de différence entre le GR maximal obtenu dans l’une ou l’autre des tâches de cette étude. Nous concluons que lorsque l’information spatiale n’est pas pertinente pour accomplir la tâche, les stimulations unilatérales et bilatérales sont équivalentes. La manipulation de la pertinence de l’information spatiale permet donc d’induire une altération du GR en fonction de la localisation des stimulations.

Lors d’une seconde étude, nous avons investigué si la différence entre les gains comportementaux résultants de l’intégration multimodale et intramodale dépend de la configuration spatiale des stimulations. Les résultats montrent que le GR obtenu pour les conditions multimodales surpasse celui obtenu pour les stimulations intramodales. De plus, le GR des conditions multimodales n’est pas influencé par la configuration spatiale des stimulations. À l’opposé, les stimulations intramodales produisent un GR plus important lorsque les stimulations sont présentées bilatéralement. Nos résultats suggèrent que l'intégration multimodale et intramodale se distinguent quant au GR qu'ils produisent et quant aux conditions nécessaires à cette amélioration.

La troisième étude examine le rôle du corps calleux (CC) dans l'observation du GR obtenu pour les stimulations multimodales et intramodales lorsque celles-ci sont présentées unilatéralement et bilatéralement. Quatre patients ayant une agénésie congénitale du corps calleux (AgCC) et un patient callosotomisé ont été comparés à des individus normaux dans une tâche de détection. Dans l'ensemble, les résultats suggèrent que le CC n'est pas nécessaire pour l'intégration interhémisphérique de stimulations multimodales. Sur la base d'études précédentes démontrant le rôle des collicules supérieurs (CS) dans l'intégration multimodale, nous concluons qu'en l'absence du CC, les bénéfices comportementaux résultants d'un traitement sous-cortical par les CS ne reflètent pas les règles d'intégration observées dans les études neurophysiologiques chez l'animal.

Mots clés : Intégration multisensorielle, gain de redondance, temps de réaction, espace, détection, discrimination, corps calleux, interhémisphérique

ABSTRACT

The integration of stimuli from the same or different modalities offers many benefits such as enhanced discrimination and accelerated reaction to objects. This thesis investigates the effects of stimuli's spatial location on the redundancy gain (RG) obtained with cross-modal and within-modal stimulations. The RG is a decrease in reaction times (RT) when two or more stimuli are presented simultaneously rather than a single stimulation.

The first study investigated cross-modal visuo-tactile integration in a single reaction time task and a choice reaction time task. Each unisensory stimulus was presented to either the left or right hemispace, and multisensory stimuli were presented in a unilateral (e.g. visual right/tactile right) or bilateral configuration (e.g. visual right/tactile left). The first task was a simple reaction time (SRT) paradigm where participants had to responded to all stimulations, irrespective of spatial position. Results showed that multisensory gain and coactivation were the same for spatially aligned and misaligned visuotactile stimulations. In the second task, a choice reaction time (CRT) paradigm where participants responded to rightsided stimuli only, bilateral stimuli yielded slower reaction times. No difference in multisensory gain was found between the SRT and CRT tasks for unilateral stimulations. Overall, the results suggest that when spatial information is task-irrelevant, multisensory integration of unilateral and bilateral stimuli is equivalent. However, manipulating task requirements can alter this effect.

In the second study, we investigated if the behavioral enhancements resulting from within-modal and cross-modal integration depend on the spatial congruency of the redundant stimuli. Results show that the redundancy gains (RG) obtained from the cross-modal conditions were far greater than those obtained from combinations of two visual or two tactile targets. Moreover, we found that the spatial alignment of the targets did not influence the RG obtained in cross-modal conditions, whereas within-modal stimuli produced a greater RG when the targets where delivered in separate hemispaces. These results suggest that within-modal and cross-modal integration are not only distinguishable by the amount of facilitation they produce, but also by the spatial configuration under which this facilitation occurs.

The third study examines the role of the corpus callosum (CC) in mediating the RG observed for unilateral and bilateral cross-modal integration. Using a simple detection task, we tested four congenitally acallosal and one callosotomized individuals. No significant difference between congenitally acallosal individuals and controls were found for unilateral within-modal conditions or for multisensory conditions. Overall, these results demonstrate that the CC in not required to integrate cross-modal information across hemispheres and that intrahemispheric processing is preserved in acallosal individuals. Based on previous studies demonstrating the role of the superior colliculus in multisensory integration, our results suggest that in the absence of the CC, the behavioral benefit resulting from subcortical processing by the superior colliculus does not reflect the neurophysiological constraints of multisensory integration.

Keywords : Multisensory integration, redundancy gain, reaction time, space, detection, discrimination, corpus callosum, interhemispheric

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LISTE DES ABBRÉVIATIONS

AES	*Anterior ectosylvian sulcus*
AgCC	*Agenesis of the corpus callosum*
CC	Corps calleux / *corpus callosum*
CDF	*Cumulative density function*
CRT	*Choice reaction time*
CS	Colliculus supérieur
GR	Gain de redondance
Hz	*Hertz*
ISI	*Interstimulus interval*
ITI	*Intertrial interval*
kPa	*kilopascal*
MG	*Multisensory gain*
ms	milliseconde / *millisecond*
MSI	*Multisensory integration*

RG	*Redundancy gain*
RT	*Reaction time*
RTE	*Redundant target effect*
SC	*Superior colliculus*
SRT	*Single reaction time*
TR	Temps de réaction

INTRODUCTION GÉNÉRALE

MISE EN CONTEXTE

Les interactions entre nos sens nous permettent d'avoir une représentation unifiée du monde qui nous entoure. Par exemple, la conduite à bicyclette exige que nous considérions la distance qui nous sépare d'un obstacle, les ajustements nécessaires au maintien de l'équilibre ainsi que l'éventuel klaxon d'un conducteur nerveux. Cette capacité du système nerveux à combiner et à intégrer ces informations nous confère des avantages comportementaux indéniables. Tandis que certaines conditions favorisent cette intégration, d'autres vont la contraindre, voire la supprimer. D'autres encore vont influencer nos perceptions ou produire des illusions. Ce projet porte sur l'intégration unisensorielle et multisensorielle des modalités visuelles et tactiles. Son but est d'évaluer l'influence de la localisation spatiale des stimuli sur nos comportements, plus spécifiquement sur notre capacité à réagir rapidement à une ou plusieurs cibles. La première étude porte sur l'influence du type de tâche sur l'intégration multimodale visuotactile. La seconde étude explore les effets de la présentation intrahémisphérique et interhémisphérique sur l'intégration de cibles redondantes d'une même modalité ou de modalités sensorielles différentes. Enfin, la troisième étude vise à évaluer la présence des effets observés dans la seconde étude chez un groupe de patients sans corps calleux. Ces trois études sont présentées sous forme d'articles et sont précédées d'une recension des écrits portant sur l'intégration sensorielle, ses bases neurophysiologiques et ses manifestations comportementales.

LES TEMPS DE RÉACTION

Lors de tâches de détection, les temps de réponse sont en moyenne plus rapides lorsque deux ou plusieurs cibles sont présentées plutôt qu'une seule (Todd, 1912; Nickerson, 1973). Ce phénomène d'accélération des temps de réaction (TR) est désigné sous le nom d'effet de redondance. La différence entre le TR moyen pour une stimulation unique et le TR moyen lorsque 2 ou plusieurs stimulations sont présentées simultanément constitue le gain de redondance (GR), principale mesure comportementale de l'effet de redondance. Cet effet a été démontré à maintes reprises sous différentes conditions expérimentales (Harrington & Peck, 1998; Diederich, Colonius, Bockhorst & Tabeling, 2003; Miller, 1982; Grice & Reed, 1992; Egeth & Mordkoff, 1991; Miller, 1991). Le GR est observé lorsque plusieurs stimulations de la même modalité sensorielle (Schröter, Ulrich & Miller, 2007; Murray, Foxe, Higgins, Javitt & Schroder, 2001; Savazzi & Marzi, 2002, 2008) ou de modalités sensorielles différentes sont présentées simultanément (Nickerson, 1973; Diederich & Colonius, 1987; Murray, Molholm, Christoph, Heslenfeld, Ritter et al., 2005).

Différentes interprétations ont été proposées afin de rendre compte de l'effet de redondance. Selon le modèle de course (Miller, 1982; Townsend & Ashby, 1993), l'effet de redondance s'expliquerait par une amélioration statistique (Raab, 1962). Ce modèle postule que lorsque plusieurs stimulations sont présentées simultanément, chaque stimulation déclenche un processus de détection indépendant s'effectuant en parallèle par rapport aux autres. Ainsi, le stimulus détecté le plus rapidement, celui qui « gagne la course », détermine le TR observé. Lorsque plusieurs signaux sont présents, le temps de détection associé au processus le plus rapide sera en moyenne plus court que lorsqu'un seul signal est présent. En assumant l'absence d'interactions entre les canaux sensoriels, l'équation d'inégalité de Miller (1982) permet d'évaluer si les distributions de probabilités cumulatives en condition de redondance excèdent la somme des distributions de ses composantes respectives. Cela permet d'établir une limite au-delà de laquelle le GR ne peut plus être expliqué par l'amélioration statistique.

Lorsque les TR observés sont trop rapides pour être conformes au modèle de course, une explication complémentaire à celle de l'approche probabiliste doit justifier le GR observé. L'hypothèse de coactivation (ou d'intégration) postule que l'activation neurale produite par chaque signal se combine pour accélérer les temps de réponse (Colonius & Diederich, 2004; Miller, 1982, 2004; Miller & Ulrich, 2003). La réponse aux stimuli redondants serait plus rapide puisque deux sources contribuent à l'atteinte d'un seul critère. Cette approche implique un locus où se combine l'activation des différents canaux préalablement à l'initiation de la réponse motrice. Malgré l'absence de consensus à l'égard du lieu où se produirait la combinaison des différents signaux, le modèle de course et le modèle de coactivation sont couramment utilisés pour discriminer les processus qui sous-tendent l'accélération des TR

(Murray et al., 2001; Zampini, Torresan, Spence & Murray, 2007; Tajadura-Jiménez, Kitagawa, Väljamäe, Zampini, Murray et al., 2008; Molholm, Ritter, Murray, Javitt, Schroder et al., 2002).

SUBSTRATS NEURONAUX DU TRAITEMENT MULTISENSORIEL CHEZ L'ANIMAL

Chez le mammifère, des neurones multisensoriels répondant à plus d'une modalité sensorielle et possédant des champs récepteurs distincts pour chacune de ces modalités se retrouvent en grande quantité dans les couches profondes des collicules supérieurs (CS). Cette structure reçoit des afférences visuelles, auditives et somatosensorielles provenant des voies sensorielles ascendantes ainsi que des projections descendantes du cortex qui convergent en différentes combinaisons sur les neurones multisensoriels. La définition opérationnelle de l'intégration multisensorielle d'un point de vue neuronal réfère à une différence statistiquement significative entre le nombre d'influx nerveux évoqués par une stimulation bimodale et sa composante unimodale la plus efficace, soit la modalité sensorielle générant le plus d'influx nerveux (Meredith & Stein, 1983). L'effet des stimulations bimodales sur ces neurones peut être supra-additif, c'est-à-dire que le nombre d'influx générés par la stimulation bimodale sera plus élevé que la somme des influx générés par ses composantes unimodales lorsqu'elles sont présentées seules (Stein & Stanford, 2008). S'appuyant sur ces principes, Alvarado, Vaughan, Stanford & Stein (2007) ont comparé la réponse des neurones du CS du chat à des stimulations bimodales audiovisuelles et des combinaisons intramodales de stimulations visuelles. Leurs résultats démontrent que les stimulations bimodales génèrent une réponse supra-additive tandis que la réponse produite par la combinaison de stimulations visuelles excède rarement la réponse de la composante unique la plus efficace. De plus, les réponses de ces neurones aux combinaisons de stimulations visuelles peuvent être réduites, voire supprimées par la présentation d'une stimulation ipsilatérale au neurone enregistré (Kadunce, Vaughan, Wallace, Benedek & Stein, 1997).

Toujours au sein du CS du chat, des études ont aussi montré que les stimulations multimodales présentées au même endroit produisent une augmentation du nombre d'influx générés par un neurone tandis que les stimuli incongruents présentés en des endroits différents tendent à produire une diminution de la réponse du neurone (p. ex. Meredith & Stein, 1986). Ces travaux ont permis de définir la règle spatiale, qui stipule que les interactions multisensorielles au sein du neurone dépendent de la congruence spatiale et du chevauchement des champs récepteurs de chacune des modalités. Par contre, les stimuli de chaque modalité sensorielle ne doivent pas nécessairement provenir d'un même endroit dans l'espace externe, pourvu qu'ils se situent à l'intérieur d'un espace dont les champs récepteurs se chevauchent ou qu'ils disposent de champs récepteurs suffisamment grands (Wallace & Stein, 2007; Stein & Meredith, 1993). Si les stimulations sont trop éloignées, de sorte que l'une des modalités ne stimule pas le champ récepteur du même neurone, il y aura absence d'interactions multimodales et donc absence de réponse supra-additive de la part du neurone.

Globalement, les études électrophysiologiques chez l'animal démontrent que l'intégration unisensorielle et multisensorielle possède des caractéristiques computationnelles et des capacités d'intégration distinctes. L'étude d'Alvarado et collaborateurs (2007) suggère que les neurones multisensoriels utilisent deux types d'intégration. Les neurones multisensoriels possèdent la capacité d'intégrer différentes modalités de façon supra-additive et possèdent de surcroît la capacité d'intégrer plusieurs stimulations unimodales. La réponse des neurones multisensoriels à plusieurs stimulations de la même modalité sensorielle produit une réponse additive analogue à celle des neurones ne répondant qu'à une seule modalité sensorielle. Gingras, Rowland & Stein (2009) ont d'ailleurs comparé les avantages comportementaux de l'intégration intramodale et multimodale chez le chat. Leurs résultats démontrent que l'intégration multimodale audiovisuelle améliore à la fois la détection et la localisation des cibles tandis que l'intégration intramodale de stimulations visuelles n'améliore que les taux de détection.

L'observation parallèle de l'activité neuronale et de l'amélioration des comportements de localisation et de détection chez l'animal suggère qu'il existe un lien causal entre les manifestations neurophysiologiques de l'intégration multisensorielle et la performance comportementale (Burnett, Stein, Chaponis & Wallace, 2004). Par exemple, les macaques chez qui l'on observe des réponses supra-additive au sein des neurones des CS démontrent un GR et un rejet du modèle de course lors de tâche de TR simple (Cappé, Murray, Barone & Rouiller, 2010). Par conséquent, les combinaisons de stimulations qui augmentent ou diminuent l'activité neuronale devraient améliorer ou nuire à la performance comportementale (Bell, Meredith, Van Opstal & Munoz, 2005). Puisque la capacité d'intégration supra-additive des neurones multisensoriels dépend jusqu'à un certain point de la congruence spatiale des stimulations, les gains comportementaux qui y sont associés devraient aussi être influencés par la configuration spatiale des stimuli. Certaines études supportent l'application de la règle spatiale au niveau neurophysiologique et comportemental chez l'animal (Stein, Huneycutt & Meredith, 1998; Frens & Van Opstal, 1998; Maier, Neuhoff, Logothetis & Gazanfar, 2004) en démontrant des réponses neuronales et des gains comportementaux plus importants lorsque les stimulations multimodales sont localisées au même endroit. Par contre l'utilisation exclusive de tâche de localisation et de discrimination spatiale chez l'animal ne permet pas d'exclure les effets attentionnels susceptibles d'influencer à la fois la réponse neuronale et le comportement (Cappé et al., 2010).

MANIFESTATION COMPORTEMENTALE DE L'INTÉGRATION SENSORIELLE ET MULTISENSORIELLE CHEZ L'HUMAIN

Le recours aux différents modèles pour expliquer le GR vise à quantifier l'amélioration observée et, indirectement, à discriminer les processus qui sous-tendent ce phénomène. L'augmentation de la vitesse de réaction peut être attribuable à la redondance de l'information. Ainsi, les stimuli sont qualifiés de redondants puisqu'un seul stimulus peut satisfaire au déclenchement d'une réponse. Ce point de vue correspond à l'amélioration statistique définie par Raab (1962). L'intégration multisensorielle fournit un cadre théorique où les différentes formes d'énergies provenant des sens vont produire un percept plus saillant et plus informatif que les stimulations redondantes provenant d'une seule modalité sensorielle. Les études neurophysiologiques et comportementales chez l'animal appuient ce point de vue (Meredith & Stein, 1986; Gingras et al., 2009). Dans ce contexte, les stimulations multimodales sont plus susceptibles de produire un GR attribuable au phénomène de coactivation. Il existe un a priori concernant les avantages des stimulations multimodales sur les stimulations unimodales malgré le peu d'études ayant comparé si le GR est plus important pour l'intégration multisensorielle que pour l'intégration intrasensorielle (Forster, Cavina-Praseti, Aglioti & Berlucchi, 2002; Laurienti, Kraft, Maldjian, Burdette & Wallace, 2004). Jusqu'à présent, les études chez l'humain démontrent que les stimulations multimodales produisent des temps de détection (Forster et al., 2002) et des TR de choix (Laurienti et al., 2004, 2006) plus rapides que les combinaisons unimodales lorsque les stimulations sont présentées bilatéralement (Forster et al., 2002) ou centralement (Laurienti et al., 2004; Laurienti, Burdette, Maldjian & Wallace, 2006). Ainsi, les effets de la localisation spatiale des stimuli n'ont pas été explorés systématiquement et n'ont pas été comparés en fonction de la nature unimodale ou bimodale des stimulations. Puisque les interactions sensorielles s'avèrent sensibles à la disparité des stimulations dans l'espace, l'avantage des stimulations multimodales sur les stimulations unimodales pourrait être influencé par la configuration spatiale des stimuli.

EFFETS DE LA LOCALISATION SPATIALE DES STIMULI MULTISENSORIELS

Un grand nombre d'études ont utilisé la règle spatiale définie selon les études neurophysiologiques chez l'animal afin de prédire et d'expliquer les résultats comportementaux chez l'humain. En conséquence, ces études vont soit appuyer ou contredire la règle spatiale. Chez l'humain, plusieurs études ont démontré les effets de la congruence spatiale sur le comportement (Spence & Driver, 2004; Spence, 2013). Cet effet se traduit par des TR plus courts pour les conditions multimodales spatialement congruentes situées dans le même hémichamp que pour les conditions incongruentes situées dans les hémichamps opposés. Nombre d'études attribuent ces effets comportementaux aux principes qui gouvernent l'intégration multisensorielle au sein des neurones des CS (Stein, Huneycutt & Meredith, 1988; Bolognini, Frassinetti, Serino & Làdavas, 2005; Sambo & Forster, 2009). Par contre, l'application de règles d'intégration neurophysiologique au comportement rencontre certaines limites.

En effet, l’application de cette règle à l’effet de redondance varie selon les études en fonction du type de stimuli, du type de tâche et du type de réponse, ce qui s’avère plus flexible que les réponses neurophysiologiques enregistrées au sein des CS. Par exemple, dans une étude de TR de saccades oculaires, Diederich et collaborateurs (2003) ont montré un déclin progressif du GR avec l’accroissement de la disparité entre des stimulations visuelles et tactiles. Des résultats similaires ont été rapportés avec des saccades oculaires pour des stimuli audiovisuels (Harrington& Peck, 1998; Hughes, Reuter-Lorenz, Nozawa & Fendrich, 1994). Les saccades oculaires pourraient être plus sensibles aux effets de la congruence spatiale puisque l’orientation du regard requiert un processus de discrimination spatial. D’autres facteurs comme l’attention sélective et les exigences de la tâche jouent un rôle important dans l’intégration multisensorielle (Spence & Driver, 2004; Talsma, Doty & Woldorf, 2007; Molholm, Ritter, Javitt & Foxe, 2004; Spence & MacDonald, 2004; Tajadura-Jiménez et al., 2009). Par exemple Sperdin, Cappé, Foxe & Murray (2010) ont suggéré que la pertinence de l’information spatiale n’était pas suffisante pour induire un effet de congruence spatiale sur les TR. Dans cette étude, pour un tiers des stimulations, les participants devaient rapporter la localisation spatiale (à droite ou à gauche) d’une des modalités. Les auteurs rapportent que le fait de porter attention à la localisation des stimuli sans devoir effectuer une réponse discriminative est insuffisant pour produire un effet de congruence spatiale. Toutefois, les tâches dont les exigences sont plus élevées, notamment les tâches de discrimination spatiale, rapportent des effets de congruence spatiale sur les TR, peu importe les modalités sensorielles combinées (Sambo & Forster, 2009; Kitagawa, Zampini & Spence, 2005; Spence & Driver ,1994). Hughes, Reuter-Lorenz, Nozawa & Fendrich (1994) ont rapporté que, lorsque la tâche exige une discrimination spatiale, les résultats démontrent une modulation des TR audiovisuels en fonction de la configuration spatiale des stimuli. Par contre, les TR sont similaires peu importe la localisation des stimuli lorsque la tâche ne nécessite pas de traitement de l’information spatiale. Dans le même ordre d’idée, Stein& Rowland (2011) indiquent que les tâches ne nécessitant pas de traitement spatial sont effectivement moins susceptibles de produire des effets de congruence spatiale. En utilisant des paradigmes de détection, plusieurs études ont obtenu des TR semblables en condition congruente et incongruente en combinant différentes modalités sensorielles (Forster et al., 2002; Murray et al., 2005; Zampini et al., 2007; Teder-Sälejärvi, Di Russo, McDonald & Hillyard, 2005). De façon générale, la variabilité des résultats des différentes études semble dépendre des paramètres de la tâche, de facteurs cognitifs et physiques plutôt que de contraintes neurophysiologiques. (Spence, 2013).

Les combinaisons des stimulations visuelles et tactiles pourraient s'avérer plus sensibles aux effets de la disparité spatiale que les combinaisons bimodales incluant une stimulation auditive. Par exemple, des études neurophysiologiques chez l'homme ont montré des interactions audiotactiles précoces dans le cortex auditif associatif indépendamment de la congruence spatiale des stimulations (Murray et al. 2005; Foxe, Wylie, Martinez, Schroeder, Javitt et al., 2002). Ces interactions sont observées au sein du cortex auditif associatif controlatéral à la stimulation tactile, peu importe la localisation du stimulus auditif. Chez le macaque, il a été démontré que les régions associatives du cortex auditif de chaque hémisphère contiennent une représentation complète de l'espace auditif (Recanzone, Guard, Phan & Su, 2000). Des observations anatomiques chez le macaque appuient l'hypothèse d'une influence directe entre les régions sensorielles primaires puisque des projections du cortex auditif primaire et associatif vers les régions visuelles primaires ont été identifiées (Falchier, Clavagnier, Barone & Kennedy, 2002; Rockland & Ojima, 2003). Contrairement aux régions auditives, les régions visuelles et somatosensorielles reçoivent majoritairement des afférences controlatérales (Fitzpatrick, 2008). Ainsi, les stimulations visuotactiles congruentes sont traitées par un seul hémisphère alors que pour les stimuli incongruents, chacune des modalités est initialement traitée par un hémisphère différent. Conséquemment, l'intégration de stimuli visuotactiles incongruents impliquerait un transfert interhémisphérique. Par exemple il a été suggéré que l'activité des régions visuelles et somatosensorielles dépende effectivement de la congruence spatiale des stimuli, des activations controlatérales plus importantes étant observées lorsque les deux modalités sont présentées au même endroit (Macaluso, Frith & Driver, 2000, 2005; Sambo & Forster 2009). Conjointement à l'absence de gains comportementaux observée pour les stimulations bilatérales incongruentes, cette étude démontre une absence d'interactions neurophysiologiques en présence de stimuli incongruents.

INTÉGRATION INTRAMODALE

Certaines études en vision ont démontré un effet de redondance équivalent avec des cibles visuelles unilatérales et bilatérales (Murray et al., 2001; Ouimet, Jolicoeur, Miller, Ptito, Paggi et al., 2009). Pour les conditions unilatérales, les stimulations visuelles étaient présentées dans des quadrants différents, soit une stimulation au-dessus et une au-dessous du méridien horizontal. D'autres études rapportent un effet de redondance plus important en condition bilatérale (Miniussi, Girelli & Marzi, 1998; Corballis, Hamm, Barnett & Corballis, 2002). Puisque toutes ces études ont utilisé des tâches de détection, la variabilité des résultats serait attribuable à la nature des stimuli ainsi qu'à leur excentricité. Toutefois, l'observation du phénomène de coactivation en modalité visuelle requiert une présentation bilatérale où les stimulations sont présentées de chaque côté du méridien vertical (Corballis et al., 2002; Hughes et al., 1994; Savazzi & Marzi, 2002).

Pour le sens du toucher, l'effet de multiples stimulations sur une main ou sur les deux mains a surtout été étudié à l'aide de paradigmes d'identification, de discrimination tactile (Craig, 1985; Evans & Craig, 1991; Haggard, Kitadono, Press & Taylor-Clarke, 2006; Tamè, Farnè & Pavani, 2011) et de jugement temporel (Craig & Baihua, 1990; Clark & Geffen, 1990). Pour l'ensemble de ces tâches, ces études démontrent un avantage lorsque les cibles sont présentées aux deux mains plutôt qu'à une seule main.

TEMPS DE RÉACTION CHEZ LES PATIENTS SANS CORPS CALLEUX

Chez les sujets sains, le corps calleux joue un rôle prédominant dans le transfert interhémisphérique (Gazzaniga, 2005; Sperry, 1967). Son rôle a été en grande partie documenté grâce aux études sur les patients ayant subi une section chirurgicale du corps calleux ou qui souffrent d'une absence congénitale du corps calleux. Dans ce contexte, les tâches qui nécessitent un transfert d'informations disponibles à un seul hémisphère sont particulièrement informatives quant à la façon dont les informations peuvent être intégrées en l'absence de corps calleux.

Dans le cas de la callosotomie, le corps calleux est partiellement ou complètement sectionné afin de traiter une épilepsie réfractaire à la médication (Gazzaniga, 1995). L'âge au moment de l'intervention chirurgicale est un facteur déterminant des symptômes observés puisque la capacité de réorganisation du cerveau est plus importante durant le développement qu'à l'âge adulte. Par exemple, les enfants ayant subi cette intervention avant la puberté démontrent très peu de symptômes de déconnexion (Lassonde & Ouimet, 2010; Lassonde, Sauerwein, Geoffroy & Décarie, 1986). À l'opposé, les patients opérés à l'âge adulte présentent un syndrome de déconnexion qui se manifeste par une interruption du transfert interhémisphérique de l'information présentée indépendamment à chacun des hémisphères (Sperry, 1974; Gazzaniga, Bogen & Sperry, 1963). Toutefois, un transfert de l'information visuomotrice demeure possible en l'absence du corps calleux, mais ce transfert est sévèrement ralenti (Jeeves, 1969).

L'agénésie du corps calleux se définit par une absence congénitale ou une interruption du développement du corps calleux généralement attribuable à des facteurs génétiques (Guerri, Pascual & Renau-Piqueras, 2001). Les individus agénésiques démontrent peu ou pas d'altération du transfert interhémisphérique (Lassonde, Sauerwein, Chicoine & Geoffroy, 1991). De plus, une multitude de tâches sensorielles, motrices et cognitives requérant un transfert interhémisphérique sont préservées chez ces patients (Lassonde et al. 1991; Brown, Jeeves, Dietrich & Burnison, 1999; Brown, Thrasher & Paul, 2001). Cette absence de symptôme serait due à la plasticité développementale au sein des structures interhémisphériques intactes. (Jeeves, 1994; Meerwaldt, 1983; Sauerwein & Lassonde, 1983; Lassonde, Sauerwein, McCabe, Laurencelle & Geoffroy, 1988). Malgré la présence de mécanismes compensatoires, certains symptômes de déconnexion peuvent être observés chez les patients agénésiques. Tel que mentionné pour les individus callosotomisés, les réponses motrices nécessitant un transfert interhémisphérique génèrent des TR anormalement longs chez les patients agénésiques (Jeeves, 1969). Toutefois, ces réponses motrices s'effectuent plus rapidement chez les sujets agénésiques que chez les individus callosotomisés (Mooshagian, Iacoboni & Zaidel, 2010).

Malgré le fait que le transfert interhémisphérique soit altéré chez ces patients, un GR supérieur est généralement observé pour les stimulations visuelles bilatérales. Paradoxalement, les sujets callosotomisés et les sujets agénésiques démontrent une réduction de TR plus importante que les sujets sains. Reuter-Lorenz (1995) a observé un GR très élevé chez un patient callosotomisé. Tandis que le modèle de course pouvait expliquer le GR observé chez les participants contrôles, les temps de réaction du patient callosotomisé surpassaient les prédictions de ce modèle. Chez les participants normaux, le GR en condition interhémisphérique est estimé à environ 10 ms tandis qu'il peut atteindre 70 à 100 ms chez certains patients. En condition intrahémisphérique, ces patients ont une performance similaire à celle des participants contrôles (Reuter-Lorenz et al., 1995; Ouimet et al., 2009), ce qui suggère qu'une présentation bilatérale soit nécessaire pour observer cet effet.

En l'absence du corps calleux, les commissures antérieures et postérieures sont susceptibles d'effectuer un transfert interhémisphérique de l'information au niveau cortical. D'ailleurs, Guenot (1998) suggère que le transfert d'information par la commissure antérieure est le principal mécanisme compensatoire chez les patients agénésiques. Dans certains cas, la taille de la commissure antérieure est plus importante chez les patients agénésiques (Wolf, Ball, Ocklenburg, Otto, Heed et al., 2011). De plus, Barr et Corballis (2002) ont rapporté le cas d'un patient ayant une commissure antérieure plus volumineuse et dont la performance était similaire aux participants contrôles. Un second sujet dont la commissure antérieure avait une taille normale démontrait un déficit de l'intégration interhémisphérique d'informations visuelles. Quant à la commissure postérieure, ses fonctions précises demeurent peu connues et son rôle dans le transfert interhémisphérique serait secondaire (Berlucchi, Buchtel, & Lepore, 1978). Toutefois, l'effet de GR observé chez les patients acalleux ne semble pas dépendre de la présence des commissures interhémisphériques. Iacoboni, Ptito, Weeked & Zaidel (2000) ont rapporté des cas de patients agénésiques et callosotomisés dont les résultats s'expliquaient par le modèle de course et d'autres par le modèle de coactivation. Leurs résultats n'étaient pas liés à une pathologie particulière ni à la préservation d'une structure spécifique.

L'hypothèse alternative serait que certaines structures sous-corticales, notamment les CS, seraient responsables du transfert interhémisphérique et de l'effet de GR supérieur observés chez les patients acalleux. Le GR supérieur observé chez les individus sans corps calleux serait attribuable à un effet de sommation neurale se produisant au sein des CS (Corballis, 1998). Contrairement à l'animal, l'organisation fonctionnelle des CS et des fibres intercolliculaires est peu connue chez l'homme. Néanmoins, une étude suggère qu'un transfert d'information visuelle s'opère au niveau colliculaire (Tardif & Clarke, 2002).

IMPLICATION DES COLLICULES SUPÉRIEURS CHEZ L'HOMME

Les propriétés d'intégration des neurones multisensoriels des CS seraient hypothétiquement à l'origine du phénomène de coactivation observé dans le comportement. Ainsi, plusieurs études suggèrent l'implication des CS dans le GR et la violation du modèle de course observés chez les participants sains et sans corps calleux. Chez les patients acalleux, les CS joueraient de surcroît un rôle dans le transfert interhémisphérique de l'information. Ces études tirent avantage du fait que les principales afférences des CS proviennent des couches magnocellulaires du corps genouillé latéral, lesquelles ne répondent pas aux longueurs d'ondes courtes (Sumner, Adamjee & Mollon, 2002; Schiller, Malpeli & Schein, 1979; Leo, Bertini, Di Pellegrino & Làdavas, 2008). Par exemple, une diminution de la différence entre une réponse motrice croisée nécessitant un transfert interhémisphérique et une réponse motrice non croisée est observée chez les patients callosotomisés lorsque les stimulations visuelles peuvent être traitées par le CS (Savazzi, Fabri, Rubolli, Paggi, Tassinari et al., 2007).

Afin d'évaluer l'implication du CS dans l'effet de redondance, des stimulations monochromatiques violettes auxquelles les CS ne répondent pas ont été comparées à des stimuli contrôles blancs chez un groupe de participants sains et un groupe de participants callosotomisés (Savazzi & Marzi, 2004). Dans la condition contrôle, les TR aux stimulations bilatérales violaient le modèle de course chez les deux groupes avec un gain plus important chez les participants callosotomisés. Pour les stimulations violettes dont la longueur d'onde est supposément invisible pour les CS, les deux groupes obtenaient des TR similaires et conformes au modèle de course. Les auteurs suggèrent l'implication des CS dans l'effet de coactivation observé pour les deux groupes et dans la présence d'un GR supérieur chez les patients callosotomisés. Dans une étude ayant une méthodologie similaire, Corballis (1998) a testé trois patients callosotomisés avec des stimulations ayant une luminance identique ou différente de l'arrière-plan. Les stimulations dont la luminance ne diffère pas du fond seraient théoriquement traitées uniquement par des structures corticales alors que les stimulations dont la luminance diffère du fond seraient traitées à la fois à un niveau cortical et sous-cortical. Pour ces deux conditions expérimentales, les TR des participants sains étaient conformes au modèle de course, malgré la présence de conditions où les stimulations étaient visibles pour les CS. Pour les patients callosomisés, les TR aux stimulations équiluminantes étaient conformes au modèle de course tandis que les TR aux stimulations non équiluminantes violaient le modèle de course. L'auteur en conclut qu'un traitement sous-cortical est nécessaire afin d'observer une violation du modèle de course chez les patients callosotomisés. Dans l'ensemble, ces études suggèrent l'implication des CS à la fois dans le transfert interhémisphérique, dans la violation du modèle de course et dans le GR supérieur observés chez les patients acalleux.

Toutefois, une étude de Tomaiuolo, Ptito, Marzi, Paus & Ptito (1997) rapporte la présence d'un GR minime chez des patients ayant subi une hémisphérectomie, mais dont les CS étaient indemnes. Ainsi, le GR ne peut être entièrement expliqué par l'intégrité des CS, ce qui suggère que des interactions cortico-sous-corticales sont nécessaires pour rendre compte de ce phénomène. Dans le même ordre d'idée, l'étude de Iacoboni et collègues (2000) démontrant que la violation du modèle de course ne dépend pas d'une pathologie ou de l'intégrité d'une structure spécifique suggère plus avant que les avantages comportementaux observés chez les patients acalleux dépendent d'interactions cortico-sous-corticales. Ils ont observé que le phénomène de coactivation était présent seulement chez les patients acalleux qui présentaient une activité du cortex extrastrié. Ces résultats suggèrent que les interactions entre les régions corticales et sous-corticales sont nécessaires afin d'expliquer le GR observé chez ces patients.

Des études chez les individus sains ont utilisé une méthodologie analogue afin d'évaluer l'implication des CS dans l'intégration multisensorielle. Dans une tâche de détection audiovisuelle, le phénomène de coactivation était observé seulement lorsqu'une stimulation auditive était jumelée à une stimulation visuelle pouvant être traitée par les CS, soit des stimulations rouges (Maravita, Bolognini, Bricolo, Marzi & Savazzi, 2008; Leo et al., 2008). Lorsque des stimulations violettes invisibles pour les CS sont pairées aux stimulations auditives, le GR s'explique par le modèle de course, ce qui suggère qu'un traitement colliculaire serait nécessaire afin d'observer une coactivation. De plus, l'étude de Leo et collègues (2008) rapporte des effets congruence spatiale démontrant que la coactivation se produit seulement lorsque les stimulations sont visibles pour les CS et spatialement congruentes. Ces résultats entrent en contradiction avec les observations de coactivation obtenues pour les combinaisons unisensorielles bilatérales (Reuter-Lorenz et al., 1995; Savazzi & Marzi, 2004; Savazzi et al., 2007). De plus, ces résultats divergent de ceux obtenus dans des études similaires où des stimulations multimodales unilatérales et bilatérales produisent un effet de coactivation et un GR identiques (Murray et al., 2005; Forster et al., 2002; Girard, Collignon & Lepore, 2011; Girard, Pelland, Lepore & Collignon, 2013).

OBJECTIFS

Comme le montre les paragraphes précédents, les résultats des études sur l'intégration multisensorielle en contexte spatial sont mitigés. Malgré l'absence de consensus sur la question de l'application de la règle spatiale au comportement humain, il est possible de distinguer les conditions nécessaires à l'observation d'un GR. En effet, la pertinence de l'information spatiale semble jouer un rôle fondamental pour l'intégration multisensorielle, mais très peu d'études ont évalué la contribution de ce facteur. Cela permettrait d'identifier quels types de paradigmes sont susceptibles de produire une modulation de l'intégration multisensorielle en fonction de la localisation spatiale des stimulations. Une étude récente supporte d'ailleurs ce point de vue (Spence, 2013). Ensuite, bien que les études sur l'intégration multimodale aient décrit les avantages des stimulations multimodales sur les stimulations unimodales simples, l'effet de redondance observé en conditions multimodales et intramodales n'a pas été exploré systématiquement. Ainsi, les avantages comportementaux associés aux stimulations multimodales pourraient dépendre de la localisation spatiale des stimuli. Cela permettrait aussi d'évaluer si l'effet de redondance observé en conditions intramodales et multimodales est gouverné par les mêmes paramètres. Enfin, la présence d'un

GR supérieur chez les patients acalleux permettrait d'explorer le rôle du corps calleux dans l'intégration interhémisphérique de stimulations intrasensorielles et multisensorielles. L'utilisation de stimulations multisensorielles afin de mesurer la vitesse de réaction n'a jamais été rapportée chez cette population clinique. Puisque plusieurs études suggèrent une implication des CS dans l'effet de redondance, il serait intéressant de voir si la performance comportementale des sujets acalleux correspond aux prédictions basées sur les effets de congruence spatiale observés au sein des neurones des CS.

ARTICLE 1

Le but du premier article est d'évaluer l'impact du type de tâche sur l'intégration multisensorielle lorsque les stimulations sont présentées unilatéralement et bilatéralement. L'utilisation d'une tâche de détection simple et d'une tâche de temps de réaction de choix permet indirectement d'évaluer la pertinence de l'information spatiale dans l'effet de redondance. Cette étude vise à démontrer que des conditions de stimulation identiques peuvent produire un GR important ou une absence complète de gain en fonction des exigences de la tâche. Nous prévoyons que les stimulations visuotactiles unilatérales et bilatérales produisent des GR identiques et indissociables dans une tâche de détection simple ne nécessitant pas de discrimination spatiale. Dans une tâche de temps de réaction de choix où les participants doivent répondre aux stimulations présentées dans l'hémichamp droit seulement, nous prévoyons obtenir une modulation du GR en fonction de la configuration spatiale des stimuli. Puisque cette tâche exige une réponse seulement pour les stimuli présentés à droite de la croix de fixation, nous prévoyons que les TR des stimulations visuotactiles bilatérales soient plus lents que les TR de la condition unilatérale. Puisque les participants doivent inhiber les stimulations situées dans l'hémichamp gauche, il est possible que celles-ci interfèrent dans le processus de réponse aux stimulations cibles lorsqu'elles seront présentées simultanément.

ARTICLE 2

Le but du second article est d'évaluer si les stimulations multisensorielles visuotactiles produisent un GR plus important que des combinaisons de cibles unisensorielles redondantes en modalités visuelles et tactiles. Un deuxième objectif est de comparer si la configuration spatiale des stimuli (c.-à-d. unilatérale ou bilatérale) a un effet identique sur le GR observé dans les conditions redondantes unimodales et multimodales. Dans ce contexte, le modèle de course sera utilisé afin de qualifier les interactions unimodales et multimodales. Nous prévoyons que les stimulations multimodales violent le modèle de course pour une proportion importante de la distribution des TR, peu importe la configuration spatiale des stimuli. Pour les stimulations intramodales, il n'y a pas de consensus quant à leur capacité de produire des TR qui sont conformes ou qui enfreignent le modèle de course. Néanmoins, nous prévoyons observer un GR pour les conditions intramodales bilatérales, possiblement attribuable à la coactivation, mais de façon moins importante que pour les stimulations multimodales. La modulation du GR selon la configuration spatiale des stimulations intramodales demeure controversée et variable selon les études. Par contre, si des cibles redondantes d'une seule modalité pouvaient produire un gain de redondance aussi important que celui de cibles bimodales, la position selon laquelle l'intégration multisensorielle surpasse l'intégration intrasensorielle serait remise en question. L'alternative suggèrerait que des processus d'intégration différents sont en jeu pour l'intégration unisensorielle et multisensorielle.

ARTICLE 3

Puisque, la majorité des études sur les patients acalleux ont porté sur l'intégration de stimulations unimodales seulement, le but du troisième article est d'explorer les capacités d'intégration multisensorielle chez cette population. Ces patients démontrent un GR supérieur pour les conditions unimodales bilatérales qui n'a jamais été investigué avec des stimulations multisensorielles. Cela permettrait d'observer si l'intégration multisensorielle est altérée, maintenue ou supérieure pour les conditions interhémisphériques chez les patients acalleux. L'utilisation de configurations unilatérales et bilatérales permettrait d'évaluer si l'intégration multisensorielle intrahémisphérique demeure intacte chez ces patients. De plus, il serait possible d'évaluer si la plasticité cérébrale joue un rôle dans l'intégration multisensorielle en comparant des patients agénésiques, des patients callosotomisés et des participants contrôles. Sur la base d'études précédentes, nous prévoyons obtenir, outre le GR supérieur observé chez les patients acalleux, une différence entre les stimulations unimodales et multimodales.

ARTICLE 1

Multisensory gain within and across hemispaces in simple and choice reaction time paradigms

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ABSTRACT

Recent studies are still inconsistent regarding the nature and limits of multisensory enhancement with stimuli presented in different regions of space. In the present experiment, visual, tactile and visuo-tactile stimuli were presented to participants in two speeded response tasks. In both tasks, each unisensory stimulus was presented either in the left or right hemispace and the bimodal stimuli were presented either as aligned (e.g. visual right/tactile right) or misaligned (e.g. visual right/tactile left). The first task was a simple reaction time (SRT) paradigm where participants were asked to respond to any stimulation, irrespective of its position in space. Results demonstrated that multisensory gain and evidence of coactivation were the same for spatially aligned and misaligned visuo-tactile stimulation. The second task was a choice reaction time (CRT) paradigm where participants were asked to respond to right-sided stimuli only. In this task, misaligned stimuli yielded slower reaction times. When comparing results from the SRT and CRT tasks for the aligned configuration, no difference in the multisensory gain were obtained. Altogether, the results suggest that if spatial information is irrelevant for the task, the processing of spatially aligned and misaligned stimuli are equivalent in terms of multisensory integration. However, we demonstrate that manipulating task requirements can easily alter this phenomenon.

INTRODUCTION

The brain's ability to integrate multiple sensory inputs represents a remarkable mechanism that improves perceptions and behaviors. Under many circumstances, simultaneous stimulation of two or more sensory modalities results in behavioral facilitation, where multisensory stimuli are detected faster than unisensory components (Hershenson 1962; Todd 1912). The advantage in reaction times (RT) observed for multiple over single stimuli, referred as redundancy gain (RG), have long been documented (e.g. Raab 1962) and can be explained by two main approaches, which are the race model and the coactivation model. The race model (Miller 1982), which is also referred to as the probability summation model, suggests that individual sensory information is processed through separate channels. The average detection speed is determined by the latency of a single detection process in trials with one stimulus, and by the fastest stimulus detection process in multisensory trials. In the case of multiple stimuli, only the fastest stimulus is necessary to reach a criterion level of activation to trigger a motor response. Hence, increasing the number of channels also increases the probability that the RT of the fastest channel will be faster than the mean RT. Based strictly on statistical assumptions, it is predicted that RTs for multisensory stimuli are faster than RTs for single stimuli. Alternatively, the coactivation model postulates that when RT facilitation exceeds the race model's prediction, a neural mechanism integrates activations from different channels to trigger the motor response, resulting in greater redundancy gain. Thus, a violation of the race model is taken as an index of neural integration (Miller 1982). However, it is important to note that a violation of the race model is not a pre-requisite for the occurrence of neural interactions since non-linear interactions were observed even when the race model was satisfied (Murray et al. 2001; Sperdin et al. 2009). Furthermore, studies showed that non-linear brain responses are also observed in passive subjects (Foxe et al. 2002) as well as for anesthesized animals (Schroeder & Foxe 2002; Schroeder et al. 2001).

The spatial principle, or the so-called "spatial rule", is an issue of particular importance to multisensory integration. This rule states that multisensory interactions are dependent on the spatial alignment and overlapping of the receptive field responsive to the stimuli. That is, facilitative interactions can be observed even when stimuli are misaligned in their external coordinates, provided that the responsive neurons contain overlapping representations or large enough receptive fields (Wallace & Stein 2007; Stein & Meredith 1993). If the stimuli are derived from spatially disparate locations, such that one stimulus falls outside of the neuron's receptive field, there will be either no interactions or even response depression. For example, pioneering studies investigating multisensory integration in the cat's superior colliculus (SC) showed that spatially congruent stimuli tend to result in an increase of firing rate in neurons whereas spatially discordant stimuli led to suppressive interactions (e.g. Meredith & Stein 1986). In humans, several studies indicate that multisensory interactions are subject to spatial limitations. Within these limits, facilitative effects on RTs were observed with spatially aligned and spatially disparate stimuli presented across hemispaces (Harrington & Peck 1998; Forster et al. 2002; Diederich et al. 2003). Furthermore, several studies investigating multisensory integration reported spatial congruency effects on RTs, that is, slower RTs for misaligned than aligned stimuli. However, most of these studies involved attentionnal factors such as directing attention to a specific sensory modality (Diederich et al. 2003; Macaluso et al. 2005) or body part (Sambo & Forster 2009).

Recent studies using audio-tactile combination reported multisensory interactions regardless of spatial alignment (Murray et al. 2005; Zampini et al. 2007; Kitagawa et al. 2005). The authors suggested that the caudal medial auditory belt cortex may play an important role in the observation of such multisensory interactions since it contains large and bilateral auditory receptive fields that respond to the full 360° azimuth. Indeed, it was demonstrated that early multisensory interactions in auditory association areas occur regardless of spatial congruence for auditory-tactile stimuli (Murray et al. 2005; Foxe et al. 2002), suggesting that these effects may rely on direct influences between sensory-specific areas. In contrast to auditory regions that contain complete representation of auditory space, somatosensory and visual regions contain representations of the contralateral space as they predominantly receive inputs from the contralateral side (Fitzpatrick 2008). Therefore, congruent visuo-tactile stimuli are processed by one hemisphere whereas incongruent or bilateral combinations may necessitate an interaction between both hemispheres in order to bound sensory informations together. For instance, the activity in visual and tactile sensory-specific cortices seems to depend on the spatial congruency of the stimuli, with stronger activation when both visual and somatosensory stimuli are presented at the same contralateral location (Macaluso et al. 2000, 2005; Sambo & Forster 2009). To date, there are no studies that have reported early low-level interactions between misaligned visual-tactile stimuli. Since early low-level multisensory interactions appear to be linked to faster behavioral performance (Sperdin et al. 2009, 2010), the integration of visual-tactile stimuli may be modulated by the spatial congruency of the stimuli. A previous study reported multisensory gain in reaction times with spatially disparate visuo-tactile stimuli (Forter et al. 2002) but lacked a comparison between aligned and misaligned conditions. To the best of our knowledge, no study has yet directly assessed violation of the race model for spatially congruent and incongruent visuo-tactile combinations. This is fundamental since, as stated above, violation of the race model serves as a robust indicator of neural summation, and hence of true multisensory integration. To resolve this issue, violation of the race model and multisensory gain (MG) obtained with spatially aligned (both stimuli in the same hemispace) and spatially misaligned (stimuli presented across hemispaces) visuo-tactile combinations were compared in a paradigm where the spatial position of the stimuli was task irrelevant (task 1).

The variability of the aforementionned findings also suggests that task requirements may influence the extent of multisensory interactions. Indeed, previous studies point out that multisensory gain might be modulated by the relevance of the spatial information in the task demand (Spence & MacDonald 2004). The hypothesis that the nature of the task may modulate multisensory enhancement was thus also tested by investigating whether multisensory gain was different in a simple reaction time paradigm (SRT; task 1) as compared to a choice reaction time paradigm (CRT; task 2) using exactly the same stimuli for both tasks. In the SRT experiment, spatial location of the stimuli was task irrelevant. Alternatively, for the CRT experiment, spatial location of the stimuli was task relevant.

METHOD

PARTICIPANTS

Twenty right-handed (Oldfield 1971) participants took part in the experiment (10 females). Their age ranged between 19 and 34 years. All participants reported normal tactile perception and normal or corrected to normal vision. The study was approved by the local ethics committee of the Université de Montréal and all subjects gave their written informed consent prior to inclusion in the study.

STIMULI AND PROCEDURE

The experiment was conducted in a dark and sound attenuated room with the participants sitting in a chair with their head positioned on a chin rest. Tactile stimuli were trains of five 1 ms biphasic square wave pulses delivered every 25 ms (40 Hz for 100 ms) applied to the skin using disposable ring electrodes (Nicolet Biomedical, Madison, USA) which were placed around the proximal and distal interphalangeal joint of the index finger of each hand. Stimuli were generated using a Grass S88 dual output stimulator connected to each hand through a PSIU6 isolation unit (Grass, Astro-Med, West Warwick, USA). Due to the very large inter-individual and inter-manual (at the individual level) differences in sensitivity to electrocutaneous stimuli, stimulus intensity was individually calibrated between the hands to equate perceived left and right intensity and to obtain a prominent but comfortable (not painful) stimulation during the task. Visual stimuli consisted of a white circle subtending 1 degree of visual angle presented against a grey background. These visual stimuli were presented to the right or left of a central fixation cross at 7.5 degree of eccentricity. This procedure ensured that visual stimuli evoked activity only in the contralateral visual cortex (Sereno et al. 1995). Visual stimuli were projected at 57 cm from the participant's head for a duration of 100 ms. Bimodal stimuli were obtained by simultaneously presenting visual and tactile stimuli. There were 4 unisensory conditions (i.e. visual left, visual right, tactile left and tactile right) and 4 multisensory conditions (i.e. visual left/tactile left, visual left/tactile right, visual right/tactile right and visual right/tactile left). These multisensory stimuli could thus either be “spatially aligned” (both stimuli originated from the same location) or “spatially misaligned” (visual stimuli presented to one side and tactile stimuli presented to the opposite side) (see Fig. 1). Catch trials (10%) with no stimulus were included to control for anticipatory responses.

Participant had to place their hands on small response boxes situated 30 cm from the body and 8 cm from the right and left of the body’s midline. Visual stimuli were projected directly next to the stimulated area of the index finger of each hand to ensure maximum spatial congruency (see Fig. 1). Participants were asked to respond as fast as possible with their right thumb by pressing a button placed on the box. Stimuli were delivered and reaction times were recorded using Presentation software (Neurobehavioral Systems Inc.).

In the first task, participants were instructed to perform a simple detection task in which they were required to make speeded responses to any stimulus, irrespective of its position in space. The second task was a CRT paradigm in which participants were asked to respond to every stimuli appearing in the right hemi-space while ignoring stimuli appearing in the left hemi-space only (left visual, left tactile and left visuo-tactile stimuli did not require a response). The order of the two tasks was counterbalanced across participants. Participants completed eight blocks of 135 experimental trials with each stimulus configuration presented 15 times per block. A total of 60 trials per conditions were recorded for each task. Each stimulus presentation was followed by a 800 ms grey background (the response period) with a fixation cross. Then the cross disappeared for 200 ms and reappeared for 200 to 1600 ms (random duration) prior to the next stimulus (Mean ISI = 2000 ms; range 1300-2700 ms). The gaze of the participants was monitored via a camera and the experimenter ensured that the subjects maintained central fixation during the experiment. Participants were asked to respond as quickly as possible and to refrain from anticipatory responses.

----------Insert Figure 1 about here----------

DATA ANALYSIS

Only RTs between 100 and 1000 ms post-stimulus were analyzed. To test for the presence of multisensory interactions in the RT data, we investigated whether the gain obtained in bimodal conditions exceeded the statistical facilitation predicted by probability summation using Miller’s race model of inequality (Miller 1982). Race model inequality was analyzed using RMITest software, which implements the algorithm described at length in Ulrich, Miller, & Schroter (2007). This procedure involves several steps. First, empirical cumulative density functions (CDFs) of the reaction time distributions are estimated for every participant and every stimulus condition (i.e. auditory alone, tactile alone and bimodal condition). Second, the bounding sum of the two CDFs obtained in the two unimodal conditions (auditory and tactile) are computed for each participant, thus providing an estimate for each participant of the upper boundary for violation of the race model inequality. Third, percentile values are calculated for every stimulus condition and bounding sum (the bound) for each participant. In the present study, bin widths of 10% were used (e.g. Martuzzi et al. 2007; Sperdin et al. 2009), which gives a good compromise between a sufficient number of bins to observe violation of the race model inequality, and a too large number of bins which requires a large number of reaction times in each condition for the computation of the race model inequality. Fourth, for each percentile, a comparison between the bimodal condition and the bound is carried out using a two-tailed t-test. If at any percentile one observes significantly faster RTs in the bimodal condition relative to the bound, it can be concluded that the race model cannot account for the facilitation in the redundant signals condition, thus supporting a multisensory integration process. The multisensory gain (MG) was calculated as the decrease (in percent) of the mean RT obtained in the multisensory condition as compared with the mean estimated RT for the race model bound. MG indices were obtained for each percentile value of the reaction time distribution and were submitted to repeated measures analysis of variance (ANOVA).

RESULTS

On average for both experiments, the participants detected 98.8 ± 1.1% of all visual targets, 95.8 ± 4.5% of all tactile stimuli and 98.5 ± 2% of all multisensory combinations. First, to test for the presence of true multisensory interactions in the RT data, we investigated whether the gain obtained in bimodal conditions exceeded the statistical facilitation predicted by probability summation using Miller's race model of inequality (Miller 1982). Significant violation of the race model prediction was observed for all bimodal conditions of task 1, irrespective of their spatial alignment (see Fig. 2). The gain obtained significantly exceeded the model prediction over the 10th to the 70th percentiles for both aligned right and left conditions (range from $P = .001$ to $P \leq .029$), over the 10th to the 70th percentiles in the "visual left/tactile right" conditions (range from $P = .001$ to $P \leq .031$) and over the 10th to the 60th percentiles in the "visual right/tactile left" condition (range from $P = .001$ to $P \leq .009$). For the second task, the model prediction was violated over the 10th to the 80th percentiles of the reaction time distribution for the aligned right condition (range from $P = .001$ to $P \leq .037$). Since participants had to react only to right-sided stimuli in task two, the race model can only be calculated for the aligned right condition.

A first ANOVA was conducted to determine if the mean MG for bimodal stimuli was modulated by the spatial location of each unisensory constituent in task 1. The within-participant factors were the alignment (aligned and misaligned) and spatial location of the visual stimuli (left or right) for common significant percentiles (10th to 70th). The analysis did not revealed any significant differences for the alignment factor ($F_{(1,19)} = .627$; *ns.*) demonstrating that the percentage of decrease in RT was similar for the aligned and misaligned conditions. There was no significant main effect of the spatial location of the visual stimuli ($F_{(1,19)} = 1.01$; *ns.*). As expected, there was a significant main effect of percentiles ($F_{(6,114)} = 6.01$; $P \leq .001$) resulting from the probability of the reaction time distribution among the participants. There was no interactions between "alignment" and "visual side" ($F_{(1,19)} = .246$; *ns.*), between "alignment and "percentiles" ($F_{(6,114)} = .254$; *ns.*), between "visual side" and "percentiles ($F_{(6,114)} = .601$; *ns.*) or between the three factors ($F_{(6,114)} = .423$; *ns.*).

To assess a potential difference between SRT and CRT (see Fig. 2 B), a second ANOVA was conducted on the aligned right (VRTR) condition from task 1 and task 2. The within-participants factors were the "task" (task 1 and task 2) and common significant percentiles (10th to 80th). There was no main effect of factor "task" ($F_{(1,19)} = .846$; *ns.*), demonstrating that the MG for this specific condition was not modulated by the task demand. As expected, there was a significant main effect of percentiles ($F_{(7,133)} = 15.40$; $P \leq .001$) resulting from the probability of the reaction time distribution among the participants. Finally, there was no interactions between the factors "task" and "percentiles" ($F_{(7,133)} = .900$; *ns.*).

----------Insert Figure 2 about here----------

Because the MG could not be calculated for the incongruent stimuli configurations, further analysis was conducted to assess RT difference between all conditions of task 2. A 1 x 5 ANOVA was conducted with stimulus type (i.e. visual right, tactile right, aligned right visuo-tactile combination and both misaligned conditions) as the within-participant factor. There was a significant main effect of stimulus type ($F_{(1,19)} = 40.49$, $P < .001$). Post-hoc comparisons revealed an advantage for multisensory stimuli but only for the aligned configuration (all $P \leq .001$). For the misaligned conditions in task 2, RTs for the "visual left/tactile right" (VLTR) condition were significantly slower than RTs for all other conditions (all $P \leq .048$), demonstrating a disadvantage for multisensory stimuli for this specific condition (see Fig. 3). There was no significant difference between the "visual right/tactile left" (VRTL) and the unisensory conditions.

----------Insert Figure 3 about here----------

DISCUSSION

The main goal of this study was to investigate if the violation of the race model and the MG were the same for spatially aligned and misaligned pairs of visual-tactile stimuli. One of the critical findings from the first task was that all conditions clearly violated the race model. Furthermore, there was no MG difference between the aligned and misaligned conditions. To the best of our knowledge, this is the first behavioral demonstration of the equivalence of VT interactions across spatial configurations using the race model violation as a criterion to investigate multisensory interaction. RTs that violate the race model can be attributed to the convergence and interaction of neural responses to the stimuli in a behaviorally facilitative manner (Murray et al. 2001). A Recent study by Sperdin et al. (2009; also see Sperdin et al. 2010) provided further evidence that early-latency low-level interactions might be linked to faster performance during simple detection task. Using visuo-auditory stimuli, they demonstrated that only trials producing RTs that exceeded simple probability summation showed non-linear neural interactions over the earlier period whereas both fast and slow trials displayed non-linear effects over the later period.

Electrophysiological studies on animal and human encephalon have revealed a multitude of cortical and subcortical brain structures where visual and tactile inputs converge and interact. In animals, the most extensively described structure is the superior colliculus, a midbrain region involved in gaze control and orientation (Stein 1998; Graziano 1999; Meredith 1986). Neurophysiological studies on the superior colliculus showed that facilitative interactions can be observed when stimuli are misaligned in their external coordinates, provided that the responsive neurons contain overlapping representations or large enough receptive fields (Wallace & Stein 2007; see Stein & Stanford 2008 for a review). Unfortunately, few studies have considered the effect of spatial disparity on multisensory integration in other brain areas.

The results of the current study are consistent with other studies wherein no modulation of multisensory integration was observed for aligned and misaligned audio-tactile stimuli (Murray et al. 2005; Zampini et al. 2007). The electrophysiological data reported by Murray et al. (2005) suggests that facilitative multisensory interactions occur at identical latencies and via indistinguishable mechanisms when stimuli are presented at the same position or on opposite hemispaces. They also suggested that the caudal medial auditory belt cortex contains large and bilateral auditory receptive fields that respond to the full 360° azimuth. Another electrohysiological study reported similar behavioral findings with pairs of audio-visual stimulations. Despite the absence of spatial modulation on reaction time data, they reported overlapping but distinctive patterns of multisensory integration at the neural level between spatially aligned and misaligned pairs of stimuli (Teder-Sälejarvi et al. 2005). On the other hand, the occurrence of visuo-tactile interactions, at the neural level, has only been reported for spatially congruent stimuli configuration (Macaluso et al. 2005; Zimmer & Macaluso 2007; Sambo & Forster 2009).

In a recent study, Macaluso et al. (2005) used visuo-tactile stimuli to investigate whether cross-modal spatial-congruence effects depend on the task relevance of the visual or tactile information in sensory-specific cortices. They found that the activity in visual and somatosensory areas was modulated by spatial congruence of the stimuli, with stronger activation when both stimuli were presented at the same spatial location. Importantly, they reported that this effect was found irrespective of which modality was task relevant. Zimmer & Macaluso (2007) demonstrated that a tactile stimulus presented at the same location as a visual target increased activity in the contralateral occipital cortex as compared to incongruent combinations. Their participants were engaged in either a visual attention or a working memory task. While they were engaged in the working memory primary task, they were also asked to perform a secondary visual discrimination task where task-irrelevant tactile stimulations were presented at spatially congruent or incongruent locations. While they performed the visual attention task, they were presented with task-irrelevant congruent or incongruent visuo-tactile pairs. They reported that the cross-modal effects were unaffected by both attentional and working memory task, leading them to conclude that visuo-tactile spatial congruency in the visual cortex does not depend on available visuo-spatial and memory resources. Another study reported that spatially disparate visual-tactile stimuli failed to produce behavioral and activity enhancement in the somatosensory area even when stimuli where presented in the same hemifield (Sambo & Forster 2009). Still, behavioral enhancements were found in a similar paradigm under conditions where the distance between the stimuli was smaller (Forster et al. 2002). Overall, these findings suggest that low-level visual-tactile interactions might be mediated by direct anatomical connection between unisensory areas (Foxe & Schroeder 2005; Rockland 2004). However this explanation only accounts for spatially congruent stimuli. Due to their lateralized cortical representations, interactions between vision and touch are less likely to occur via direct anatomical connections between unisensory areas when stimuli are presented across hemifields. Therefore, if spatially congruent and spatially disparate stimuli are mediated by partially segregated pathwayss, the present results suggest that these pathways are equally effective for behavioral performance. The present demonstration with visuo-tactile stimuli is of considerable importance in determining whether the crossed anatomical pathways and the corresponding representations of these sensory systems could yield the same behavioral pattern as audio-tactile and audio-visual multisensory signals. Recent studies also demonstrated that auditory-somatosensory interactions were modulated by the specific body part that was stimulated (see Kitagawa & Spence 2006 for a review). For example, Tajadura-Jiménez et al. (2009) reported faster RTs for aligned stimuli than for misaligned stimuli when somatosensory stimuli were delivered to the participants' heads. However, no such spatial modulation was observed when somatosensory stimuli were delivered to the participants' hands. Indeed, the current result might have been different if the somatosensory stimuli were delivered to another body part (e.g. the head), possibly revealing a spatial modulation effect. In the present study, tactile stimuli were delivered to both hands whereas the responses were only produced with the right hand. Since there was no difference between the MG for all multisensory conditions, effects related to inter-hemispheric transfer time did not seem to modulate the multisensory enhancement. It is possible however, that using only the right hand to respond marginaly modulated the MG for misaligned conditions.

The results of the current study also show that the race model prediction was exceeded over a similar range of the reaction time distribution in the CRT and in the SRT (see Fig. 2 B). As opposed to findings by Hecht et al. (2008), the absence of differences in the MG between SRT and CRT suggests that there is no further advantage for multisensory processing in more demanding tasks such as the CRT paradigm. In task 2, when both unisensory components were task-relevant (VRTR), the MG was not modulated by the task demand and despite the fact that this task involved more no-go trials than go trials. It is important to note that due to the experimental paradigm, this comparison between the two tasks was only possible with one stimulation condition (VRTR). Furthermore, the MG for the other conditions in the second task was inaccessible because of the absence of responses for the left unisensory stimuli. Furthermore, different behaviors were also observed with the same stimuli under conditions where the spatial information was task relevant (task 2) as opposed to when it was task irrelevant (task 1). As opposed to the second task, the absence of any contingencies in the first task allowed the observation of visual-tactile interactions without the additionnal influence of top-down, attention-related and task-related constraints (Spence et al. 1998). Moreover, the results for the second task support the view that task requirements may influence the spatial limitations of multisensory integration (Talsma et al. 2007). Few explanations have been proposed to account for such phenomenon. An explanation was proposed by Murray et al. (2005) suggesting that higher-order cognitive and/or attentional processes might possibly act as a top-down influence on multisensory interactions. This would either involve dynamic shifts of the spatial representations or strategies that emphasize on the temporal aspect of the stimuli instead of their spatial location. Further investigations are now needed to investigate the cerebral basis of the multisensory effects observed in the present study.

In the CRT, when both stimuli were task relevant (visual right/tactile right; VRTR), reaction times exceeded the race model prediction. However, one misaligned condition (visual left/tactile right; VLTR) yielded slower RTs than the unisensory conditions, demonstrating multisensory inhibition (see Fig. 3). Therefore, when responding to a right tactile target, the left visual stimulation interfered with performance. On the other hand, no interference was seen with a task irrelevant tactile stimulation when responding to a visual target. This difference may be related to visual dominance in multisensory paradigms (Spence & Driver 2004; Colavita 1974; McGurk 1976). For example, Hecht et al. (2009) reported that haptic and auditory signals are more likely to be undetected when combined with a visual signal. Thus, the results from both tasks are consistent with prior findings indicating that behavioral advantage for multisensory processing occurs when both modalities are fully attended (Talsma et al. 2007). Overall, the results of task 2 suggest that stimuli presented at an unattended location are not beneficial for the task. This could also be indicative of subject attempting to filter out irrelevant sensory information instead of integrating this information with the relevant stimuli, which could then result in a behavioral cost when processing misaligned multisensory stimuli.

In summary, this study contributes to our understanding of the mechanisms underlying multisensory integration in humans. First, we compellingly demonstrate that the race model was violated for spatially congruent and incongruent visuo-tactile stimuli when the spatial position of the stimuli is task irrelevant. Furthermore, there was no MG difference for aligned and misaligned stimuli, suggesting that both conditions yield the same behavioral enhancement. Second, the results also demonstrate that the MG was not modulated by the task constraint (SRT or CRT) for stimuli that were relevant in both tasks. Third, results showed that both multisensory enhancement and inhibition can be obtain with the same physical stimuli, providing further evidence that multisensory integration is modulated by task requirements and relevance of spatial information.

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FIGURE CAPTIONS

*Figure 1***.** Schematic view of the experimental setup and stimulation conditions. Electrocutaneous stimulations were delivered on the index finger of each hand and visual stimuli were projected next to the stimulated area of the fingers. There were a total of eight conditions of stimulation: four unisensory and four multisensory.

*Figure 2***.** Test for violation of race model inequality (Miller 1982). The multisensory gain (MG) represents the decrease, in percent, of the mean RT obtained for the multisensory condition as compared with the mean estimated RT for the race model bound. The MG was calculated for each percentiles of the reaction time distribution. In the present study, bin widths of 10 percent were used. Positive values on the Y-axis indicate race model violation whereas negative values indicate race model satisfaction. (A) The race model of inequality was significantly violated for all conditions of task 1, irrespective of their spatial alignment. (B) The race model was violated over similar range of the reaction time distribution in task 1 (SRT) and in task 2 (CRT).

*Figure 3***.** (A) Mean reaction times (in miliseconds) and standard error for multisensory pairs (gray bars) and their corresponding visual (black bars) and tactile (white bars) unisensory stimuli in task 1. Capital letters refer to the modality and the spatial location of each stimulus. When participants were asked to respond to any stimulus, irrespective of the spatial location, multisensory facilitation was found for all multisensory conditions. (B) Mean reaction times for common conditions of tasks 1 (black bars) and 2. When participants were asked to respond only to stimuli presented on the right side, the results show facilitative interaction only for the aligned (VRTR) condition and show a disadvantage for one misaligned condition (VLTR).

Figure 1.

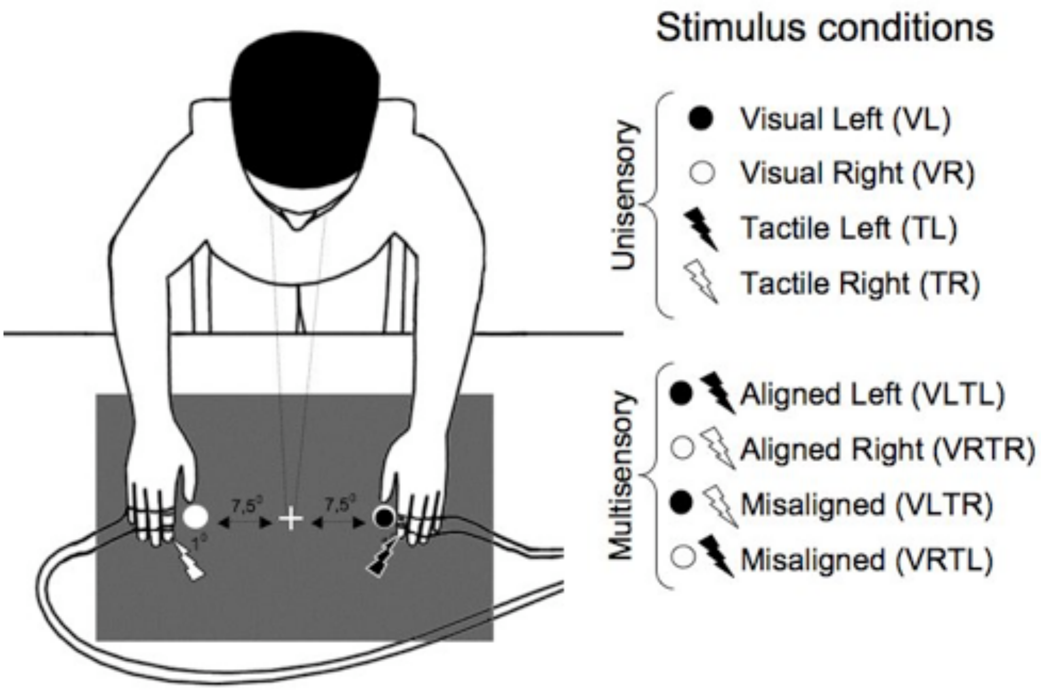

7,5°
7,5°
1°
Stimulus conditions
Unisensory
Visual Left (VL)
Visual Right (VR)
Tactile Left (TL)
Tactile Right (TR)
Multisensory
Aligned Left (VLTL)
Aligned Right (VRTR)
Misaligned (VLTR)
Misaligned (VRTL)

Figure 2.

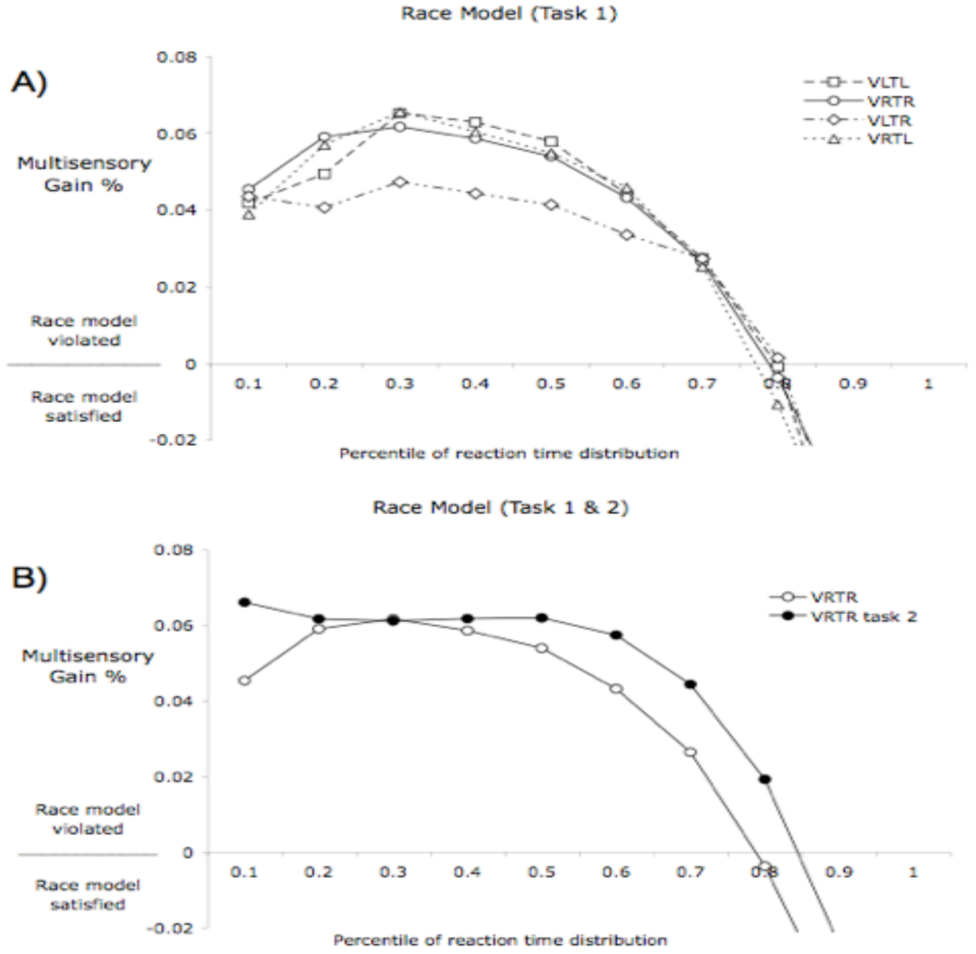
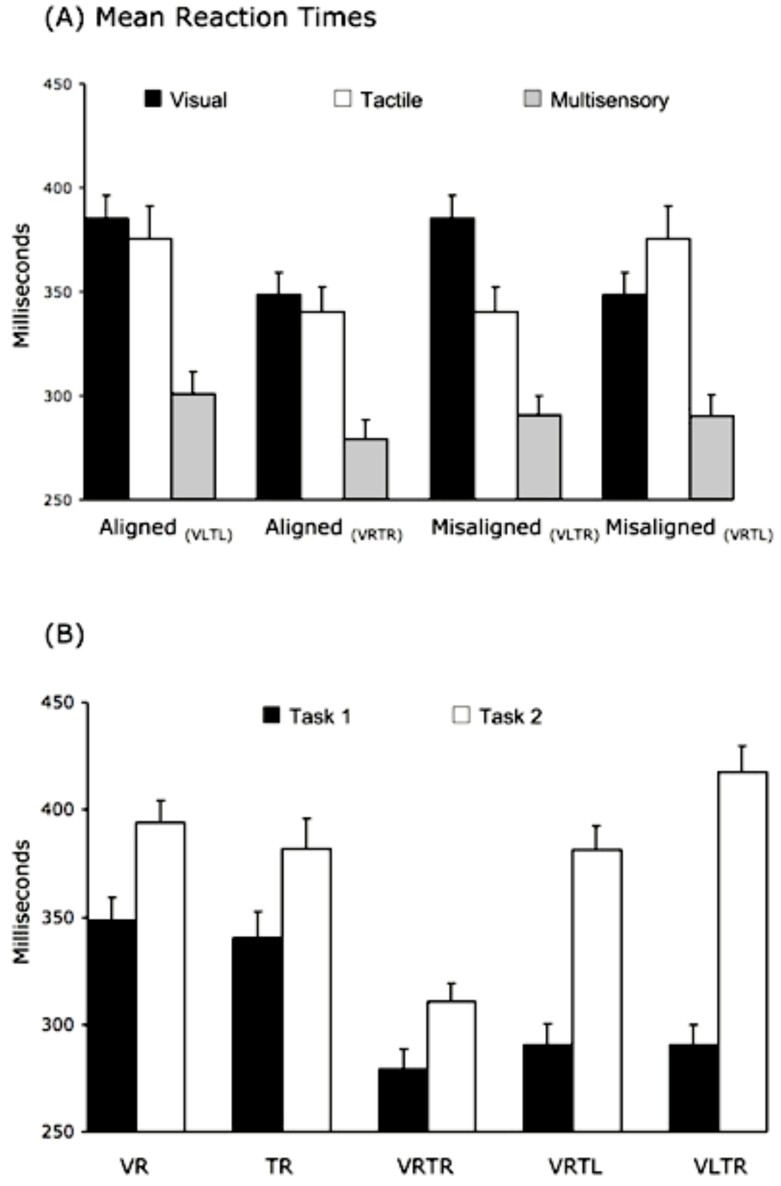

Race Model (Task 1)
A)
Multisensory Gain %
0.08
0.06
0.04
0.02
0
-0.02
Race model violated
Race model satisfied
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
Percentile of reaction time distribution
VLTL
VRTR
VLTR
VRTL
Race Model (Task 1 & 2)
B)
Multisensory Gain %
0.08
0.06
0.04
0.02
0
-0.02
Race model violated
Race model satisfied
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
Percentile of reaction time distribution
VRTR
VRTR task 2

Figure 3.


(A) Mean Reaction Times
Visual
Tactile
Multisensory
Milliseconds
450
400
350
300
250
Aligned (VLTL)
Aligned (VRTR)
Misaligned (VLTR)
Misaligned (VRTL)
(B)
Task 1
Task 2
Milliseconds
450
400
350
300
250
VR
TR
VRTR
VRTL
VLTR

ARTICLE 2

Impact of the spatial congruence of redundant targets on within-modal and cross-modal integration

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S.G. : Collecte des données
S.G. & M.P. : Analyse des résultats
S.G. : Rédaction de l'article
S.G., & O.C. : Interprétation des résultats
S.G., O.C., M.P. & F.L. : Révision du manuscrit

ABSTRACT

Although the topic of multisensory integration has raised increasing interest, the reaction time facilitation elicited by redundant cross-modal stimuli compared with those obtained with redundant stimuli of the same sensory modality has only been scarcely investigated. In the present experiment, observers were required to respond as fast as possible to (1) lateralized visual or tactile targets presented alone, (2) double stimulation within the same modality or (3) double stimulation across modalities. Each combination was either delivered within the same hemispace (spatially aligned) or in different hemispaces (spatially misaligned). Results show that the redundancy gains (RG) obtained from the cross-modal conditions were far greater than those obtained from combinations of two visual or two tactile targets. Consistently, we observed that the reaction time distributions of cross-modal targets, but not those of within-modal targets, surpass the predicted reaction time distribution based on the summed probability distributions of each constituent stimulus presented alone. Moreover, we found that the spatial alignment of the targets did not influence the RG obtained in cross-modal conditions whereas within-modal stimuli produced a greater RG when the targets where delivered in separate hemispaces. These results suggest that within-modal and cross-modal integration are not only distinguishable by the amount of facilitation they produce, but also by the spatial configuration under which this facilitation occurs. Our study strongly supports the notion that estimates of the same event that are more independent produce enhanced integrative gains.

INTRODUCTION

The brain's ability to integrate information coming from single or multiple sources or modalities is critical for perceiving the world as a unified and coherent percept. The integration of cross-modal (Spence and Driver 2004; Stein and Stanford 2008; Meredith and Stein 1986) and within-modal (Schröter et al. 2007; Murray et al. 2001; Savazzi and Marzi 2002; 2008) stimuli offers many benefits such as enhanced discrimination and accelerated reaction to objects. Surprisingly, only very few studies explored how the beneficial effects obtained in multisensory conditions differ from those obtained when combining redundant stimuli of the same sensory modality (Forster et al. 2002; Laurienti et al. 2006; Gingras et al. 2009).

Whereas inputs derived from different senses provide independent estimates of the same event, inputs from the same modality can exhibit substantial covariance in the information they provide. Thus, it might be expected that two spatio-temporally concordant stimuli from two different modalities will produce a greater gain in performance than the combination of two concordant stimuli from the same modality (Ernst & Banks 2002; Stein et al. 2009). In contrast, one might assume that both multisensory and unisensory integration would yield equivalent results because multisensory response enhancement simply reflects the presence of more environmental energy or multiple, redundant stimuli (Miller 1982; Stein et al. 2009). Supporting the first assumption, a recent study contrasting the behavioral consequences of cross-modal and within-modal integration in cats involved in a localization task demonstrated that cross-modal stimuli lead to an enhanced performance compared to within-modal pairs (Gingras et al. 2009). Similarly, neurophysiological studies point to major distinctions between multisensory and unisensory integration. When integrating multiple cues from different senses, neurons of the superior colliculus (SC), a primary site where inputs from different senses converge (Stein and Meredith, 1993), show additive or super-additive responses that are equal to or greater than the sum of the responses of the individual components. In contrast, multiple inputs from the same modality presented to the same neurons produce responses that are typically lower than the sum of their component response

(Alvarado et al. 2007). Further demonstrating that different neurophysiological mechanisms underlie unisensory and multisensory integration, reversibly deactivating cortico-collicular inputs from anterior ectosylvian sulcus (AES) disrupts the multisensory integrative capabilities of their target neurons in the SC, but not their capacity to integrate within-modal stimuli (Jiang et al. 2001; Alvarado et al. 2007b). These animal studies have received support from a network model study that accounts for the underlying computations that characterizes cross-modal and within-modal integration (Cuppini et al. 2010). Altogether, these findings are suggestive that within-modal and cross-modal stimulations produce different neurophysiological responses and behavioral outcomes, with cross-modal stimulations usually leading to enhanced gains.

In humans, the behavioral outcome of sensory integration can be investigated through simple reaction time (SRT) paradigms showing significant decrease in reaction time (RT) when two or more stimuli are presented simultaneously rather than individually (Todd 1912). This effect is classically referred to as the redundancy gain (RG) (Hershenson 1962; Raab 1962). Different explanations have been put forward to account for the observation of such RG. The most common are the race model and the co-activation model. The race models propose that each individual stimulus elicits a detection process performed in parallel to the others. For a given trial, the fastest stimulus to be processed determines the observable RT. On average, the time to detect the first of several redundant signals is faster than the detection time for single signal. In that case, the speeding up of reaction time is attributable to statistical facilitation. When the observable RTs are too fast to result from statistical facilitation, the race model inequality is violated. To account for violations of the race model inequality, the coactivation model (Miller 1982) proposes that the neural activations of both stimuli combine to induce faster responses. The race model inequality is widely used as a measure of integrative processes underlying RT facilitation (Murray et al. 2001; Forster et al. 2002; Zampini et al. 2007; Tajadura-Jiménez et al. 2008; Molholm et al. 2002; Gielen et al. 1983).

To date, the only SRT study directly comparing the RG produced by cross-modal and within-modal stimulations demonstrated that cross-modal stimuli violated the race model inequality over a substantial proportion of the reaction time distribution whereas the gain associated with redundant unimodal targets could be accounted for by statistical facilitation (Forster et al. 2002). In this experiment however, the redundant unisensory stimuli were only presented bilaterally, leaving unanswered how the spatial configuration of the stimuli differentially affects cross-modal and within-modal integration.

SRT studies investigating the impact of stimuli's spatial configuration on the RG typically show comparable facilitative effects with spatially aligned and spatially misaligned stimuli presented across hemispaces for visuo-tactile (Forster et al. 2002; Girard et al. 2011), audio-tactile (Murray et al. 2005; Zampini et al. 2007) and audio-visual stimuli (Teder-Sälejärvi et al. 2005). It is worth noting here that the processing of spatially aligned and misaligned stimuli is equivalent in terms of multisensory integration when spatial information is irrelevant for the task (e.g. in SRT paradigms; but see Gondan et al. 2005 for small spatial congruency effects in a task that doesn't require spatial discrimination). However, when the spatial information is made relevant for the task, cross-modal stimuli presented at different locations result in a smaller RG than stimuli presented at the same spatial location (Diederich et al. 2003; Harrington and Peck 1998; Bolognini et al. 2005). Indeed, we recently emphasized that task requirements are crucial in triggering spatial congruency effects on multisensory integration (Girard et al. 2011).

In comparison to the cross-modal literature, the impact of the spatial configuration on redundant unimodal targets has been scarcely investigated. In vision, SRT studies investigating within-modal interactions yielded inconsistent results. Some studies showed comparable RG for redundant stimuli in both unilateral and bilateral configurations (Murray et al. 2001; Ouimet et al. 2009) while other studies demonstrated larger RG for bilateral than unilateral pairs of visual stimuli (Miniussi et al. 1998; Corballis et al. 2002). To date, evidences of coactivation have been observed only for bilateral presentations (Corballis et al. 2002; Hughes et al. 1994; Savazzi & Marzi, 2002). In touch, the effect of double tactile stimulations within or between hands has mainly been used to investigate tactile identification and discrimination (Craig 1985; Evans and Craig 1991; Haggard et al. 2006; Tamè et al. 2011) and temporal order judgment (Craig and Baihua 1990; Clark and Geffen 1990). If these studies suggest a clear advantage of stimulating both hands in identification and discrimination tasks, no study has compared the RG for within and between hands stimulations in a SRT experiment.

To the best of our knowledge, no study has directly investigated how the spatial congruence of the redundant targets might differentially influence cross-modal and within-modal integration. This is of major importance since the advantage of cross-modal over within-modal integration may depend on specific spatial configurations. Since it has been suggested that a RG only occurs when each stimulus of a pair produces its own independent percept (Mordkoff & Yantis 1993; Schröter et al. 2011), it could be hypothesized that the integration of spatially adjacent and physically identical stimuli from the same modality has minimal impact on RT because they produce overlapping internal or neural representations which might covary up to the point that their integration is not beneficial for behaviors. Indeed, a RG would only emerge when stimuli possess a distinct characteristic such as a spatial discrepancy. With cross-modal stimuli however, a RG might be observed regardless of the spatial congruency of the targets because they originate from different sensory systems. Testing the extent of cross-modal and within-modal integration under different spatial configurations should provide further insight on whether the spatial alignment of the redundant targets (and therefore the independence of the sensory estimates of this event) has the same effect on the behavioral outcome of both types of integration. We therefore designed the present experiment to compare the RG and violations of the race model inequality yielded by both cross-modal and within-modal combinations when visual and tactile targets are presented in spatial congruence or not. If the magnitude of behavioral enhancement resulting from within-modal and cross-modal combinations differs according to the spatial configuration, this would indicate that spatial information has a critical but differing impact on within and cross-modal interactions.

METHODS

PARTICIPANTS

Sixteen right-handed (Oldfield 1971) participants (8 males; mean age of 24 years, SD = 2.3 years; range from 20 to 29 years) were recruited to take part in the experiment. None of the participants reported a history of neurological or psychiatric problems. They all reported normal tactile sensitivity and normal or corrected to normal vision. The study was approved by the "Comité d'Éthique de la Recherche de la Faculté des Arts et des Sciences" (CÉRFAS) of the Université de Montréal and all subjects gave their written informed consent prior to inclusion in the study.

APPARATUS AND STIMULI

Somatosensory stimuli were delivered using a pneumatic tactile stimulator (Institute for Biomagnetism and Biosignal Analysis, University of Muenster, Germany) for 100 ms. A plastic membrane (1 cm in diameter) was attached to the distal volar part of the index and middle finger and was inflated by a pulse of air pressure delivered through a rigid plastic tube. The plastic tube connecting the stimulator to the participant's fingertips were inserted into the testing room through a hole padded with sound attenuating foam to ensure that tactile stimulations were completely silent from the inside of the room. Due to large inter-individual differences in sensitivity to somatosensory stimuli, intensity was individually calibrated to obtain low salient, but above tactile threshold, stimulations. This procedure resulted in a mean pressure of 13.99 kilopascals (kPa; range from approximately 9.99 to 25.03 kPa). Participant's hands were positioned at a distance of approximately 56 cm from their head and their fingertips were placed at 7.5 (index) and 9.5 (middle finger) visual degrees of eccentricity to the right and left of a central fixation cross (see Fig. 1). Since tactile stimulations could produce small but perceptible finger movements, participant's hands were placed under a white plastic board.

Visual stimuli consisted of white circles subtending 1 degree of visual angle presented against a grey background for 100 ms. These visual stimuli were delivered to the right or left of the central fixation cross at 7.5 and 9.5 degree of eccentricity. This procedure ensured that the initial neural representation in the visual cortex was lateralized (Sereno et al. 1995). Visual stimuli were presented on a plastic board located 105 to 155 mm above the stimulated fingertips by a projector fixed to the room ceiling. Stimuli were displayed and reaction times were recorded using Presentation software (Neurobehavioral Systems, Inc., Albany, US).

PROCEDURES

Participants sat in a silent and dimly lit room with their head on a chinrest. They were instructed to respond as fast as possible to the onset of any stimulus by pressing a button fixed on a small box with their right or left thumb. After each blocks, observers were told to change the hand they were using to respond. The hand that was initially used to respond in the first block was counterbalanced across participants. Breaks were encouraged between blocks to maintain a high concentration level and prevent mental fatigue. Participants' gaze was monitored throughout the experiment via a camera to ensure that they maintained central fixation.

Participants were presented with (1) a tactile stimulus alone, (2) aligned double tactile stimuli, (3) misaligned double tactile stimuli, (4) a visual stimulus alone, (5) aligned double visual stimuli, (6) misaligned double visual stimuli, (7) aligned visuo-tactile stimuli and (8) misaligned visuo-tactile stimuli. This yielded 24 stimuli configurations (4 tactile alone, 4 visual alone, 2 aligned double tactile, 2 aligned double visual, 2 misaligned double tactile, 2 misaligned double visual, 4 aligned visuo-tactile, 4 misaligned visuo-tactile). Aligned conditions consisted of two stimuli presented in the same hemifield whereas misaligned conditions consisted of two stimuli presented in different hemifields. All the conditions of stimulation are presented in the schematic view of the experimental setup (Fig. 1). Whenever double unimodal or cross-modal stimuli were presented in the same hemifield, one of the stimulation was presented either to the index (tactile) or above the index (visual) and the second stimulation was presented either to the middle finger or above the middle finger. The same logic was applied to misaligned stimuli. Hence, all misaligned stimuli were presented to the left at 7.5° and simultaneously to the right at 9.5° and vice-versa.

Participants completed six blocks of 260 experimental trials with each of the 24 stimuli configurations presented 10 times per block. Each block contained 20 catch trials (8%) in which no stimulus was presented. They were used in order to restrain participants from anticipatory responses. A total of 60 trials per conditions were recorded. Intertrial interval randomly varied between 1600 and 3600 ms (Mean ITI = 2600 ms). The fixation cross was displayed throughout the experiment. Each block lasted approximately 11 minutes.

----------Insert Figure 1 about here----------

DATA ANALYSIS

Only RTs between 100 and 1000 ms were considered for analyses. As a result, less than 1 percent of trials per conditions were discarded. Since there was no main effect of the responding hands in the RT data, RT obtained with both hands were averaged. Furthermore, RTs obtained for each redundant condition (either within-modal or cross-modal) were averaged separately as aligned (both stimuli presented in the same hemifield) or misaligned (each stimuli presented in opposite hemifields) depending on their spatial locations.

The RG was computed by calculating the decrease (in percent) of the mean RTs obtained in the redundant conditions as compared with the mean RTs obtained for the best single condition (Stein and Meredith 1993, Buccholz et al. 2012). For each condition and each participant separately, the mean RT of a redundant condition was subtracted from the mean RT of the fastest stimuli of the pair and then divided by the RT of the fastest stimulus of the pair, which yield to the percentage decrease of RT between the redundant condition of stimulation and its best constituent [(RT best stimulation - RT redundant)/ RT best stimulation]. The RG were then submitted to repeated measures analysis of variance

(ANOVA). Post hoc analyses using a Bonferroni correction were used when appropriate.

To further investigate RG differences obtained for within-modal and cross-modal conditions, the race model inequality was analyzed using RMITest software, which implements the algorithm described at length in Ulrich, Miller, & Schröter (2007). This procedure involves several steps. First, empirical cumulative density functions (CDFs) of the RT distributions are estimated for every participant and every condition (i.e., visual alone, tactile alone, redundant unimodal and cross-modal condition). Second, the bounding sum of the two CDFs obtained from the two unimodal conditions (visual and tactile) are computed for each participant. This measure provides an estimate of the boundary at which the race model inequality is violated. Third, percentile points are determined for every distribution of RT, including the estimated bound for each participant. In the present study, the race model inequality was evaluated at the 5th, 15th, 25th… 95th percentile points of the RT distributions.

Fourth, for each percentile, the mean RTs for redundant conditions and the bound are compared using a two-tail one-sample t-test. A Bonferroni correction is applied to avoid Type I errors due to multiple comparisons (Ulrich et al. 2007). If any percentile shows significantly faster RTs in the redundant condition relative to the bound, it can be concluded that the race model cannot account for the facilitation of the redundant signal conditions, supporting the existence of an integrative process.

RESULTS

On average, participants detected 97.8 percent of all tactile stimuli (range from 94.8 to 99.8%), 98.4 percent of visual stimuli (range from 97.7 to 99.1%) and 99.0 percent of multisensory pairs (range from 98.8 to 99.4%). Participants responded to less than 1 percent of catch trials throughout the experiment. Mean RTs obtained for single, within-modal and cross-modal conditions can be found in Figure 2.

----------Insert Figure 2 about here----------

RGs (in percents; Fig. 3) were submitted to a 3 [Modality: visual, tactile, visuo-tactile] x 2 [Alignment: aligned or misaligned] repeated measures ANOVA. The results showed a main effect of "Modality" [$F(2,30)=72.53$, $p \leq .001$] demonstrating that cross-modal visuo-tactile stimuli produced greater RT facilitation compared to both double tactile ($p \leq .001$) and double visual stimuli ($p \leq .001$). However, the RGs of double tactile and double visual stimuli did not differ significantly ($p = 1$). There was also a main effect of "Alignment" [$F(1,15)=47.72$, $p \leq .001$] demonstrating that RGs were greater for the misaligned conditions than for the aligned conditions. There was a significant interaction effect between "Modality" and "Alignment" [$F(2,30)=5.92$, $p \leq .007$]. Follow-up comparisons showed that the RGs of the misaligned conditions were larger than the RGs of the aligned conditions for double visual stimuli ($p \leq .001$) and double tactile stimuli ($p \leq .041$). However, there was no spatial alignment difference in RGs for the cross-modal conditions ($p = .47$). As assessed with separate one-sample Students' *t*-test, the RG for cross-modal combinations was significantly different from zero for aligned [$t(15) = 13.71$, $p \leq .001$] and misaligned configurations [$t(15) = 12.65$, $p \leq .001$] whereas only the misaligned configuration yielded RG that were significantly different from zero for within-modal pairs of visual [$t(15) = 4.84$, $p \leq .001$] and tactile stimuli [$t(15) = 4.38$, $p \leq .001$].

----------Insert Figure 3 about here----------

To further test the advantage of cross-modal over within-modal integration, we investigated whether the RTs obtained in the redundant conditions exceeded the statistical facilitation predicted by Raab's race model inequality (Miller 1982). For cross-modal stimuli, the race model inequality was significantly violated up to the 40th percentiles of the RT distribution in the aligned conditions (all $p \leq .001$) and in the misaligned conditions (all $p \leq .004$). No significant violation of the race model inequality was found for any redundant visual or tactile condition, suggesting that the faster RTs in these conditions could be explained by simple probability summation (Fig. 4).

----------Insert Figure 4 about here----------

CONTROL EXPERIMENT

In the main experiment, intrahemispheric (aligned) stimuli were always presented closer to each other's in an Euclidian (external) space when compared to stimuli presented interhemispherically (misaligned). In order to test if the greater RG observed for within-modal misaligned conditions depends on interhemispheric stimulation or on the external spatial separation between stimuli, we conducted a control experiment in which the spatial separation between stimuli was held constant in external space for redundant intrahemispheric and interhemispheric conditions.

----------Insert Figure 5 about here----------

METHOD

PARTICIPANTS

Thirteen right-handed (Oldfield 1971) participants (6 males; mean age of 25 years, SD = 2.3 years; range from 20 to 29 years) were recruited to take part in the control experiment. None of the participants reported a history of neurological or psychiatric problems. They all reported normal tactile sensitivity and normal or corrected to normal vision.

Procedures and stimuli were the same as the main experiment. However, intrahemispheric and interhemispheric within-modal conditions were presented with a constant Euclidean distance between both stimuli. For the tactile experiment, participant's hands were positioned at a distance of approximately 56 cm from their head and their fingertips were positioned parallel to the horizontal meridian to form an imaginary rectangle (Fig. 5). Both index fingers were placed at 1 visual degree below the fixation cross and middle fingers placed at 1 visual degree above the fixation cross. Left and right fingertips were positioned as close as possible to the vertical midline in order to maintain an equal distance between stimuli for intrahemispheric and interhemispheric conditions.

For the visual experiment, all visual stimuli were presented at 2.5 degrees of visual angle to the right and left of a central fixation cross. This ensured that visual stimuli were presented outside the naso-temporal retinal overlap region and that their initial representations were lateralized (Sugishita et al. 1993). Briefly, for intrahemispheric conditions, one stimulus was presented at 2.9 visual degree above (upper), and a second stimulus was presented at 2.9 visual degree and below (lower) the fixation cross. For interhemispheric conditions, one stimulus was presented to the left at 1.5 visual degree above the fixation cross while the second stimulus was presented to the right at 1.5 degree below the fixation cross and vice versa. Hence, there was a constant 5.83 visual degree separation between redundant stimuli for both intrahemispheric and interhemispheric conditions (Fig. 5). There were 8 single visual conditions and 4 redundant visual conditions. For the visual control experiment, participant's hands were located at the same location as the main experiment. Participant completed 4 blocks in the visual condition and 4 blocks in the tactile condition for a total of 60 trials per conditions. First block modality and responding hand were counterbalanced between participants.

RESULTS

On average, participants detected 99.0 percent of all tactile stimuli (range from 96.6 to 100%) and 99.5 percent of visual stimuli (range from 98.9 to 100%). Mean RGs obtained for single tactile, double tactile, single visual and double visual can be found in Figure 6.

RGs (in percent; Fig. 6) were submitted to a 2 [Modality: visual, tactile] x 2 [Alignment: intrahemispheric or interhemispheric] repeated measures ANOVA. First, no main effect of "Modality" was found, [$F(1,12)=2.36$, $p = 0.150$], demonstrating that the RGs of double tactile and double visual stimuli did not differ significantly. The results showed a main effect of "Alignment", indicating that the RGs for interhemispheric conditions were greater than for intrahemispheric conditions [$F(1,12)=7.96$, $p \leq 0.015$]. Finally, no interaction was found between "Modality" and "Alignment", [$F(1,9)=0.014$, $p = 0.907$]. As assessed with separate one-sample Students' *t*-test, the RG for visual stimuli was significantly different from zero for interhemispheric [$t(12) = 5.27$, $p \leq .001$] and intrahemispheric [$t(12) = 2.329$, $p \leq .038$] conditions. For tactile stimuli, only the interhemispheric yielded a RG that was significantly different from zero [$t(12) = 3.574$, $p \leq .004$].

----------Insert Figure 6 about here----------

These results are consistent with what was found in the main experiment (Fig. 6). First, it suggests that even with a constant distance held between the stimuli, the RGs appear to be greater for interhemispheric conditions than intrahemispheric conditions for both modalities. Secondly, a small increase in the distance between visual stimuli produced a small increase in the RG for the intrahemispheric condition, suggesting that the RG might be influenced by stimuli's spatial separation under specific circumstances. Further studies including parametric variations of the distance between stimuli are needed to better understand the relative impact of the external spatial distance and the stimulation of the same or separate hemispheres on the within-modal RG.

DISCUSSION

We compared the RGs yielded by cross-modal and within-modal combinations when targets were presented within or across hemispaces. The aim was to test how the spatial congruency of the stimuli affects cross-modal and within-modal integration. As measured by RTs, the behavioral benefits resulting from redundant stimuli are far greater for combinations of cross-modal stimuli than for combinations of within-modal stimuli. This result replicates previous findings obtained in simple (Forster et al. 2002) and choice (Laurienti et al. 2006; Bernstein et al. 1972) RT paradigms and parallels those obtained in animals, which also point toward a behavioral advantage of integrating cross-modal over within-modal stimuli (Gingras et al. 2009). Whereas statistical facilitation could account for within-modal RTs, all cross-modal conditions violated the race model inequality. Such RT advantage of multisensory over unisensory integration might appear surprising since the former relies on the integration of different kinds of energy captured by different sensory organs and transmitted to separate sensory regions of the brain. However, several studies have demonstrated that multisensory interactions can occur at low-level stages in the cortical hierarchy of perception and at very early latencies after stimuli presentation (Molholm et al. 2002; Ghazanfar and Schroeder 2006; Giard and Peronnet 1999; Foxe et al. 2000). Crucially, recent findings suggest that such early-latency and low-level interactions of sensory information from different modalities are functionally linked to both reaction time facilitation (Sperdin et al. 2009; 2010) and detection accuracy (Van der Burg et al. 2011).

The main results of the present study relate to how within-modal and cross-modal integration are modulated by the spatial congruency of the stimuli. We observed that RTs of multisensory stimuli were significantly and equally facilitated for both aligned and misaligned conditions (Fig. 3) and that the race model inequality was violated over the same range of the RT distributions in both conditions (Fig. 4). These results contrast with studies showing enhanced behavioral gains for spatially congruent over incongruent multisensory conditions (Diederich et al. 2003; Harrington and Peck 1998; Hughes et al. 1994; Kitagawa and Spence 2006; Sambo and Forster 2009; Kitagawa et al. 2005; Spence and Driver 1994; Bolognini et al. 2005, Frassinetti et al. 2002). However, unlike in the present study, most of these studies required an explicit processing of the spatial position of the targets. A critical aspect of the present study is that we used a SRT paradigm where no explicit processing of the target's spatial location was required. This is consistent with other studies showing no modulation of the RG according to the spatial position of the stimuli (Murray et al. 2005; Zampini et al. 2007; Tajadura-Jiménez et al. 2008; Teder-Sälejärvi et al. 2005; Forster et al. 2002; Girard et al. 2011). Therefore, when no explicit spatial discrimination is required, there is no effect of the spatial congruence of multisensory targets on the RG (see also Sperding et al., 2010). It has indeed been shown that the same misaligned stimuli could produce a RG when presented in a SRT task or a decrease in RT when presented in a spatial discrimination task (Girard et al. 2011). These results are consistent with the proposition that higher-order cognitive or attentional processes, which are task-dependent, might have a top-down influence on multisensory interactions (Spence and Driver 2004; Talsma et al. 2007; 2010; Spence and MacDonald 2004; Hecht et al. 2008). This influence might involve dynamic shifts of spatial representations or strategies that emphasize the stimuli's temporal aspect over its spatial location (Murray et al., 2005). More generally, this hypothesis is consistent with the idea that different computational goals might dictate different multisensory integrative principles (Stein and Stanford 2008).

In contrast to what was observed for cross-modal combinations, we observed that the RG for double tactile or visual stimuli was greater when the unisensory targets were delivered in separate hemispaces compared to situations where the unisensory targets were delivered in the same hemispace. These results are supported by our control experiment which demonstrate greater RG for interhemispheric than intrahemispheric presentation even when the distance is held constant between the stimuli. This indicates that the greater RG for interhemispheric and misaligned conditions likely depends on the simultaneous stimulation of both hemispheres rather than the physical distance that separates the stimuli. In the control experiment, intrahemispheric visual targets generated a significant RG, which was not observed in the main experiment, suggesting that the distance between visual stimuli might also influence the RG under specific conditions. To ensure an initial lateralization and constant distance between visual targets, the stimuli in the intrahemispheric conditions of the control experiment were slightly more distant than the aligned conditions of the main experiment.

The results for visual stimuli are consistent with previous findings showing that the RG for bilateral pairs was larger than for unilateral pairs and that this effect is present for symmetric and diagonal arrangements (Corballis et al. 2002). However, other studies previously reported a redundant target effect that was independent of the spatial configuration (unilateral, bilateral or vertical midline) of the stimuli (Murray et al. 2001; Ouimet et al. 2009). All these studies used SRT tasks with similar spatial configurations and distances. Hence, the discrepancies regarding the spatial congruency effects for visual stimuli are presumably related to methodological factors such as the type of stimuli, response method and experimental settings. The results obtained with tactile stimuli are consistent with several studies showing the advantage of delivering stimuli to both hands rather than adjacent fingers for identification or discrimination (Craig 1985; Evans and Craig 1991; Haggard et al. 2006; Tamè et al. 2011). The current experiment therefore extends such bilateral tactile advantage to the RG observed in SRT paradigms.

In the aligned conditions, the representations of the stimuli from the same modality may largely overlap, resulting in similar internal or neural representations for single and redundant trials. Because both stimuli are not processed independently, such overlapping representations would contribute to the smaller or the absence of RG observed for these conditions. On the other hand, interhemispheric stimuli are initially processed independently by each hemisphere, resulting in distinct and non-overlapping internal representations that produce enhanced RG. In line with such interpretation, a recent study showed that the fusion of redundant targets into a single visual percept failed to produce a RG (Schröter et al. 2011). Using stereoscopic presentation where double visual stimuli could elicit either a single or distinct percepts, the authors demonstrated that the redundant target effect emerged only when the stimulations produced two distinct percepts. In addition, similar findings have been reported in the auditory domain (Schröter et al. 2007), suggesting that the number of percepts drives the appearance of the RG.

In line with this view, cross-modal stimuli would produce greater RGs than within-modal combinations because they originate from different sensory systems that provide independent and non-redundant estimates about the same external event. To some extent, this relates to the probabilistic “bayesian” view of sensory integration stating that individuals take the reliability of the sensory estimates into account when making behavioral decisions. They weight each modality according to its reliability to improve discrimination and localization (Ernst & Banks, 2002; Alais & Burr, 2004). Accordingly, combinations that do not provide more accurate information to the nervous system are less likely to improve behavior. Therefore, the combined information of two stimuli from different modalities should have lower variance because they are processed by independent sensory systems and are not influenced by the same noise source (Hillis et al. 2002). However, two identical sensory stimuli from the same modality presented at the same time and approximately at the same place might covary up to the point that their integration is only minimally beneficial (Gingras et al. 2009).

Since the physical features of a stimulus such as intensity can influence RTs (Piéron 1952; Bonnet et al. 1992; Bell et al. 2006), it may appear surprising that increasing a stimulus’ energy through double unimodal stimulation only had marginal or no effect on the RTs to unilateral pairs of stimuli in our study. Since the amount of energy was the same for within-modal pairs in aligned and misaligned configurations, our results suggest that the redundant target effect does not depend on stimulus’ energy, but rather appears to be under the influence of the stimuli’s spatial locations, with interhemispheric stimuli yielding to an enhanced gain compared to intrahemispheric stimulation even when the absolute spatial distance between the targets is equal (Fig. 6). Nevertheless, it is still unclear whether increasing a single stimulus intensity or increasing stimulus intensity through double stimulation produce similar neurophysiological responses. For example, in a study investigating the effect of stimulus intensity on saccadic RTs and response onset latency in SC neurons of monkeys, Bell and collaborators (Bell et al. 2006) reported that increasing single stimulus intensity shortened both the latency of neuronal responses and saccadic RTs to visual targets. On the other hand, Alvarado and collaborators (2007) showed in the same structure that unisensory integration of within-modal (visual) pairs yielded responses that were similar to those evoked by their best component stimulus. Although they also varied the intensity of the visual stimuli, they did not report any response latency effect on SC neuronal activity. Thus, increasing a stimulus’ energy by presenting multiple stimuli does not seem to invariably produce neurophysiological or behavioral response enhancement, as appears to be the case for single stimuli.

In summary, in addition to our observation that cross-modal stimuli produce far greater RG than combinations of within-modal stimuli in every conditions of stimuli presentation, the results of the present experiment demonstrate that the spatial locations from which the sensory inputs occur had differential impacts on cross-modal and within-modal integration. Whereas aligned and misaligned cross-modal stimuli yielded identical enhancements, performance was affected by the spatial location of within-modal stimuli. Indeed, behavioral facilitation for redundant visual and redundant tactile stimuli was greater when stimuli were presented in a misaligned or interhemispheric configuration (see Fig. 3 & 6). These results provide novel insights regarding the impact of the spatial congruence of redundant targets on within-modal and cross-modal integration and support the notion that more independent estimates of a single event produce greater behavioral benefits.

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FIGURE CAPTIONS

Figure 1. Schematic view of the experimental setup and stimulation conditions. Tactile stimuli were delivered to the index and middle fingers of each hand and visual stimuli were projected on a surface above the stimulated fingers. All conditions including two stimuli were presented either in an aligned configuration (both stimuli in the same hemispace) or misaligned configuration (both stimuli presented in different hemispaces).

Figure 2. Mean reaction time (in milliseconds) and standard errors of the mean (SEM) for pooled single, within-modal and cross-modal conditions. Capital letters refer to the modality (V for visual, T for tactile) and spatial configuration (A for aligned, M for misaligned) for each combination. $\text{SEM}^{\text{L\&M}}$, which reflect within-subject pattern were computed following Loftus & Masson (1994) method for confidence intervals.

Figure 3. Mean RGs and SEM for within-modal and cross-modal pairs obtained under aligned and misaligned spatial configurations. RGs were calculated as the decrease (in percent) of the mean RT obtained in redundant conditions compared with the mean RT obtained for its best constituent stimulus. The X-axis refers to sensory combinations (V for visual, T for tactile) and spatial alignment ("A" for aligned and "M" for misaligned). Asterisks indicate that the RGs were significantly ($p < .05$) different from zero as assessed by one-sample Students' *t*-test. Cross-modal stimuli produced greater enhancement than within-modal stimuli combinations, supporting the advantage of combining multiple sensory cues for behavioral performance. Moreover, a RG was observed for within-modal pairs of both modalities only when the stimuli were presented in a bilateral configuration.

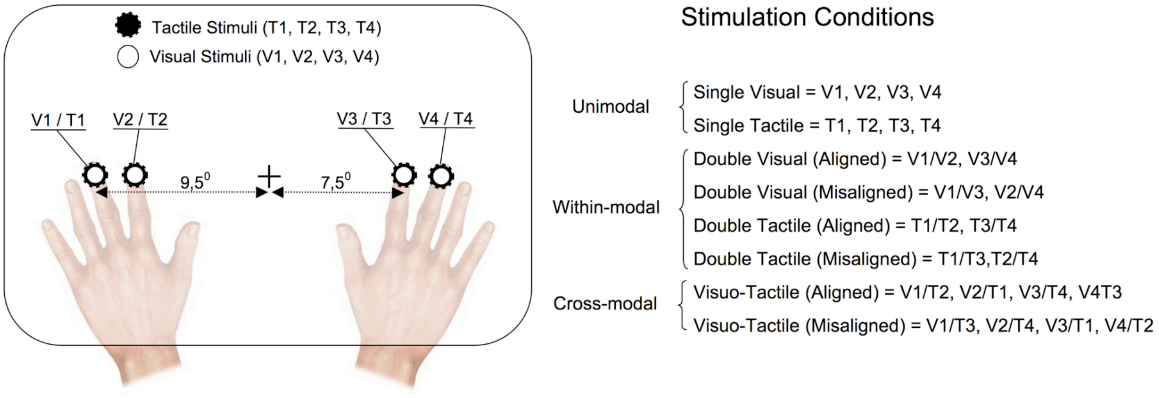
Figure 4. Test for violation of the race model inequality (Miller, 1982; Ulrich et al., 2007). The graph represents the difference in milliseconds (on the Y-axis) between the model prediction computed from the RTs of each unisensory counterpart (the model bound) and the RTs obtained in the redundant conditions. Positive values on the graph refer to RTs that were faster than the race model prediction. RTs that were significantly faster than the race model

prediction are marked with an asterisk, which indicates race model inequality violation. Negative values on the graph refer to RTs that were slower than the race model prediction. The difference between the bound and the RTs of the redundant condition are found for each percentile of the RT distribution (on the X-axis). Cross-modal stimuli significantly violated the race model inequality irrespective of their alignment whereas both double visual and double tactile stimuli were consistent with simple probability summation.

Figure 5. Schematic view of the experimental setup and stimulation conditions for the control experiment. Visual stimuli (A) were projected on a surface above the stimulated hands and tactile stimuli (B) were delivered to the index and middle fingers of each hand. The distance between redundant stimuli was held constant for same hemispace and different hemispaces configurations.

Figure 6. Mean RGs and SEM for within-modal pairs obtained under intrahemispheric and interhemispheric spatial configurations. The X-axis refers to sensory combinations (V for visual, T for tactile) and spatial configurations ("SH" for same hemispace and "DH" for different hemispaces). Asterisks indicate that the RGs were significantly ($p < .05$) different from zero as assessed by one-sample Students' *t*-test. For both modalities, stimuli presented in different hemispaces produced greater enhancement than stimuli presented in the same hemispace.

Figure 1



Stimulation Conditions

Unimodal
- Single Visual = V1, V2, V3, V4
- Single Tactile = T1, T2, T3, T4

Within-modal
- Double Visual (Aligned) = V1/V2, V3/V4
- Double Visual (Misaligned) = V1/V3, V2/V4
- Double Tactile (Aligned) = T1/T2, T3/T4
- Double Tactile (Misaligned) = T1/T3,T2/T4

Cross-modal
- Visuo-Tactile (Aligned) = V1/T2, V2/T1, V3/T4, V4T3
- Visuo-Tactile (Misaligned) = V1/T3, V2/T4, V3/T1, V4/T2

Figure 2

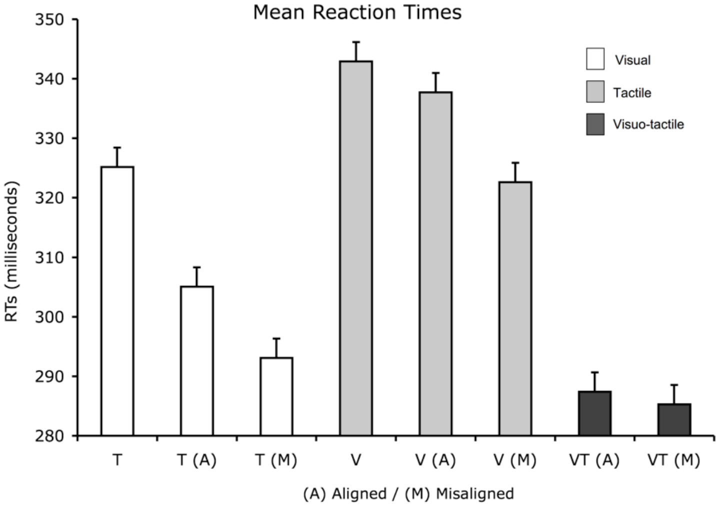


Figure 3

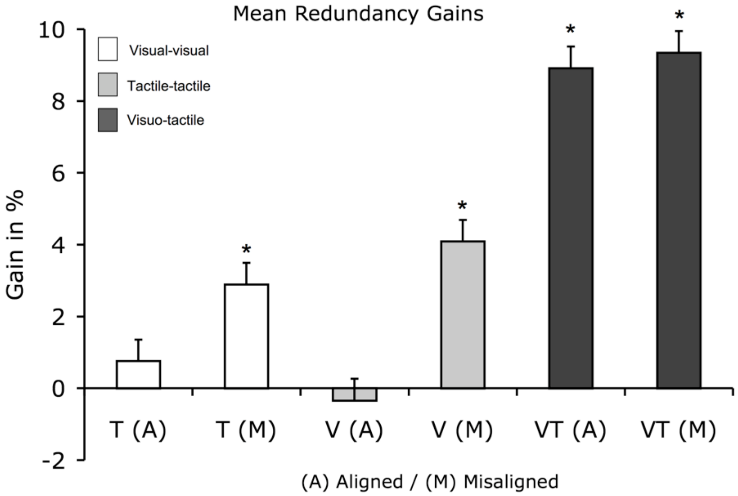


Figure 4

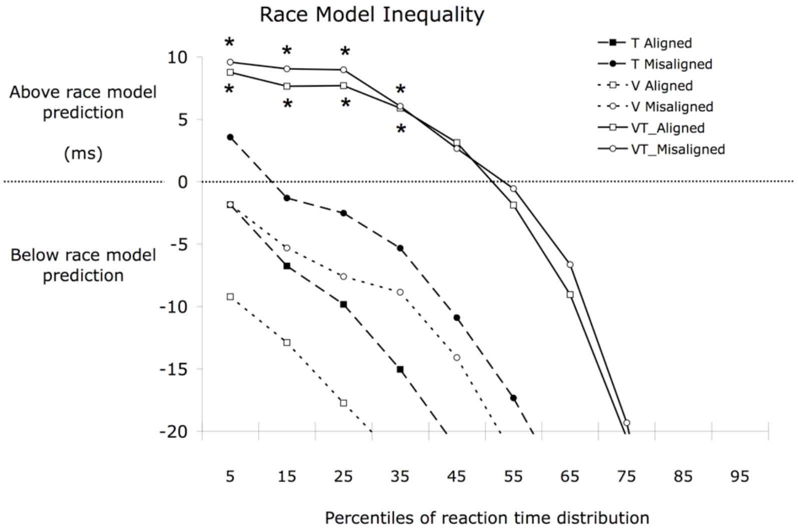


Figure 5

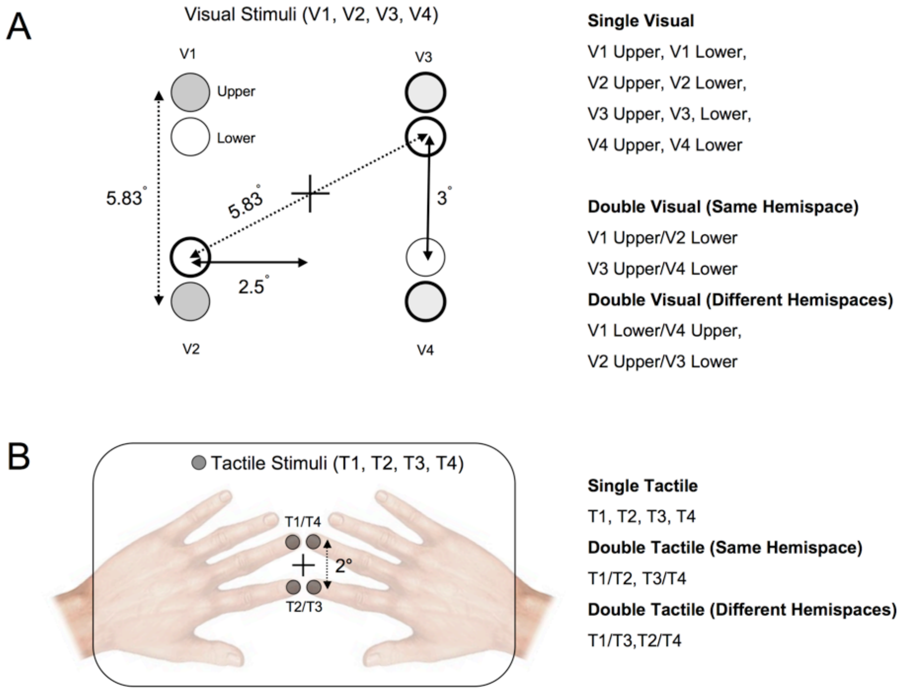
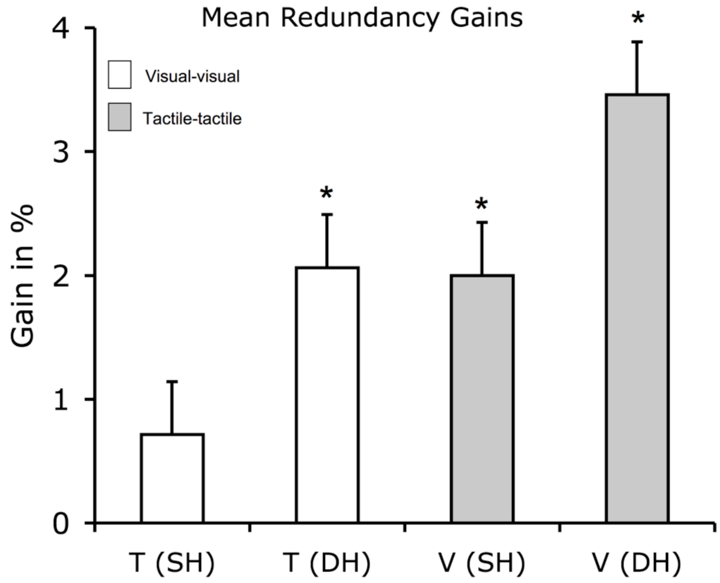


Figure 6


Mean Redundancy Gains
Visual-visual
Tactile-tactile
Gain in %
0
1
2
3
4
*
*
*
T (SH)
T (DH)
V (SH)
V (DH)

ARTICLE 3

Integrating uni and multisensory targets across hemispaces without the corpus callosum

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Article en préparation

Contribution des coauteurs :
S.G., O.C., & F.L. : Conception du projet
S.G. : Recrutement des participants
S.G, M.V. & G.C. : Collecte des données
S.G. : Analyse des résultats et rédaction de l'article
S.G., & O.C. : Interprétation des résultats
S.G., O.C. & F.L. : Révision du manuscrit

ABSTRACT

When one observer has to rapidly detect sensory events occurring in peripersonnal space, the simultaneous occurance of multiple targets produce a redundancy gains (RG), which manifests as a robust acceleration in reaction times. Since such RG can be observed with unisensory or multisensory targets simultaneously presented in separate hemifields, it has been supposed that interhemispheric communication supports this effect. In the present study, we examine the role of the corpus callosum in mediating unilateral and bilateral unisensory and multisensory integration by testing four congenitally acallosal, one callosotomized and a group of individually matched control individuals. Participants were involved in a simple detection task with redundant within-modal (double visual or tactile) and cross-modal (visuo-tactile) stimuli delivered in the same or in separate hemifields. The integrative processes underlying the RG was assessed by comparing the reaction time distributions of redundant stimulations to the predicted reaction time distribution of the summed probability distributions of each constituent stimulus presented alone. Our results demonstrate that AgCC and split-brain patients perform comparably to control participants in a cross-modal visuo-tactile detection task. This suggests that cross-modal integration is not altered in the absence of the corpus callosum, even when stimuli from different modalities are initially presented to different hemispheres. These results suggest that the behavioral benefit resulting from sensory integration putatively at the subcortical level does not follow a “spatial rule” which would predict that integration is only observed for spatially congruent stimuli.

INTRODUCTION

A fundamental aspect of our sensory experience is that information from different modalities is often seamlessly integrated into a unified percept. Through their seminal works investigating the neurophysiology of the superior colliculus (SC), Stein and colleagues (e.g. Stein and Meredith 1993) disclosed some general principles that still define multisensory integration (MSI) today. The SC hosts multiple sensory inputs and contains integrative multisensory neurons in its deep layers, with the role of facilitating the detection, localization and orientation to external events (Stein et al. 1989; Jiang et al. 2002; Burnett et al. 2004). One of the key principles or rules of MSI derived from the study of the SC is the "spatial rule", which states that MSI is more likely or stronger when its unisensory components arise from approximately the same location or that the respective receptive fields for each modality overlap (Meredith and Stein 1986; Stein and Meredith 1993; Wallace and Stein 2007). Actually, spatially congruent stimuli tend to result in neuronal response enhancement, whereas spatially discordant stimuli give rise to suppressive interactions (e.g. Meredith and Stein 1986, 1996). In summary, multisensory function in collicular neurons is gated by the requirement of spatial coincidence.

The parallel observation of multisensory responses of SC neurons and the enhancement of overt detection, orientation and localisation behaviors have led to the assumption that there is a causal relationship between the neural manifestations of multisensory interactions and behavioral performance (Burnett et al. 2004). Thus stimuli combinations that enhance or depress neural activity would result in enhanced or depressed behavioral performance in animals (Stein et al. 1988, 1989; Jiang et al. 2002) Given the underlying neuronal interactions seen with spatially congruent and incongruent stimulations, behavioral results should in principle reflect the spatial rule. However, studies of the behavioral impact of multisensory stimulation in cats and monkeys have focused on saccadic eye movements (Wang et al. 2008; Frens and Van Opstal 1998) or localisation and discrimination tasks (Stein et al. 1988; Maier et al. 2004; Ghazanfar and Logothetis 2006). While some of these studies provide evidence for the spatial rule at both a neural and behavioral level (Stein et al. 1988; Frens and Van Opstal

1998; Maier et al. 2004), one of their downside of is that they cannot exclude the role of selective attention to one or the other modality (Cappé et al. 2010).

In line with animal findings, studies in humans investigated the role of the SC in mediating cross-modal integration in simple detection task. Pairing visual stimuli of different wavelength with audio stimuli, it was shown that cross-modal behavioral enhancement occurred only when the visual stimulus's wavelength could reach the SC (Maravita et al. 2008; Leo et al. 2008). Consistently with the multisensory responses in the SC of the cat (Stein and Meredith 1993), the redundancy gain (RG) only occured for spatially coincident audiovisual stimuli (Maravita et al. 2008). These findings argue for a critical role of the SC in cross-modal integration and suggest that neural interactions at a collicular level might be functionally linked to behavioral performance in humans.

However, cross-modal studies investigating the spatial rule in humans have reported inconsistent findings, suggesting that this rule applies under specific and rather restricted experimental conditions. A recent review by Charles Spence (2013) sheds light on the circumstances in which behavioral findings are consistent or not with the spatial rule in humans. The spatial rule is typically observed with task requiring either orienting responses or spatial discrimination in which the spatial information is relevant to the participants (Girard et al. 2011; Spence and Driver, 1997; Spence et al. 2004; Sambo and Forster 2009). In contrast, various studies have demonstrated that the integration of spatially adjacent and disparate stimuli is equivalent when the spatial information is irrelevant for the task (e.g. simple detection task) (Hughes et al. 1994; Girard et al. 2011, 2013; Murray et al. 2005). In a recent experiment we simply manipulated the task demand on the same multisensory stimulus in order to involve the participants either in a simple reaction time (SRT) paradigm where participants responded to all stimulations irrespective of their spatial positions, or a choice reaction time (CRT) in which stimuli position had to be processed. The same spatially incongruent stimulus produced either reaction times facilitation (SRT) or impairment (CRT) depending on the task demand (Girard et al. 2011). Although there are exceptions (Gondan et al. 2005; Fiebelkorn et al. 2011), these studies suggest that the spatial limitations of multisensory integration in human observers depends on top-down, attention-related and task related processes rather than bottom-up contraints (Girard et al. 2011; Talsma et al. 2007; Spence 2013).

The finding that stimuli from different modalities presented simultaneously to different cerebral hemispheres can produce as much MSI as spatialy coincident stimuli presented to a single hemisphere (Murray et al. 2005; Girard et al. 2011, 2013; Forster et al. 2002) contradicts the link between the MSI abilities of the SC, which depend on spatial coincidence, and behavioral performance. Thus, it has been proposed these effects might rely on the early convergence of information through feed-forward projections between primary sensory areas (Murray et al. 2005; Foxe et al. 2000; Schroeder and Foxe 2004). If the cortex indeed supports integrative functions (Giard and Perronet 1999; Hughes et al. 1994), the transfer of information across the corpus callosum (CC) via heterotopic connections linking functionally different regions (Lassonde and Ouimet 2010) may play a critical role in MSI when interhemispheric integration is required. This is especially relevant for visuo-tactile interactions because somatosensory and visual brain regions receive inputs primarily from the contralateral hemispace (Fitzpatrick 2008). A striking example comes from Spence and colleagues (2001) who demonstrated the complete absence of visuo-tactile remapping in the split-brain for cross-modal conditions that required interhemispheric transfer. Thus, the integrity of the corpus callosum might be a prerequisite for cross-modal integration when stimuli are presented to the different hemispheres. However, interhemispheric visuo-tactile remapping has been found to be intact in agenesis of the corpus callosum (AgCC) individuals (Wolf et al. 2011).

Experiments on split-brain individuals are probably among the most fascinating studies to probe the biology of the brain. This condition arises from surgical interventions severing the nerve fibres connecting both hemispheres. Split-brain experts Michael Gazzaniga and Roger Sperry (Gazzaniga 1963; Sperry 1966, 1967) were among the firsts to show that a patient which has undergone such intervention suffers from disconnexion syndrome in which a host of sensory and cognitive functions are impaired due to the absence of interhemispheric transfer (Sperry 1974; Gazzaniga et al. 1963, 1996). In contrast, the reduced disconnection deficits in AgCC, individuals born without CC, is argued to be due to developmental plasticity favoring the reinforcement of alternative neural pathways such as the anterior commissure, posterior commissure and intercollicular commissure (Lassonde et al. 1991; Wolf et al. 2011). However, when compared to healthy individuals, both callosotomized and AgCC patients show a lenghtening of interhemisperic transfer (Jeeves 1965). For example, crossed motor responses to lateralized visual input are abnormally long in acallosal subjects (Jeeves 1969), with AgCC patients typically showing faster interhemispheric transfer than split-brain subjects (Mooshagian et al. 2009). Thus, one would expect interhemispheric integration to be severely affected by the absence of the corpus callosum.

Surprisingly, an enhanced redundant target effect (RTE), namely a reduction in reaction times observed when two or more stimuli are presented simultaneously instead of one stimulus (Miller 1982; Hershenson 1962; Raab 1962), has consistently been found in the split-brain with interhemispheric presentation (Reuter-Lorenz et al. 1995; Savazzi and Marzi 2004). More specifically, split-brain and AgCC individuals show a RT decrease to bilateral pairs beyond predictions based on a simple race between independent unilateral processes, while those of the normal subjects were actually longer than predicted by the race model (Reuter-Lorenz et al. 1995; Savazzi and Marzi 2004; Corballis et al. 2002). These results do imply interhemispheric interaction in the split-brain despite the absence of the main interhemispheric fiber tract (Corballis et al. 2002), possibly via subcortical pathways and in particular the SC. To investigate the possibility that interhemispheric RG is subserved by the SC, Corballis (1998) tested three split-brain patients with stimuli presumably visible or invisible to the SC. The use of monochromatic purple stimuli, that are claimed to be undetectable by the SC, take advantage of the neurophysiological properties of short wave sensitive cones (S-cones) which do not send or send very few projections to the SC (Savazzi and Marzi 2004). In both conditions, healthy individuals' RTs following bilateral presentation were compatible with the race model. In split-brain individuals, RTs to stimuli visible to the SC exceeded simple probability summation whereas the RG was greatly reduced with stimuli invisible to the SC. Comparable results have been reported in AgCC individuals, suggesting that subcortical processing via the SC is critical for the occurrence of RG enhancement in acallosal patients (Savazzi et al. 2007). Taken together, these findings suggest that RT enhancement and race model violation, which are likely subserved by the superior colliculus, are observed only for bilateral conditions in acallossal patients.

Taken together, these results create a paradoxical situation when contrasted with the known integrative properties of the SC, which are thought to require spatial coincidence for unisensory and multisensory integration to occur (Alvarado et al. 2007; Stein and Stanford, 2008). However, most of the research carried out in AgCC and split-brain patient have focused on interhemispheric transfer with unisensory visual stimuli. With the current experiment we therefore aimed to identify the role of the CC in the integration of sensory information by directly comparing intrahemispheric and interhemispheric integration of unisensory and multisensory stimuli in split-brain, genetically acallosal and neurotypical individuals. Participants were tested with unilateral and bilateral within-modal pairs of visual and tactile stimuli and cross-modal visual-tactile pairs (see fig. 2 for a schematic diagram). Comparing within-modal and cross-modal conditions will help us determine if the enhanced RG found in acallosal individuals is present with stimuli from different modalities as it is the case in neurotypical individuals (Girard et al. 2013). Furthermore, if we observe a spatial modulation of cross-modal integration in acallosal patients, one could hypothesize that cross-cortical connections through the corpus callosum are required for the integration of bilateral cross-modal stimuli. If the integration of spatially congruent and incongruent stimuli is identical, it would indicate that the corpus callosum is not required for cros-modal integration and would suggest that the behavioral enhancement resulting from subcortical or extra-callosal processing is not subject to spatial constraints.

METHOD

PARTICIPANTS

Four acallosal subjects (MG, SG, SP, MD), one callosotomized patient (ML) and five neurologically intact control participants took part in the study. Control subjects were individually matched to experimental subjects on the basis of sex, age and handedness determined by the Edinburgh handedness inventory (Oldfield 1971). Control subjects and experimental subjects were not matched for intelligence quotient (IQ). The age of patients ranged between 24 and 53 (M = 42.3, SD = 12.7), the age of controls ranged between 27 and 55 (M = 41, SD = 13.9).

ML is a 31-year-old left-handed man who underwent complete surgical resection of the corpus callosum, with sparing of the anterior commissure at the age of 22. The surgery was performed as a last resort for intractable epilepsy. His postoperative IQ was of 76. MG is a 44 years-old left handed man with a complete agenesis of the corpus callosum and sparing of the anterior commisure. He has an IQ of 77. At the time of testing, MG was taking prozac for depression. SG is a 53 years-old right-handed woman with a complete agenesis of the corpus callosum and sparing of the anterior commissure. Her IQ is of 84. SP is a 48-year-old right-handed man with a total agenesis of both the corpus callosum and the anterior commissure. He has an IQ of 107. MD is a 24-year-old right-handed woman with a total agenesis of the corpus callosum and sparing of anterior commissures. MD was a university student at the time of testing. Her IQ is unknown. Midsagittal MRI images for all acallosal participants and one healthy individual can be seen in figure 1.

All participants reported normal tactile sensitivity and normal or corrected to normal vision. Participants were naive to the experimental hypothesis, were paid for their participation and gave written informed consent. The study was approved by the ‘‘Comité d’Éthique de la Recherche de la Faculté des Arts et des Sciences’’ of the University of Montreal.

----------Insert Figure 1 about here----------

APPARATUS AND STIMULI

A more extensive description of the material and procedure can be found in Girard et al. (2013). Somatosensory stimuli were delivered using a pneumatic tactile stimulator (Institute for Biomagnetism and Biosignal Analysis, University of Muenster, Germany) for 100ms. A plastic membrane (1 cm in diameter) was attached to the distal volar part of the index and middle finger and was inflated by a pulse of air pressure delivered through a rigid plastic tube. The mean pressure of tactile stimulations was 14.06 kilopascals (kPa; range from approximately 10 to 25 kPa). Participant's hands were positioned at a distance of approximately 56 cm from their head and their fingertips were placed at 7.5 (index) and 9.5 (middle finger) visual degrees of eccentricity to the right and left of a central fixation cross (see Fig. 2). Participant's hands were placed under a white plastic board.

Visual stimuli consisted of white circles subtending 1 degree of visual angle presented against a grey background for 100 ms. These visual stimuli were delivered to the right or left of the central fixation cross at 7.5 and 9.5 degree of eccentricity. This procedure ensured that the initial neural representation in the visual cortex was lateralized (Sereno et al. 1995). The onset of visual and tactile stimuli was perfectly synchronized during the experiment.

PROCEDURES

Participants sat in a silent and dimly lit room with their head on a chinrest. They were instructed to respond as fast as possible to the onset of any stimulus. Participants responded bimanually by pressing a button fixed on a small box located under each hand with their right and left thumb. Breaks were encouraged between blocks to maintain a high concentration level and prevent mental fatigue. Participants' gaze was monitored throughout the experiment via a camera to ensure that they maintained central fixation.

Participants were presented with visual, tactile and visuo-tactile stimuli. Within-modal and cross-modal pairs were either presented in a unilateral (aligned) or bilateral (misaligned) configuration. Unilateral conditions consisted of two stimuli presented in the same hemifield whereas bilateral conditions consisted of two stimuli presented in different hemifields. All the conditions of stimulation are presented in the schematic view of the experimental setup (Fig. 2). Participants completed six blocks of 260 experimental trials with each of the 24 stimuli configurations presented 10 times per block. Each block contained 20 catch trials (8%) in which no stimulus was presented to restrain participants from anticipatory responses. A total of 60 trials per conditions were recorded. Intertrial interval randomly varied between 1600 and 3600 ms (Mean ITI = 2600 ms). The fixation cross was displayed throughout the experiment. Each block lasted approximately 11 minutes. Since split-brain patient ML had trouble to maintain fixation due to distractions or cognitive impairment, stimulations were self-triggered by the experimenter after ensuring that the participant was fixating the central cross via an online camera image centered on the eye of the participant.

----------Insert Figure 2 about here----------

DATA ANALYSIS

Only RTs between 100 and 1000 ms were considered for analyses. For each trial, the first response initiated by either hand was analysed. Furthermore, RTs obtained for each redundant condition (either within-modal or cross-modal) were averaged separately as aligned (both stimuli presented in the same hemifield) or misaligned (each stimuli presented in opposite hemifields) depending on their spatial locations. The RG was computed by calculating the decrease (in percent) of the mean RTs obtained in the redundant conditions as compared with the mean RTs obtained for the best single condition (Stein and Meredith 1993: Girard et al. 2013). For each condition and each participant separately, the mean RT of a redundant condition was subtracted from the mean RT of the fastest stimulus of the pair and then divided by the RT of the fastest stimulus of the pair, which yield the percentage decrease of RT between the redundant condition of stimulation and its best constituent [(RT best stimulation - RT redundant)/ RT best stimulation]. The RG in the Control and AgCC were submitted to repeated measures analysis of variance (ANOVA). Additionnally, single case analysis for AgCC and split-brain patients were conducted using a modified t-test to compare an individual score to a small control sample (Crawford and Howell 1998). This test was applied using the program SINGLIMS.exe (Crawford and Garthwaite 2002).

Different explanations have been put forward to account for the observation of the RG (Miller 1982; Hershenson 1962; Raab 1962). The most common are the race model and the co-activation model. The race models propose that each individual stimulus elicits a detection process that entails a probabilistic race between the sensory channels to access the motor response. On average, the time to detect the first of several redundant signals is faster than the detection time for single signal. In that case, the speeding up of reaction time is attributable to statistical facilitation or probability summation. When the observable RTs are too fast to result from statistical facilitation (violation of the race model), the co-activation models (Miller 1982; Miller and Ulrich 2003; Colonius and Diederich 2004) proposes that the neural activations of both stimuli combine to induce faster responses. To further investigate RG differences obtained for within-modal and cross-modal conditions, the race model inequality was analyzed using RMITest software, which implements the algorithm described in Ulrich et al.(2007). This procedure involves several steps. First, empirical cumulative density functions (CDFs) of the RT distributions are estimated for every participant and every condition (i.e., visual alone, tactile alone, redundant unimodal and cross-modal condition). Second, the bounding sum of the two CDFs obtained from the two unimodal conditions (visual and tactile) are computed for each participant. Miller's bound represent the maximal RT gain that can be explained by purely statistical facilitation when decisions are based on two independent sources of information. This is ilustrated mathematically by the *race model inequality* :

$$F_{\mathrm{vt}}(\mathrm{t}) \leq F_{\mathrm{v}}(\mathrm{t}) + F_{\mathrm{t}}(\mathrm{t}),$$

where the cumulative probability distribution of RT for visuotactile signal $F_{\mathrm{vt}}(\mathrm{t})$ should not exceed the sum of the observed distribution in visual $F_{\mathrm{v}}(\mathrm{t})$ and tactile $F_{\mathrm{t}}(\mathrm{t})$ conditions. Because the race model predictions are derived from individual participants' data for each modality, the MSI measurement is normalized to any individual differences in the unisensory RTs. Third, percentile points are determined for every distribution of RT, including the estimated bound for each participant. In the present study, the race model inequality was evaluated at the 5th, 15th, 25th… 95th percentile points of the RT distributions.

----------Insert Figure 3 about here----------

RESULTS

ACCURACY

Control (CTRL) participants detection accuracy ranged between 94% and 100%. On average, they detected 99% of single and double visual stimuli, 98% of single tactile, 99% of double tactile stimuli and 99% of visuo-tactile stimuli. AgCC patients' detection accuracy for all conditions ranged between 89% and 100%. On average, they detected 92% of single and 97% of double tactile stimuli, 97% of single and 97% of double visual stimuli and 97% of visuo-tactile stimuli.

ML's detection accuracy for all conditions ranged between 56.7% and 80%. On average, he detected 66.3% of single and 69% of double tactile stimuli, 69% of single and 72% of double visual stimuli and 73.1% of visuo-tactile stimuli. To investigate the possibility that ML's RG for within-modal and cross-modal pairs were related to his detection accuracy, we computed Pearson product-moment correlation coefficient. The data shows that for all redundant conditions, there was no significant correlation between the detection accuracy of the least effective stimulus of a pair and the RG [$r(14) = -.125$, $p < .644$], between the mean detection accuracy of a redundant stimulation's components and the RG [$r(14) = -.033$, $p < .904$] or between redundant conditions detection accuracy and the RG [$r(14) = .005$, $p < .987$]. Hence, ML's detection accuracy cannot account the RG differences.

REACTION TIMES

RTs for single unisensory stimulus were submitted to a repeated measures ANOVA with 2 "Modalities" [visual, tactile] as within subject factor and the 2 "Groups" [AgCC, Control] as between subject factor. First, there was no main effet of factor "Modality" [$F(1,7)= 3.44$, $p \leq$

.106]. However, we found a main effect of factor “Group” [F(1,7)=6.351, $p \leq .040$, $\eta\rho^2 = .476$] demonstrating that RTs for single stimulus conditions were slower in the AgCC compared to the the CTRL group.

RGs for the CTRL group were submitted to a 3 [Modality: visual, tactile, visuo-tactile] x 2 [Alignment: aligned or misaligned] repeated measures ANOVA. The results showed a main effect of “Modality” [F(2,8)=17.53, $p \leq .001$, $\eta\rho^2 = .814$] demonstrating that cross-modal visuo-tactile stimuli produced greater RT facilitation compared to both double visual ($p \leq .039$) and double tactile stimuli ($p \leq .001$). However, the RGs of double visual and double tactile stimuli did not differ significantly (p = 1). There was also a main effect of “Alignment” [F(1,4)=30.12, $p \leq .005$, $\eta\rho^2 = .883$] demonstrating that RGs were greater for the misaligned conditions than for the aligned conditions. There was a significant interaction effect between “Modality” and “Alignment” [F(2,8)=12.75, $p \leq .003$, $\eta\rho^2 = .761$]. Follow-up comparisons showed that the RGs of the misaligned conditions were larger than the RGs of the aligned conditions for double visual stimuli ($p \leq .001$) and double tactile stimuli ($p \leq .023$). However, there was no spatial alignment difference in RGs for the cross-modal conditions (p = .064). Equivalent results were obtained using non-parametric statistics (Friedman’s test) for “Modality” [$X^2(2) = 7.60$, $p \leq .022$] and “Alignment” [$X^2(1) = 5.00$, $p \leq .025$]. These results reproduce those obtained in a previous study using identical procedures (Girard et al. 2012).

RGs for the AgCC group were submitted to the same 3 [Modality: visual, tactile, visuo-tactile] x 2 [Alignment: aligned or misaligned] repeated measures ANOVA. As opposed to the CTRL group, there was no significant difference between modalities, demonstrating that double visual, double tactile and visuo-tactile combination yielded similar RGs [F(2,6)= .526, p = .616]. There was a main effect of “Alignment” [F(1,3)=29.74, $p \leq .012$, $\eta\rho^2 = .908$] demonstrating that RGs were greater for the misaligned conditions than for the aligned conditions. There was a significant interaction between “Modality” and “Alignment” [F(2,6)=6.79, $p \leq .029$, $\eta\rho^2 = .693$]. Follow-up comparisons showed that the RGs of the misaligned conditions were larger than the RGs of the aligned conditions for double visual stimuli ($p \leq .008$) and marginally, for double tactile stimuli ($p \leq .059$). There was no spatial alignment difference in RGs for the cross-modal conditions (p = .479). Results were further confirmed using non-parametric statistics (Friedman's test) for "Modality" [X^2(2) = 1.50, p ≤ .472] and "Alignment" [X^2(1) = 4.00, p ≤ .046].

We then submitted the RG to a 3 [Modality: visual, tactile, visuo-tactile] x 2 [Alignment: aligned or misaligned] repeated measures ANOVA with the 2 groups [AgCC, Control] as between subject factor. First, there was no main effet of factor "Group" [F(1,7)=.186, p ≤ .679]. As observed for both groups, there was also a main effect of "alignment" [F(1,7)=61.87, p ≤ .001, $\eta\rho^2$ = .898] demonstrating that RGs were greater in bilateral than unilateral conditions. There was also a main effect of "Modality" [F(2,14)=9.38, p ≤ .012, $\eta\rho^2$ = .573] showing that visuo-tactile conditions produced greater RG than visual (p ≤ .023) or tactile condition (p ≤ .008). There was an interaction between "Modality" and "Alignment" [F(2,14)=15.57, p ≤ .001, $\eta\rho^2$ = .690] demonstrating that misaligned produced faster RT than aligned conditions with visual (p ≤ .001) and tactile (p ≤ .002) stimuli. Finally, there was an interaction between "Modality" and "Group" factors [F(2,14)=4.71, p ≤ .027, $\eta\rho^2$ = .402] which showed that RG was greater in the AgCC than CTRL group for tactile stimuli (p ≤ .034). It is worth noting that the mean RGs of the AgCC group for cross-modal conditions (see fig. 3) are influenced by the fact that patient MD had virtually no RG for these conditions. As such MD's results for cross-modal conditions are aberrant relative to acallosal patients and control individuals (see fig. S1).

We used Crawford and Garthwaite (2002)'s test (Singlims_ES.exe, one-tailed) to compare if each AgCC patient's RG was significantly greater than the mean RG of the CTRL group. Results from the single case analysis revealed that patient MG had greater RG than CTRL participants for misaligned tactile [t(4) = 2.52, p ≤ .033] and misaligned visual conditions [t(4) = 3.10, p ≤ .018]. SP, the only patient with agenesis of both the CC and anterior commissure, demonstrated a greater RG only for the aligned tactile condition [t(4) = 2.97, p ≤ .021]. Consistently with her RT data, participant MD demonstrated lower RG than what was found in CTRL participants for aligned [t(4) = -6.47, p ≤ .001] and misaligned [t(4) = -4.62, p ≤ .005] visuo-tactile conditions.

Overall, ML showed similar results to what was found in CTRL and AgCC participants. He demonstrated an enhanced RG for bilateral within-modal conditions and a RG similar to control participants for unilateral and bilateral cross-modal conditions. We used Crawford and Garthwaite (2002)'s test (Singlims_ES.exe, one-tailed) to compare if ML's RG was significantly greater than the RG of the CTRL or AgCC group. The results showed that ML had a significantly greater RG than the AgCC group only for the misaligned tactile condition [$t(3) = 2.73$, $p \leq .036$]. When compared to the CTRL group, ML's RG were significantly greater for aligned tactile [$t(4) = 2.67$, $p \leq .028$], misaligned tactile [$t(4) = 4.997$, $p \leq .007$] and aligned visuo-tactile conditions [$t(4) = 3.40$, $p \leq .013$]. Overall, ML's results show a consistently greater RG than CTRL group for all conditions (see fig. 3).

----------Insert Figure 3 about here----------

To further investigate possible differentiation between the Split-brain patient, CTRL and AgCC group, we investigated whether the RTs obtained in the redundant condition exceeded the statistical facilitation predicted by Raab's race model inequality (Miller 1982). First, we found that CTRL and AgCC participants had similar results. For both groups, aligned and misaligned visuo-tactile conditions exceeded the summing bound of their unisensory counterparts (see fig. 4). The same pattern was found for misaligned tactile conditions, although this finding was more pronounced in AgCC subjects. In ML, with the exception of intrahemispheric visual condition, all redundant conditions produced RT that exceeded simple probability summation over variable proportions of the RT distributions.

----------Insert Figure 4 about here----------

DISCUSSION

The aim of the present study was to investigate within-modal and cross-modal integration across space in neurotypical, congenitally acallosal and split-brain individuals. Using a simple detection task, we found that there was no major difference between the AgCC group and control participants. The AgCC patients did not exhibit the classical feature of an abnormally enhanced RG with bilateral within-modal pairs (Corballis 1998). A trend toward an enhanced RG for misaligned presentation was present for both modalities in three of the four AgCC patients relative to their control participants (see fig S1). This is supported by the RT distributions of bilateral visual and tactile stimuli, which exceeded probability summation of each sensory constituent to a greater extent in AgCC patients than control participants (see fig. 4). However, the single case analysis revealed that MG was the only participant demonstrating a significantly greater RG for misaligned visual and tactile conditions. Furthermore, RT data suggest that RTs for single stimulus conditions were slower in the AgCC compared to the CTRL group. According to the inverse effectiveness principle, which states that the maximal multisensory intergation is observed with weakly effective stimuli, these results raise the possibility that the slower RTs observed in the AgCC group might have influenced the RG observed in redundant within-modal or cross-modal conditions. Thus, the greater RG observed in the AgCC group for tactile stimuli may be related to the inverse effectiveness principle.

Redundant stimuli presented to the same hemifield did not yield differential RG in AgCC and control participants, except for participant SP who demonstrated and enhanced RG for the aligned tactile condition. An enhanced RG was also observed in the split-brain patient ML who showed greater RG than the control group for unilateral and bilateral tactile conditions and unilateral visuotactile conditions. ML's RG were different from the AgCC group only for bilateral tactile condition. ML's reaction time distribution consistently exceeded probability summation for bilateral visual stimuli and for unilateral and bilateral tactile stimuli, revealing a surprisingly robust RG for intrahemispheric redundant tactile stimulation. Findings of similar gains with intra and interhemipheric presentation have previously been reported in a split-brain in a visual discrimination task (Pollman and Zaidel 1999). Overall, these results confirm that the corpus callosum is not required for interhemispheric within-modal integration in simple detection task and extend this finding to the tactile modality.

For cross-modal conditions, there was no difference between the AgCC and the control group. With the exception of MD (see, fig. S1), cross-modal RG in acallosal individuals were consistent with the behavioral performance seen in healthy individuals. Cross-modal RT distributions exceeding the probability summation boundary was highly consistent between the AgCC and control groups, but was however more pronounced in the split-brain in the unilateral visuo-tactile condition (see fig. 4). Since the RG were not different for intra and interhemispheric visuo-tactile conditions, the results suggest that cross-modal integration is preserved in acallosal individuals and that the CC is not a mandatory structure for interhemispheric cross-modal RT enhancement.

Our results also indicate that the enhanced and abnormally robust RG typically observed for bilateral within-modal pairs in AgCC is not found for bilateral cross-modal combinations. Actually, the results suggest that there was no behavioral advantage of cross-modal stimulation over within-modal stimulation in bilateral configuration for acallosal patients. This contrasts with the advantage of cross-modal over within-modal integration observed in healthy individuals (Girard et al. 2013) and with the inherent difference that exist between unisensory and multisensory processing in the SC. Indeed studies in animals demonstrated that cross-modal stimuli produced enhanced neurophysiological and behavioral responses compared to within-modal stimuli (Alvarado et al. 2007; Gingras et al. 2009).

In acallosal individuals, subcortical processing via the SC appears to play a critical role in interhemipheric integration and its resulting behavioral benefits (Corballis 1998; Savazzi and Marzi 2004; Savazzi et al. 2008). Moreover, the SC appears to be involved in the RTE observed with redundant within-modal (Savazzi and Marzi 2004) and cross-modal stimuli (Leo et al. 2008; Maravita et al. 2008) in healthy individuals. The primary visual afferent to the SC consist of inputs from the magnocellular layers of the lateral geniculate nucleus, which have been found to be blind to short wavelength (e.g. purple) stimuli (Sumner et al. 2002; Schiller et al. 1979). Thus, studies in humans have taken advantage of this finding to investigate the role of the SC in interhemispheric integration and the RTE. Previous studies have reported that the enhanced RTE and race model violation found in split-brain and AgCC patients is altered or even eliminated with stimuli to which the SC is unresponsive (Corballis 1998; Savazzi and Marzi 2004). With the exception of patient ML, bilateral presentation appear to be a prerequisite for coactivation to occur with unisensory stimuli since there was no violation when redundant stimuli were presented to the same hemisphere (Corballis et al. 2002; Hughes et al. 1994; Savazzi and Marzi 2002). Overall, race model violation for within-modal combinations occurs in healthy individuals and acallosal patients when stimuli are visible to the SC and presented bilaterally.

Several behavioral studies in humans suggest that the SC is also a major contributor to cross-modal behavioral enhancement (Klemen and Chambers 2012; Maravita et al. 2008; Bertini et al. 2008; Murray et al. 2005; Leo et al. 2008). In line with studies investigating the role of the SC in unisensory RTE, it was showed that when auditory stimuli were coupled with purple stimuli that are assumed to be invisible to the SC, participant's RTs were consistent with simple probability summation. Race model violation occurred only when the visual stimulus's wavelength could reach the SC (Maravita et al. 2008; Leo et al. 2008). Consistently with the spatial rule of MSI, the race model violation only occured for spatially coincident audiovisual stimuli (Maravita et al. 2008). In a similar paradigm, Leo et al. (2008) paired red and purple stimuli with a spatially congruent or incongruent auditory stimulus and demonstrated a similar coactivation effect only for spatially congruent red stimulus. They also reported that unlike peripheral presentation, audiovisual stimuli presented at a central location produced neural coactivation regardless of stimulus colour. These studies therefore suggest that race model violation occurs when the visual information can reach the SC and when cross-modal stimuli are spatially coincident (Leo et al. 2008; Maravita et al, 2008).

These studies highly contrast with the current and previous results where spatial congruency was not required for coactivation to occur with lateralized stimuli. Although we used different sensory modalities, a host of studies reported violation of the race model for spatially aligned and misaligned audio-visual stimuli (Hughes et al. 1994; Teder-Salejarvi et al. 2005; Bertini et al. 2008). The discrepency between these results suggest that the rules governing multisensory interactions may vary according to the pathways used by a particular task or set of stimuli (Hughes et al, 1994). As noted by Spence (2013), whether the visual stimulus activates the magnocellular or parvocellular pathway may play a role in the behavioral outcome of multisensory integration. However, contrasting with the findings by Leo et al. (2008) and Maravita et al. (2008), our data suggest that the activation of the SC through the magnocellular system may not produce spatial congruency effets on cross-modal RTs. Indeed, we observed race model violation in bilateral condition with visual stimuli that may predominantly have activated the magnocellular system, since it is primarily responsive to transient, peripheral low contrast and low spatial frequency stimuli (Azzopardi et al. 1999; Schiller 1990; Kaplan and Shapley, 1986).

Assuming the SC is a primary site for cross-modal integration, our results in acallosal individuals provide clear evidence that the behavioral enhancement subserved by subcortical processing is not constrained by the spatial rule of MSI since both unilateral and bilateral cross-modal conditions produced highly consistent behavioral enhancement. It is unlikely that interhemispheric integration depends on the anterior commissure (Barr and Corballis 2002), since patient SP, and other patients from various studies, either with a congenital absence or a section of the anterior commissure, demonstrate a normal or enhanced RG (Corballis, 1998; Pollman and Zaidel 1999). Thus, the current and previous findings converge toward a role of the SC for the integration of spatially congruent and incongruent cross-modal stimuli. Although there are no direct evidence for the involvement of the SC in the integration of spatially disparate cross-modal stimuli, the absence of differences between unilateral and bilateral visuo-tactile stimulations in acallosal patients support this hypothesis. Since the SC is the main candidate for the preservation of interhemispheric integration and RT enhancement in the absence of the CC, our results suggest that the behavioral enhancement resulting from subcortical processing, possibly at a collicular level, may not reflect the spatial constraints observed in SC neurons. Paradoxically, this hypothesis remains compatible with the spatial rule. Indeed, sufficiently large or misaligned receptive fields (Wallace and Stein 2007; Stein and Meredith 1993) and coding of cross-modal stimulation at a population level (McAlpine 2005) provide viable explanation for these effects. In line with animal studies (Worgotter and Eysel, 2000; Tolias et al. 2001), the hypothesis that receptive fields properties may be flexible or dynamically shaped by higher cognitive processes has been proposed as a modulating factor on multisensory integration (Murray et al. 2005; Spence 2013). The idea that behavioral enhancement in humans does not follow the rules derived from neurophysiological studies is also supported by our previous study investigating the ventriloquist effect (Charbonneau et al. 2013). In this study, our group demonstrated that the inverse effectiveness principle, according to which the maximal multisensory integration is observed with weakly effective stimuli, does not strictly apply to audio-visual localization in humans.

Another possibility is that the SC subserves interhemispheric transfer in acallosal individuals without compromising the integration of spatially disparate stimuli that might occur at a cortical level. Several studies have demonstrated that multisensory interactions can occur in low-level areas in the cortical hierarchy of perception and at very early latencies after stimuli presentation (Schroeder and Foxe 2004; Giard and Peronnet 1999; Foxe et al. 2000, 2002). Recent findings further suggest that such early latency and low-level interactions of sensory information from different modalities are functionally linked to both reaction time facilitation (Sperdin et al. 2009, 2010) and detection accuracy (Van der Burg et al. 2011). Crucially, early multisensory interactions between auditory and tactile stimuli were observed regardless of stimuli's alignement in the auditory belt cortex ipsilateral to the tactile stimulation (Murray et al., 2005). Furthermore, these interactions were accompanied by a decrease in RT for both aligned and misaligned stimuli. However, current neuroimaging data would suggest that low-level multisensory interactions between visual and tactile stimuli occur only when the constituent stimuli are presented in the same hemifield (Macaluso et al. 2000, 2005; Zimmer and Macaluso, 2007). Thus, further studies are needed to identify how spatially disparate visual and tactile stimuli are integrated at a cortical level and how these interactions contribute to behavioral enhancement.

The preserved capacity for intrahemispheric cross-modal integration supports the idea that the absence of the corpus callosum does not interfere with intrahemispheric cross-modal processing. To some extent, intact intrahemispheric cross-modal integration contradicts models where response inhibition must be released through the activation of both hemisphere to enable faster RTs (Reuter-Lorenz et al. 1995, Roser and Corballis 2002). Our data are also inconsistent with the possibility that the lack of CC releases the SC from an interhemispheric inhibitory influence (Savazzi and Marzi 2004; Iacoboni and Zaidel 2003), since we demonstrate that rapid motor response exceeding simple probability summation occur with intrahemispheric cross-modal stimuli in both AgCC and the split-brain patients. Thus, with the exception of patient MD, split-brain and AgCC participants showed intact intrahemispheric and interhemispheric visuo-tactile processing, suggesting that the absence of the corpus callosum, or developmental plasticity does not affect cross-modal RTs in simple detection paradigm.

Our results are to some extent consistent with a previous study indicating that AgCC patients had normal remapping of visuo-tactile space in trials that required interhemispheric interactions (Wolf et al. 2011). Thus, the effect of a task irrelevant visual distractor on tactile RTs is the same when both stimuli are presented to the same or different hemispheres. These results imply that information is shared between the hemispheres and suggest that early brain plasticity in AgCC can compensate for the absence of the corpus callosum. Accordingly, Wolf and colleagues (2011) mention the SC as a possible contributor to their finding, but report that developmental plasticity, notably in the anterior commissure which was enlarged in four of their patients, is mainly reponsible for the preservation of the spatial congruency effect in interhemispheric trials. Using a very similar paradigm, it was demonstrated that in the split-brain, the visual influence on tactile targets only occur when both stimuli are presented to the same cerebral hemisphere (Spence et al. 2001a; 2001b), demonstrating that some form of interhemispheric communication is required for intact processing and remapping of visuotactile information across space. In the split-brain, it appears that subcortical or extra-callosal pathways are insufficient to ensure visuo-tactile remapping, suggesting that more complex task may require cross-cortical connections. Our results however demonstrate that bilateral cross-modal integration is preserved in the split-brain and that extracallosal pathways can cope with the lower requirement of the simple detection task. This also support that in simple detection tasks, developmental plasticity does not play a critical role for bilateral cross-modal integration in AgCC.

Recent findings suggests that MSI is influenced by higher order and perceptual processes (Girard et al. 2011, 2013; Spence 2013; Talsma et al. 2007). To some extent, our findings relate to the Bayesian framework of sensory integration which states that individuals take the reliability of the sensory estimates into account when making behavioral decisions (Ernst and Banks 2002; Alais and Burr 2004). According to this view, combinations that do not provide more accurate information to the nervous system are less likely to improve behavior. Moreover, sensory cues have different degrees of reliability that are subject to change in different contexts (Deneve and Pouget 2004). Therefore, the combined information of two stimuli from different modalities should have lower variance because they are processed by independent sensory systems and are not influenced by the same noise source (Hillis et al. 2002). However, two identical sensory stimuli from the same modality presented at the same time and approximately at the same place might covary up to the point that their integration is only minimally beneficial (Gingras et al. 2009). In the aligned conditions, the representations of the stimuli from the same modality may largely overlap, resulting in similar internal or neural representations for single and redundant trials. Because both stimuli are not processed independently, such overlapping representations would contribute to the smaller or the absence of RG observed for these conditions. On the other hand, interhemispheric stimuli are initially processed independently by each hemisphere, resulting in distinct and non-overlapping internal representations that produce a RG. In line with this view, cross-modal stimuli would produce greater RGs than within-modal combinations because they originate from different sensory systems that provide independent and non-redundant estimates about the same external event. In the absence of the CC, bilateral stimulations from the same modality might be represented as completely indepedent and non-redundant information about an external event. Thus, bilateral within-modal combinations may provide an especially robust estimate of an event in acallosal individuals because of the independent processing of information in the isolated hemipheres. As a result, spatially incongruent within-modal and cross-modal stimuli could possibly enhance performance in acallosal individuals. Interestingly, a behavioral study in behaving animals suggests that the violation of the spatial principle at the behavioral level remains consistent with statistically-optimal integration in a Bayesian model. One hypothesis that have received support from animal data would be that the increased variability of stimuli presented in periphery is compensated by an increase in the receptive field size with eccentricity (Rowland et al. 2007).

CONCLUSION

Our results demonstrate that AgCC and split-brain patients perform comparably to control participants in a cross-modal visuo-tactile detection task. Although AgCC and the split-brain patient did not show a systematic enhancement for bilateral within-modal conditions, some patients demonstrated an increased RG relative to the control group. Nevertheless, our results suggest that behavioral enhancement in these patients are similar to what is observed in neurotypic individuals for within-modal and cross-modal integration. Overall, these results suggest that cross-modal integration is not altered in the absence of the corpus callosum, even when stimuli from different modalities are initially presented to different hemispheres. Based on previous studies demonstrating that the SC is a primary site for cross-modal integration in acallosal patients and healthy individuals in simple detection tasks, our results suggest that the behavioral benefits resulting from subcortical processing, putatively by the SC, do not reflect the spatial rule of multisensory integration.

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FIGURE CAPTIONS

Figure 1. Midsagittal MRI scans of (A) MD, (B) MG, (C) SG, (D) SP, (E) ML and (F) an intact brain.

Figure 2. Experimental setup. Schematic view of the experimental setup and stimulation conditions. Tactile stimuli were delivered to the index and middle fingers of each hand, and visual stimuli were projected on a surface above the stimulated fingers. All redundant conditions were presented either in an aligned configuration (both stimuli in the same hemispace) or misaligned configuration (both stimuli presented in different hemispaces).

Figure 3. Reaction times. Mean reaction time (in milliseconds) and standard errors of the mean (SEM) for single, within-modal and cross-modal conditions. Capital letters refer to the modality (V visual, T tactile) and spatial configuration (A aligned, M misaligned) for each combination.

Figure 4. Mean RGs and SEM for within-modal and crossmodal pairs obtained under aligned and misaligned spatial configurations. The X axis refers to sensory combination (V visual, T tactile) and spatial alignment (‘‘A’’ for aligned and ‘‘M’’ for misaligned). Cross-modal stimuli produced greater RT enhancement than within-modal stimuli in CTRL participants. In AgCC patients, there was no difference between cross-modal and within-modal combinations, possibly because of enhanced gains in misaligned within-modal conditions. It’s worth noting that the mean RG of AgCC participants for cross-modal conditions are influenced by the fact that MD had virtually no RG for these conditions. The split-brain (ML) had a significantly greater RG than controls in condition TA, TM and VTA.

Figure 5. Race model inequality. Test for violation of the race model inequality (Miller 1982; Ulrich et al. 2007). The graph represents the difference in milliseconds (on the Y axis) between the model prediction computed from the RTs of each unisensory counterpart (the model bound) and the RTs obtained in the redundant conditions. Positive values refer to RTs

that were faster than the race model prediction. Negative values refer to RTs that were slower than the race model prediction. The difference between the bound and the RTs of the redundant conditions is computed for each percentile of the RT distribution (on the X axis). Cross-modal stimuli significantly violated the race model inequality irrespective of their alignment whereas both double visual and double tactile stimuli were consistent with simple probability summation.

SUPPLEMENTAL DATA

Figure S1. RG for each patient and their respective control participants.

Figure 1.

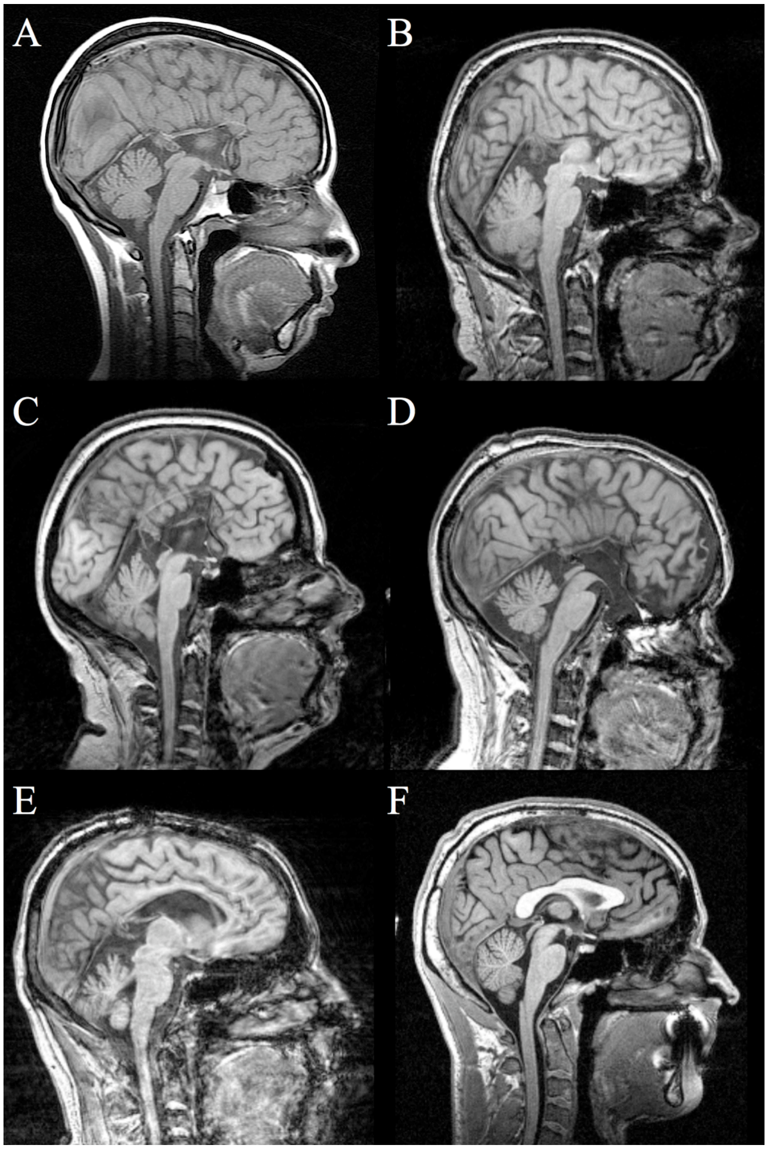
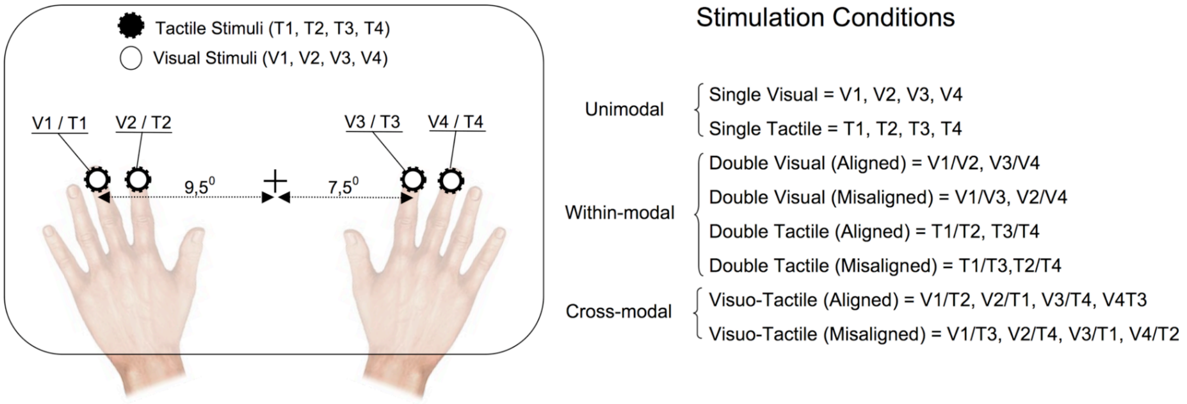


Figure 2.



Stimulation Conditions

Unimodal
- Single Visual = V1, V2, V3, V4
- Single Tactile = T1, T2, T3, T4

Within-modal
- Double Visual (Aligned) = V1/V2, V3/V4
- Double Visual (Misaligned) = V1/V3, V2/V4
- Double Tactile (Aligned) = T1/T2, T3/T4
- Double Tactile (Misaligned) = T1/T3,T2/T4

Cross-modal
- Visuo-Tactile (Aligned) = V1/T2, V2/T1, V3/T4, V4T3
- Visuo-Tactile (Misaligned) = V1/T3, V2/T4, V3/T1, V4/T2

Figure 3.

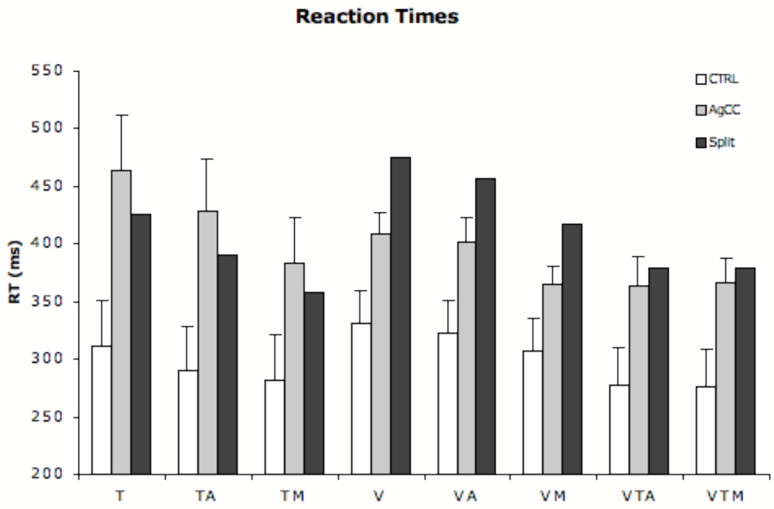


Figure 4.

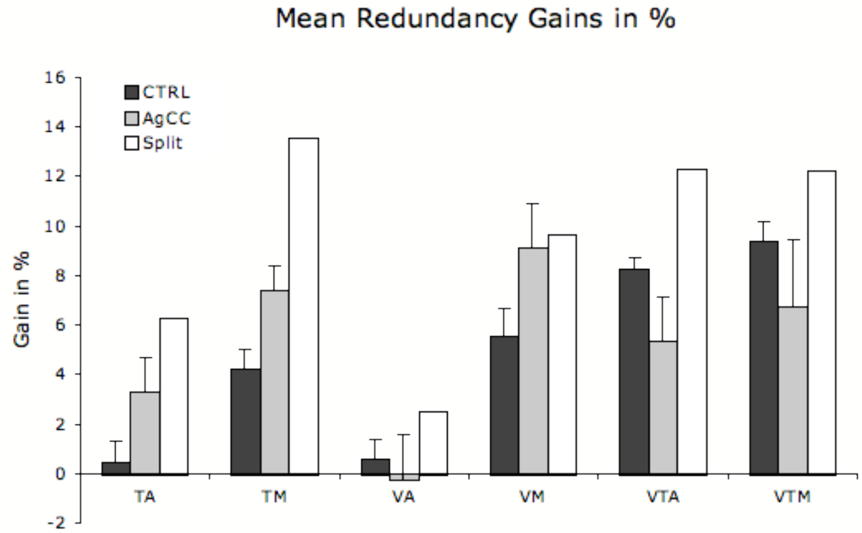
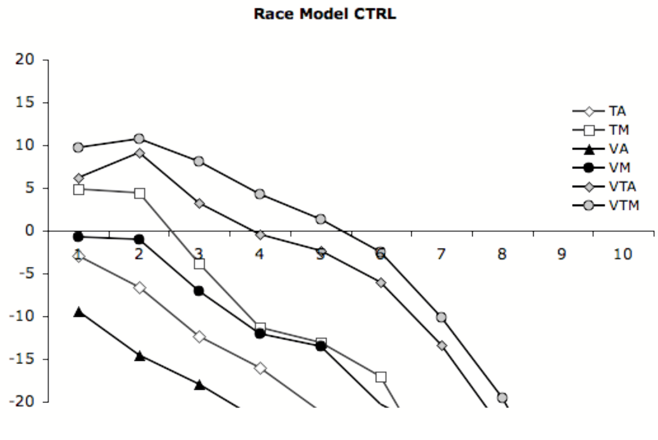
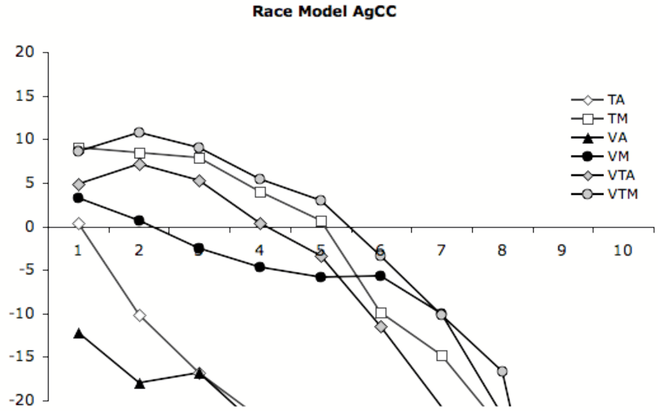
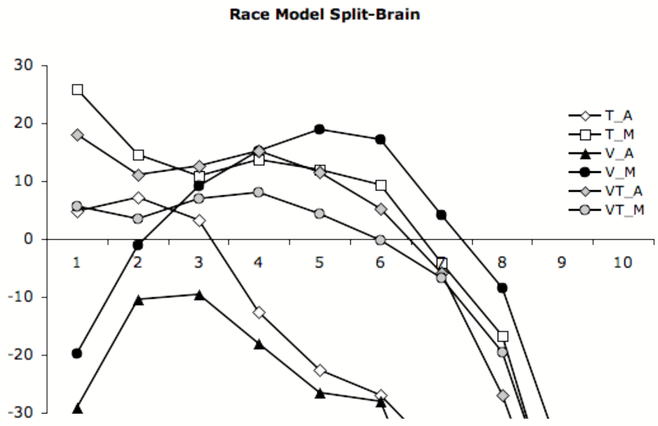

Mean Redundancy Gains in %
CTRL
AgCC
Split
Gain in %
16
14
12
10
8
6
4
2
0
-2
TA
TM
VA
VM
VTA
VTM

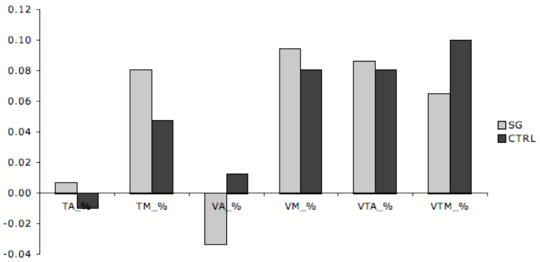
Figure 5.

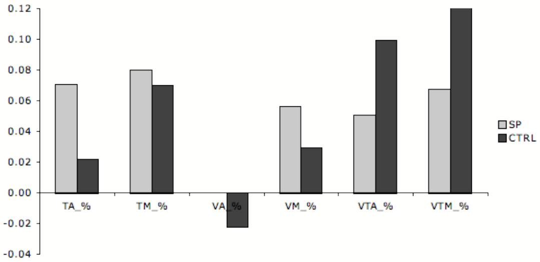

Race Model CTRL

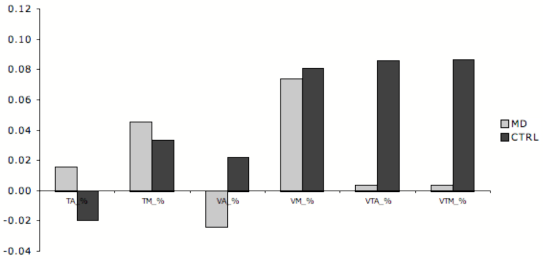

Race Model AgCC

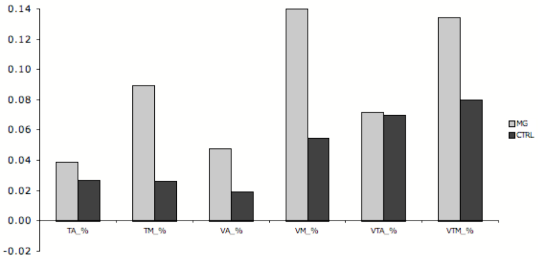

Race Model Split-Brain

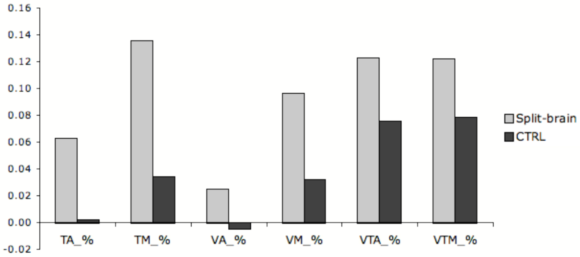
Supplemental data.











DISCUSSION GÉNÉRALE

RAPPEL DES OBJECTIFS EXPÉRIMENTAUX ET DES PRINCIPAUX RÉSULTATS

La présente thèse a permis d'approfondir nos connaissances sur l'intégration multimodale visuotactile, les facteurs qui l'influencent et qui la distinguent de l'intégration intramodale. Dans une première étude, il a été démontré que la manipulation des exigences de la tâche influence la capacité d'intégration d'informations visuelles et tactiles dans l'espace. Dans une seconde étude, l'utilisation d'un paradigme de temps de réaction simple montre que les stimulations multimodales produisent une réduction des TR plus importante que les stimulations intramodales. Une seconde distinction démontre que contrairement aux conditions intramodales, les stimulations multimodales produisent des gains comportementaux qui sont indépendants de la configuration spatiale des stimulations. Enfin, une troisième étude suggère que l'intégration multimodale est préservée chez les patients callosotomisés et agénésiques. L'analyse conjuguée de ces trois études permet de dégager différentes conclusions quant aux principes qui régissent l'intégration intramodale et multimodale sur le plan comportemental. Plusieurs propositions sont mises de l'avant afin d'expliquer la modulation des TR et du GR selon les modalités présentées et la configuration spatiale des stimulations. Enfin, certaines limites sont considérées dans l'interprétation et la généralisation des résultats et des avenues de recherches futures sont proposées.

MODULATION DE L'INTÉGRATION SENSORIELLE SELON LES EXIGENCES DE LA TÂCHE

Nos résultats indiquent que dans une simple tâche de détection, les TR, le GR et la proportion de la distribution des TR qui excède l'estimation du modèle de course sont indissociables, peu importe la configuration spatiale des stimulations. Ces résultats complémentent ceux d'études précédentes ne démontrant pas de modulation spatiale du GR pour les combinaisons audiovisuelles et audiotactiles (Murray et al., 2005; Zampini et al., 2007). Ce résultat suggère que les différentes voies impliquées dans la représentation et le traitement intrahémisphérique et interhémisphérique sont équivalentes pour l'intégration visuotactile. L'utilisation d'une tâche de détection simple nous a permis d'observer des interactions visuotactiles sans influences descendantes (traduction par l'auteur de « top-down »), sans effets attentionnels et sans contraintes liées à la tâche (Spence, Nicholls, Gillepsie & Driver, 1998), outre l'emphase sur la vitesse de réaction.

À l'opposé, dans une tâche de temps de réaction de choix où les participants doivent effectuer une discrimination spatiale, les TR, le GR et la violation du modèle de course sont modulés par la configuration spatiale des stimuli. Les résultats de la seconde tâche supportent l'idée que les exigences de la tâche peuvent imposer des contraintes spatiales sur l'intégration multisensorielle (Spence, 2013). Peu d'explications ont été proposées afin d'expliquer comment des processus cognitifs ou attentionnels sont susceptibles d'influencer l'intégration multisensorielle. Une hypothèse proposée par Murray et al. (2005), suggère que des processus descendants pourraient modifier de façon dynamique la représentation spatiale des stimuli en influençant l'étendue des champs récepteurs. De façon générale, nos résultats démontrent que des stimulations physiques identiques peuvent produire différentes formes d'intégration multimodale, suggérant ainsi que les propriétés physiques des stimuli, et par conséquent leurs localisations spatiales, ne sont pas suffisantes pour prédire la performance comportementale chez l'humain.

Dans la tâche de temps de réaction de choix, une inhibition de la réponse aux stimulations tactiles a été observée lorsqu'une stimulation visuelle non pertinente pour la tâche était présentée simultanément du côté opposé à la stimulation tactile, démontrant ainsi que les stimulations multimodales peuvent nuire au comportement sous certaines conditions. Cela suggère qu'il puisse y avoir un coût lorsque les participants essaient de filtrer l'information multimodale, notamment lorsque les stimulations sont présentées bilatéralement. Par ailleurs, les stimulations tactiles n'interféraient pas avec la réponse visuelle. En accord avec le phénomène de dominance visuelle (Colavita, 1974, McGurk & MacDonald, 1976), ces résultats démontrent que le poids accordé aux stimulations diffère selon la modalité dans les interactions sensorielles, la vision dominant généralement l'audition et le toucher.

Les résultats de cette étude supportent la proposition selon laquelle les manifestations comportementales de l'intégration multimodale ne dépendent pas nécessairement de la congruence spatiale des stimulations. Conséquemment, nous proposons que la règle spatiale de l’intégration multisensorielle, définie selon les propriétés neurophysiologiques des neurones colliculaires chez l’animal, ne s’applique pas de façon systématique au comportement humain. Cette interprétation s’accorde d’ailleurs avec la position de Spence (2013), selon laquelle les effets de congruence spatiale sont observés seulement dans des conditions expérimentales spécifiques et bien définies.

Tel que nous l’avons démontré, les résultats d’une tâche n’exigeant pas de discrimination spatiale de l’information sensorielle ne seront pas modulés en fonction de la configuration spatiale des stimulations. À l’opposé, une tâche nécessitant une discrimination spatiale va induire une modulation de l’intégration multimodale, démontrant des avantages comportementaux moindres pour les stimulations spatialement incongruentes. Cette interprétation supporte l’hypothèse selon laquelle l’intégration multimodale chez l’humain serait dépendante des processus perceptuels et cognitifs.

DIFFÉRENCIATION DE L’INTÉGRATION UNIMODALE ET MULTIMODALE

La deuxième étude compare les effets de la configuration spatiale sur les TR produits lors de l’intégration intramodale et multimodale. Le premier but de cette expérience était de mesurer le GR optimal pour les combinaisons intramodales et multimodales afin d’obtenir une démonstration empirique de leurs avantages comportementaux respectifs. Les résultats démontrent que la réduction des TR est plus importante pour les stimulations multimodales qu’unimodales, peu importe la configuration spatiale des stimulations. Tel qu’obtenu dans la première étude, les stimulations multimodales spatialement congruentes et incongruentes produisent un GR et une violation du modèle de course indissociables. À l’inverse, le GR associé aux stimulations unimodales est modulé par la configuration des stimuli. Contrairement aux conditions multimodales, le GR en condition unimodale demeure conforme au modèle de course et se produit uniquement lorsque les stimulations visuelles ou tactiles sont présentées bilatéralement.

Ces résultats suggèrent que des stimulations redondantes de la même modalité sensorielle présentées au même endroit n’améliorent pas la performance. De plus, il semble possible que ces stimulations soient perçues comme un événement unique si le chevauchement des représentations interne est important. Par exemple, il a été démontré que l'effet de redondance en vision (Schröter, Fiedler, Miller & Ulrich, 2011) et en audition (Schröter, Ulrich & Miller, 2007) émerge seulement lorsque les stimulations redondantes produisent des percepts distincts.

La dissociation des résultats en fonction des modalités combinées et de la configuration spatiale s'accorde avec l'approche bayésienne de l'intégration, laquelle fournit un support théorique à nos résultats. Cette approche stipule que les individus attribuent un poids aux stimulations dans leur processus décisionnel (Ernst & Banks 2002; Alais & Burr 2004). Par conséquent, les stimulations dont la combinaison n'est pas plus informative sont moins susceptibles d'améliorer le comportement. Tel que démontré chez l'animal, la combinaison de deux stimulations identiques de la même modalité sensorielle qui sont présentées au même endroit pourrait covarier au point de ne pas être bénéfique pour le comportement (Gingras et al., 2009). À l'opposé, les combinaisons de stimulations des différentes modalités partagent moins de variances communes puisqu'elles sont initialement traitées par des systèmes sensoriels différents qui ne sont pas influencés par les mêmes sources de bruits. Bien que les résultats de la seconde étude correspondent aux prédictions des modèles bayésiens, d'autres études doivent être menées afin de déterminer dans quelle mesure cette approche pourrait expliquer une réduction des TR.

RÔLE DU CORPS CALLEUX DANS LES INTERACTIONS SENSORIELLES

La troisième étude explore l'effet de l'absence du corps calleux sur l'intégration intramodale et multimodale. Les résultats de cette étude suggèrent qu'il n'y a pas de différence majeure entre les sujets normaux et les participants sans corps calleux. Ces résultats permettent d'inférer que le corps calleux n'est pas une structure indispensable pour l'intégration unisensorielle et multisensorielle. Les hémisphères cérébraux d'individus callosotomisés et agénésiques peuvent communiquer par l'entremise de connections extracallosales (traduction par l'auteur de «extracallosal») ou sous-corticales qui sont suffisantes pour assurer une intégrité de l'effet de redondance.

Contrairement aux participants contrôles, certains patients acalleux peuvent démontrer un GR supérieur et une violation du modèle de course pour les conditions unisensorielles bilatérales (Corballis, 1998; Reuter-Lorenz et al., 1995). Quant au GR observé pour les conditions unilatérales, ils ne différaient pas entre les groupes. Pour les conditions multimodales, le GR ne différait pas selon les groupes ni la configuration spatiale des stimulations, démontrant que l'intégration multimodale est totalement préservée chez les sujets acalleux. L'absence du corps calleux et la réduction du transfert interhémisphérique n'interfèrent pas dans la réduction des TR obtenus pour les conditions multimodales intrahémisphériques et interhémisphériques.

La préservation de l'effet de redondance chez les sujets acalleux est généralement attribuée à un transfert et un traitement sous-cortical par la commissure intercolliculaire et les CS (Corballis et al., 2002; Savazzi & Marzi, 2004). Par ailleurs, les études sur l'effet de redondance chez les participants normaux suggèrent l'implication des CS dans la violation du modèle de course pour les stimulations bilatérales unimodales et multimodales (Savazzi & Marzi, 2004; Leo et al., 2008). Or, ces résultats entrent en contradiction avec la règle spatiale de l'intégration multisensorielle.

Les résultats du groupe de patients acalleux suggèrent que l'intégration multimodale, même lorsqu'elle dépend hypothétiquement d'un traitement colliculaire, ne reflète pas la règle spatiale. Paradoxalement, cette constatation demeure compatible avec la règle spatiale. En effet, la présence de champs récepteurs non alignés ou suffisamment grands ainsi que l'encodage des stimuli par une population de neurones fournissent des explications viables quant au maintien du GR en conditions bilatérales (Wallace & Stein, 2007; Stein & Meredith, 1993). En accord avec les données chez l'animal (Worgotter & Eysel, 2000; Tolias et al., 2001), la possibilité que les propriétés des champs récepteurs soient flexibles ou dynamiques sous l'influence de processus cognitifs de plus haut niveau pourrait expliquer nos résultats. Une seconde hypothèse serait que les CS soient impliqués dans le transfert interhémisphérique, mais que le phénomène d'intégration menant à une amélioration de la performance se produirait au niveau du cortex. En effet, plusieurs études ont démontré des interactions multimodales précoces au sein de régions corticales primaires (Schroeder & Foxe, 2004; Giard & Peronnnet, 1999; Foxe, Morocz, Murray, Higgins, Javitt & al., 2000; Foxe et al., 2002). Ces interactions seraient fonctionnellement liées à l'accélération des TR (Sperdin, Cappé, Foxe & Murray, 2009, 2010) et à l'augmentation du taux de détection (Van der Burg et al., 2011). Toutefois, cette hypothèse nécessite un support empirique plus substantiel, notamment quant à la possibilité d'observer des interactions multimodales précoces en l'absence du corps calleux lorsque les stimulations sont latéralisées. Néanmoins, nos résultats supportent l'idée selon laquelle les manifestations comportementales de l'intégration multisensorielle ne reflètent pas les règles issues d'études neurophysiologiques chez l'animal (Charbonneau et al., 2013).

AVENUES DE RECHERCHES FUTURES

L'utilisation de modèles alternatifs au modèle de course tel que celui proposé par Otto & Mamassian (2012), qui tient compte à la fois de la corrélation entre la latence des différents essais et des effets de l'historique de présentation des stimuli, pourrait fournir des informations complémentaires sur les processus qui permettent l'accélération des TR. De plus, la comparaison des différents modèles pourrait permettre d'identifier si certains modèles s'appliquent plus spécifiquement à certaines conditions expérimentales. D'autres modèles axés sur la préparation ou l'amorçage (Los & Van der Burg, 2013), qui nécessitent l'utilisation de paradigmes de TR de choix plutôt que de TR simple seraient aussi pertinents à évaluer dans un contexte où les stimulations sont latéralisées, notamment afin d'évaluer si l'amorçage sensoriel prime sur l'amorçage spatial.

Nos résultats chez les patients acalleux suggèrent qu'une intégration multimodale de stimulations simples est préservée en l'absence de toute contrainte attentionnelle. Puisque nous avons observé peu de différences entre les groupes, il serait pertinent d'évaluer si l'intégration de stimulations plus complexes est aussi préservée chez ces patients. À titre d'exemple, Wolf et collègues (2011) suggère que l'intégration de stimulations multimodales requérant un traitement plus complexe de l'information est préservée chez les patients agénésiques tandis qu'elle est absente chez un sujet callosotomisé. Ainsi, l'utilisation de stimulations ou de tâches plus complexes permettrait de spécifier les conditions nécessaires pour que l'intégration soit possible. De plus, cela permettrait de mieux évaluer la contribution du corps calleux, des structures sous-corticales et de la plasticité cérébrale dans l'intégration multisensorielle. L'exploration de ces avenues de recherches fournirait des informations nous permettant d'avoir une meilleure compréhension des facteurs qui gouvernent les avantages comportementaux associés à l'intégration multisensorielle chez l'humain.

LIMITES DES ÉTUDES

Les résultats de cette thèse doivent être interprétés en considérant certaines limites associées aux études présentées. Certaines de ces considérations reflètent des difficultés inhérentes à l'étude d'une population clinique.

LIMITES STATISTIQUES

Les études chez les individus callosotomisés et agénésiques s'appuient généralement sur de petits nombres de participants. Dans le cas présent, le faible nombre de participants agénésiques ainsi que l'importante variabilité intrasujet retrouvée chez cette population réduisent considérablement la puissance statistique des résultats. Le participant callosotomisé représente un cas unique dont les résultats demeurent ambigus dû à sa capacité d'accomplir la tâche correctement, ce qui limite la portée des conclusions à ce sujet. En somme, ces facteurs limitent la généralisation des conclusions que nous proposons à l'ensemble de cette population clinique. Néanmoins, les résultats obtenus sont en partie congruents avec ceux retrouvés chez les participants contrôles et sont conformes aux prédictions basées sur les études antérieures. D'autres études doivent tenter de reproduire et confirmer les résultats obtenus afin de préciser les différences attribuables au type de pathologie dans des tâches de temps de réaction simple.

LIMITES RELATIVES À L'ÉCHANTILLON DE PATIENT

Les sujets contrôles de la troisième étude ont été appariés selon l'âge, le sexe et la latéralité manuelle seulement. Idéalement, l'appariement du groupe contrôle et du groupe de patients devrait de surcroît se baser sur le quotient intellectuel. Il est donc possible que certaines variables confondantes aient pu influencer les résultats de cette étude.

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