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Modèle attentionnel à deux étapes de la planification des mouvements de portée du bras et des saccades

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Résumé

La planification des saccades ou des mouvements de la portée du bras vers un espace spécifique dans l’environnement dépend des mécanismes attentionnels pour sélectionner un espace pertinent, et des systèmes moteurs pour correctement guider les mouvements à leur destination. Cependant, l’interaction entre l’attention et l’action sont encore loin d’être compris. Le but notre recherche était de déterminer si la planification des mouvements des yeux et des bras était basée sur des représentations partagées ou indépendantes. Dans notre premier article, nous avons investigué comment la modulation de l’attention exogène avec un indice visuel influençait les caractéristiques temporelles et spatiales des mouvements des yeux et des mains durant des mouvements simples ou combinés. Nos résultats suggèrent deux étapes de la planification des mouvements; la première étant dépendante de l’effecteur, l’autre indépendante de l’effecteur. Dans notre deuxième article, nous avons investigué l’influence de l’indiçage exogène sur les mouvements de la portée du bras durant une tâche d’adaptation visuomotrice afin d’identifier si les mécanismes attentionnels facilitent la planification motrice ou la détection de la cible visuelle. Nos résultats ont démontré une affectation attentionnelle au niveau de la détection visuelle qu’à la planification motrice du bras, en contraste aux saccades, tel que démontré par une étude précédente. Ensemble, ces deux articles permettent de mieux comprendre les mécanismes opérationnels de l’attention sur les mouvements des yeux et des bras, en plus de l’interaction entre les systèmes sensoriels et moteurs. Nous proposons un modèle attentionnel à deux étapes afin d’unifier plusieurs études ayant des conclusions divergentes par rapport aux processus de planification des mouvements des yeux et des bras.

Mots-clés: attention visuelle, attention exogène, mouvements visuellement guidés, mouvements coordonnés, saccades, mouvements de portée du bras, coordination œil-main, adaptation visuo-motrice, temps de réaction, indiçage

Abstract

Planning saccades or reach movements to a specific location in the environment relies on attentional mechanisms to select a relevant location and on motor systems to correctly guide the movements to their destination. However, the interaction between attention and action are still far from being completely understood. We wished to determine whether planning of eye and arm movements is based on shared or independent representations. In our first article, we investigated how exogenous attentional modulation through the use of behaviorally irrelevant cues influenced the temporal and spatial characteristics of the eye and the arm during single or combined movements. We found both similar and differential effects of eye and arm reaction times, which we suggest is based on two stages of motor planning; one effector-independent and one effector-dependent. In our second article, we investigated the influence of exogenous cueing on arm movements during visuomotor adaptation to identify whether attentional mechanisms facilitate motor planning or visual target detection. Our findings demonstrated that motor planning during a visuomotor adaptation task relied more on the visual target than on arm motor planning, contrastingly to saccades, as has been shown in a previous study. Taken together, our papers provide better understanding of the operating mechanisms of attention on eye and arm movements and the interaction between sensory and motor systems. We propose a dual-stage attentional model to bring together a number of divergent findings in the field with respect to eye and arm planning processes.

Keywords: visual attention, exogenous attention, visually-guided movements, coordinated movements, saccades, reach movements, hand-eye coordination, visuomotor adaptation, reaction times, cueing

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DISCUSSION

Liste des abréviations

ACV: Accident vasculaire cérébral

COF: Champ oculaires frontaux

CPP: Cortex postérieur pariétal

CS: Colliculi/us supérieur(s)

FEF: Frontal eye fields

ITI: Inter-trial interval

LIP: Lateral intraparietal area

PLI: Partie latérale intrapariétale

PPC: Posterior parietal cortex

PRR: Parietal reach region

RRT(s): Reach reaction time(s)

RT(s): Reaction time(s)

SC: Superior colliculus

SMT: Stimulation magnétique transcrânienne

SOA: Stimulus-onset asynchrony

SRT(s): Saccade reaction time(s)

TCC: Traumatisme crânio-cérébral

tDCS: Stimulation transcrânienne à courant continu

TEP: Tomographie par émission de positrons

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1. Introduction

1.1. Aperçu général

Planifier un mouvement vers un objet ou un espace repose grandement sur l'attention et le système moteur. D'une part, les mécanismes attentionnels permettent une sélection de l'information qui priorise une certaine région aux dépens d'autres dans l'environnement visuel. D'une autre part, le système moteur permet l'exécution de mouvements jusqu'à destination en réponse à la sélection attentionnelle initiée précédemment. Cependant, les mécanismes à travers lesquels l'attention affecte les mouvements, notamment ceux des yeux et des mains, sont encore peu connus.

Les mouvements des yeux rapides, appelés saccades, et les mouvements de portée du bras ont des fonctions fondamentalement différentes. Les saccades permettent d'acquérir de l'information sur notre environnement, tandis que les mouvements des bras permettent principalement de le manipuler. Les mécanismes attentionnels ont été démontrés comme étant impliqués dans la planification des mouvements de ces deux effecteurs, yeux et bras, modifiant certaines de leurs caractéristiques, tels que le temps de réaction et l'amplitude. Notre projet de recherche vise à mieux comprendre comment la modulation attentionnelle influence les caractéristiques temporelles et spatiales des yeux et du bras durant la planification de mouvements.

Le mémoire qui suit est subdivisé en six chapitres : une introduction globale, les objectifs de recherche, un premier article, un deuxième article, une discussion synthèse et une conclusion. L'introduction consistera à développer un contexte théorique sur l'attention visuelle, les mouvements visuellement guidés, et sur l'interaction entre ces deux concepts. Ensuite, nous allons décrire les objectifs, les hypothèses ainsi que la méthodologie de la recherche présentée. Ceci sera suivi d'un premier article qui traite de l'attention exogène lors des saccades et des mouvements de portée du bras, puis d'un deuxième article qui traite de l'influence de l'attention exogène sur les mouvements de la portée du bras lors d'une tâche d'adaptation visuomotrice. Enfin, nous discuterons des résultats présentés, des limites du projet de recherche, et nous développerons une ouverture sur les possibilités des recherches futures.

1.2. L’attention visuelle

L’attention visuelle est un concept ancré dans la science de la vision, englobant plusieurs sous-concepts à la croisée de la neuropsychologie, la neurophysiologie et les sciences de la perception. L’attention visuelle est elle-même qu’une partie, quoique primordiale, de l’attention, mais représente un grand domaine de recherche qui vise à élucider les mécanismes et les structures neurophysiologiques affectant la perception et le comportement humain. Tout d’abord, il est important de circonscrire le cadre conceptuel selon lequel nous allons analyser l’attention visuelle tout au long de ce mémoire. Nous définissons l’attention visuelle comme étant un concept impliquant plusieurs mécanismes gérant en partie l’entrée, la filtration et le traitement des informations sensorielles. Ces mécanismes qui construisent l’attention visuelle ont été étudiés sous plusieurs facettes afin de souligner et de mesurer les effets que ceux-ci peuvent notamment avoir sur la perception et le traitement de l’information. Nous acquiesçons que l’attention visuelle est un construit complexe composé d’une multitude de processus et mécanismes qui influent sur le comportement humain et qu’il serait réductionniste de la considérer comme un mécanisme unitaire qui a pour but de générer une carte de priorité spatiale.

Dans le mémoire qui suit, nous essayons d’éclaircir les effets de l’attention visuelle dans un contexte précis, et, de par la nature limitée de nos expériences, nous examinerons qu’une fraction bien définie du construit qu’est l’attention visuelle. Le modèle attentionnel à deux étapes que nous proposons et soutenons grâce aux résultats de nos études se limite à un contexte de planification motrice des bras et des yeux, mais pourrait être généralisable à d’autres contextes où l’attention visuelle est engagée. Les prochains paragraphes vont explorer l’attention visuelle en tant que processus de sélection, par ses mécanismes d’orientation et, enfin, les différents moyens de moduler l’attention vont être présentés.

1.2.1. La sélection attentionnelle

Notre environnement visuel est constamment parsemé d'une multitude d'objets ayant plusieurs caractéristiques vastement différentes. Dû à la quantité importante d'information visuelle à traiter à tout moment, à la capacité de traitement limitée de notre système visuel et aux ressources limitées de nos systèmes cognitifs, tels que la mémoire et la prise de décision, un processus de sélection de l'information est nécessaire afin d'avoir une représentation valide des objets (Alvarez & Cavanagh, 2004; Luck & Vogel, 1997; Sperling, 1960; Todd & Marois, 2004; Vogel & Machizawa, 2004). Le mécanisme au cœur de ce processus est la sélection attentionnelle.

L'attention visuelle est souvent comparée à un projecteur envoyant un faisceau de lumière sur une partie délimitée de l'espace visuel, afin de permettre un traitement plus limité spatialement, mais approfondi visuellement (Ericksen & Yeh, 1985; Posner & Petersen, 1990; Posner, Snyder & Davidson, 1980). Cependant, cette représentation de l'étendue spatiale de l'attention a été considérée comme étant trop simpliste et présentait des lacunes importantes, notamment dans sa manière d'expliquer l'attention divisée (Tong, 2004). Au cours des dernières décennies, plusieurs théories complémentaires à la théorie du projecteur attentionnel (de l'anglais « spotlight of attention ») ont vu le jour.

Une des théories contemporaines de la sélection et l'allocation attentionnelle est celle des cartes de priorité (« priority maps ») (Bisley & Goldberg, 2010; Deco & Zihl, 2001; Fecteau & Munoz, 2006; Shomstein & Yantis, 2004). La sélection d'un espace visuel pour un traitement approfondi, similairement à la théorie du projecteur attentionnel, a été suggérée de se produire suite à une composition d'une carte de priorité intégrant des entrées ascendantes « bottom-up », c'est-à-dire les caractéristiques physiques des objets se démarquant de leur environnement visuel, et des entrées descendantes « top-down », composées des buts et des motivations de l'observateur (Bisley & Goldberg, 2010; Fecteau & Munoz, 2006; Kamkar, Moghaddam, & Lashgari, 2018; Serences, Yantis, Culberson, & Awh, 2004; Zelinsky & Bisley, 2015). La combinaison et l'intégration de ces deux entrées permettraient de créer une représentation topographique de la priorité dans l'environnement visuel selon laquelle la sélection attentionnelle se produit (Itti & Koch, 2001; Ptak, 2012; Treue, 2003).

Les études sur la neurophysiologie des cartes de priorité proposent que ce mécanisme de sélection attentionnelle intégrant les influences « top-down » et « bottom-up » se produise dans les champs oculaires frontaux, le cortex latéral intrapariétal, ainsi que dans les colliculi supérieurs, et a même été suggéré d'opérer dans l'ensemble du réseau pariéto-frontal (Bisley & Goldberg, 2010; Boehnke & Munoz, 2008; Fecteau & Munoz, 2006; Goldberg, Bisley, Powell, & Gottlieb, 2006; Keller and McPeek, 2002; Liu, Yttri & Snyder, 2010; Song, Rafal & McPeek, 2011; Thompson & Bichot, 2005).

1.2.2. L'orientation attentionnelle

Afin de parcourir un champ visuel efficacement, une série de saccades est générée pour porter le centre de notre rétine, la fovéa, sur différentes parties de l'environnement. Bien que l'attention visuelle soit généralement associée à la fovéa, elle peut également être dissociée de la vision centrale. Cette différenciation sépare l'attention en deux catégories d'orientation : l'attention explicite et implicite. D'un côté, l'attention explicite accompagne les mouvements oculaires et est portée directement au centre de la vision ou aux alentours immédiats de la fovéa. D'un autre côté, l'attention implicite peut être orientée indépendamment des mouvements oculaires et peut être portée sur l'ensemble de la périphérie visuelle. L'attention implicite peut être modulée par un nombre de facteurs que l’on peut catégoriser en deux types d’orientation, exogène et endogène.

L’attention exogène, aussi appelée « bottom-up » est une forme d’orientation automatique et abrupte contrôlée par des facteurs externes, tel un éclair apparaissant soudainement dans la périphérie du champ visuel. L’attention endogène, appelée « top-down », est régulée par des facteurs internes, tels les buts et motivations de l’observateur, est contrôlée de façon volontaire, et est soutenue, c’est-à-dire qu’il est possible de la maintenir pendant un relativement long temps comparativement à l’attention exogène qui est transitoire (Nakayama & Mackeben, 1989). L’attention endogène peut être allouée volontairement vers un endroit de l’environnement (Posner, 1980), ou vers certaines caractéristiques physiques, telles la forme, la couleur ou la grosseur, afin de réduire la distraction causée par des stimuli qui ne concordent pas avec les buts de l’observateur, et qui sont en dehors du faisceau de l’attention (Yantis & Johnston, 1990). En termes neurophysiologiques, cela suggère que l’activité des circuits neuronaux se rapportant soit à l’endroit ou aux caractéristiques priorisés par les buts de l’observateur est facilitée (Mangun, 1995; Hillyard et al., 1998; Kastner et al., 1999). La conséquence directe d’une facilitation de l’attention endogène est démontrée dans les études rapportant une meilleure performance à des tâches de recherche visuelle où les caractéristiques des stimuli valides étaient différentes de celles des stimuli invalides, et étaient connues d’avance (Wolfe, 1994; Wolfe, Cave, & Franzel, 1989).

Plusieurs études tentent de démystifier si l’attention exogène et endogène sont deux parties complémentaires distinctes d’un système attentionnel unitaire ou s’ils sont deux systèmes complètement séparés (Funes, Lupiáñez, & Milliken, 2007; Godijn & Theeuwes, 2002;

Hopfinger & West, 2006). Cela dit, ces deux types d'attention divergent sur plusieurs différences fondamentales, notamment par leurs bases neurophysiologiques, leur décours temporel, et leurs effets sur les mouvements et les comportements. Des recherches de neurostimulation récentes ont soulevé des différences au niveau des structures neurophysiologiques entre l'attention endogène et exogène (Chica, Bartolomeo, & Lupiáñez, 2013; Coull, Frith, Büchel, & Nobre, 2000; Mayer, Dorflinger, Rao, & Seidenberg, 2004).

Un chevauchement dans l'activité des parties du cerveau impliquées lors de l'engagement de ces deux systèmes attentionnels a aussi été soulevé (Egeth & Yantis, 1997; Peleen, Heslenfeld, & Theeuwes, 2004). Cela expliquerait les différents types d'interactions observées dans les études comportementales impliquant ceux-ci. En effet, pour avoir une image complète de l'attention spatiale et visuelle, il est nécessaire de prendre en compte les effets d'interaction de ces deux systèmes attentionnels. Les interactions peuvent être de nature concurrente ou synergique (Berger, Henik, & Rafal, 2005; Jonikaitis & Deubel, 2011). Bien que plusieurs études aient démontré que l'attention exogène et endogène sont partiellement distincts sur le plan des substrats neuronaux, tous deux peuvent néanmoins contribuer à une interaction bénéfique menant à une meilleure perception visuelle quand ils sont engagés simultanément (Theeuwes, 1991). À l'inverse, ces deux systèmes peuvent entrer en compétition par rapport à l'orientation de l'attention si les entrées des stimuli « top-down » et « bottom-up » sont non concordantes (Godijn & Theeuwes, 2002). Cette interaction compétitive mène à une résolution où le gagnant emporte tout (« winner-takes-all ») c'est-à-dire que le comportement qui en découle est ultimement modulé par le système attentionnel qui présentait la plus grande valence prioritaire (Macaluso & Doricchi, 2013). Ce mécanisme du contrôle attentionnel a été démontré au niveau de la neurophysiologie, notamment dans des études sur des neurones dans la partie latérale intrapariétale (PLI) du cortex postérieur pariétal (CPP), et dans les champs oculaires frontaux (COF) (Bogler, Bode, & Haynes, 2011).

1.2.3. La modulation attentionnelle

L'indiçage attentionnel est des techniques les plus populaires permettant d'étudier de façon détaillée l'orientation de l'attention. Pour ce faire, l'indiçage attentionnel est utilisé pour moduler l'attention en exerçant une influence sur celle-ci. Michael Posner, un des fondateurs du domaine de la neuroscience cognitive de l'attention, a développé une tâche visuelle simple permettant la modulation de l'attention de façon exogène ou endogène (Posner, 1980; Posner & Cohen, 1984). La tâche, nommée « Posner cueing task » ou « Posner paradigm », consiste à répondre le plus rapidement à un stimulus visuel constituant une cible présentée dans un carré à gauche ou à droite d'une position centrale où l'observateur fixe son regard. Dépendant de l'instruction donnée à l'observateur, il est possible soit de mesurer la modulation endogène ou exogène de l'attention (Peleen, Heslenfeld, & Theeuwes, 2004). Notre projet de recherche a porté exclusivement sur l'indiçage exogène, puisqu'il est impliqué de façon plus prononcée dans la préparation motrice (Smith, Schenk, & Rorden, 2012). Néanmoins, l'indiçage endogène va être abordée dans certaines parties de la discussion, notamment dans les limites (partie 5.3.1) et les directions futures (partie 5.5.1).

D'un côté, l'indiçage endogène est un type d'indiçage qui, par l'entremise d'un stimulus central, force une modulation attentionnelle volontaire vers un autre espace périphérique de l'environnement visuel. Par exemple, si une flèche est présentée au milieu d'un espace visuel, un observateur serait incité à porter son attention vers la direction de la flèche. Dû à la nature symbolique et prédictive de la flèche, l'orientation de l'attention doit être faite de façon consciente, volontaire et contrôlée (Berger, Henik, & Rafal, 2005). Malgré le fait que certaines études suggèrent que la modulation attentionnelle est gérée exclusivement par des mécanismes attentionnels « bottom-up » (Hickey, McDonald, & Theeuwes, 2006; Theeuwes, 1994, 2004), les mécanismes attentionnels « top-down » semblent être impliquées de façon importante, surtout lors des tâches de recherche visuelle durant lesquelles des entrées « bottom-up » sous forme de distracteurs hautement saillants pouvaient être relativement ignorés (Theeuwes, 1991; Yantis & Jonides, 1990).

D'un autre côté, l'indiçage exogène est une technique de modulation automatique de l'attention et consiste généralement de stimuli visuels présentés abruptement, ou d'un changement soudain d'une caractéristique physique du stimulus, tel un changement de contraste ou de couleur. Dans la tâche classique de Posner, les bordures du carré dans lequel la cible allait apparaitre sous peu étaient momentanément élargies, présentant un changement visuel transitoire dans la périphérie de l'observateur. Cet indiçage exogène permettait donc de moduler l'attention automatiquement vers le carré avant même que la cible y apparaisse, menant notamment à un effet facilitateur en termes de temps de réaction des saccades et des bras puisque l'attention était déjà déployée à l'endroit indicé. Inversement, si l'indice incitait un déploiement de l'attention vers le carré à l'opposé de la cible, le temps de réaction des saccades et des bras vers la cible serait généralement ralenti (Kustov & Robinson, 1996).

La modulation attentionnelle exogène présente une influence sur la perception en priorisant certains endroits de l'environnement visuel, menant principalement à un traitement visuel amélioré (Carrasco, Giordano, & McElree, 2004, 2006; Carrasco & McElree, 2001) et une meilleure performance à des tâches de perception, telles qu'une discrimination de contraste

(Carrasco, Talgar, & Eckstein, 2000), de détection (Smith, Wolfgang, & Sinclair, 2004) et d’identification de stimuli (Talgar, Pelli, & Carrasco, 2004).

Les effets de la modulation de l’attention endogène et exogène sur les mouvements des yeux et des bras varient de façon importante dépendant de l’application des indices ou des conditions dans lesquelles ils sont présentés. Ils vont être explorés en détail dans la partie 1.4 de ce mémoire, intitulée « Interactions entre l’attention visuelle et les mouvements visuellement guidés ».

1.3. Mouvements visuellement guidés

Afin d'interagir avec notre environnement physique, nous effectuons régulièrement des mouvements visuellement guidés. Que ce soit pour ouvrir une poignée de porte ou pour préparer une tasse de thé, le déplacement volontaire de nos bras et mains vers un espace défini de notre environnement visuel représente un des mouvements les plus exécutés au courant de notre vie.

La génération des mouvements visuellement guidés est le résultat de l'interaction entre le système visuel, qui a comme entrée l'information visuelle sur la position des membres par rapport à une cible donnée, et les systèmes oculomoteur et moteur des membres supérieurs, qui ont comme sortie les commandes appropriées pour mener les mouvements des yeux et des bras à terme. L'interaction entre ces systèmes s'appelle la transformation visuomotrice.

Afin de planifier et d'exécuter adéquatement un mouvement de la portée du bras, plusieurs critères doivent être initialement établis, notamment la trajectoire et la position finale du mouvement, ainsi que des caractéristiques cinétiques et cinématiques du mouvement, telles la vitesse, la distance et la direction générale (Kalaska, 2009). Par la suite, une série de rotations des articulations des membres supérieurs sous-tendant aux mouvements de la main est calculée par le système moteur utilisant les critères initiaux pour établir un plan moteur, puis est ultimement mise en action par une activation coordonnée des muscles impliqués dans le mouvement final.

Les mouvements volontaires des bras, tout comme les mouvements des yeux, nécessitent une période de préparation de mouvement. En introduisant un délai entre l'instruction d'un mouvement et un signal de départ du mouvement, plusieurs études ont démontré que les temps de réaction des mouvements de la portée du bras étaient plus rapides quand le délai était plus long (Riehle & Requin, 1989; Rosenbaum, 1980), suggérant la présence d'une période de préparation de mouvement qui nécessite un certain décours temporel. Une série d'études neuronales investiguant cette période de délai avant l'exécution des mouvements ont soulevé une activité importante dans l'aire pré-motrice suggérant son implication dans la préparation du mouvement (Tanji and Evarts, 1976, Weinrich and Wise, 1982).

La planification et l'exécution des mouvements des bras sont des processus impliquant une interaction non-sérielle et distribuée dans plusieurs parties des cortex pariétaux et frontaux (Marconi et al., 2001). Bien qu'une grande partie du cerveau soit impliquée dans les fonctions motrices, le cortex moteur est primordialement associé aux mouvements volontaires. Celui-ci est composé de plusieurs aires, tels le cortex moteur primaire, l'aire pré-motrice et l'aire motrice supplémentaire. L'aire pré-motrice est particulièrement importante puisqu'elle est impliquée dans l'intégration sensorimotrice nécessaire dans les mouvements visuellement guidés, et est également activée lors de tâches d'attention visuelle.

L'aire pré-motrice joue un rôle important dans la sélection des mouvements. Lors d'une étude sur des primates non humains (Cisek & Kalaska, 2005), plusieurs cibles potentielles de mouvement étaient reflétées indépendamment dans l'activité de l'aire pré-motrice. Suite à la présentation d'un indice endogène identifiant la cible correcte, l'activité dans l'aire pré-motrice correspondant à celle-ci était augmentée tandis que l'activité qui correspondait à la cible incorrecte était inhibée. Le processus de sélection du mouvement, faisant partie de l'étape de planification du mouvement, a aussi été démontré chez les humains lors d'une étude utilisant la tomographie par émission de positrons (Deiber et al., 1997). Cette étude a comparé des mouvements nécessitant une sélection suite à la présentation d'indices endogènes avec des mouvements prédéfinis fixes et a démontré que l’activité liée à la sélection du mouvement était fortement localisée dans l’aire pré-motrice, ainsi que dans le cortex pariétal (Deiber et al., 1997; Grafton, Fagg, & Arbib, 1998).

L’activité reliée à la préparation des mouvements n’est pas limitée à ces deux aires, et a aussi été démontrée dans le cortex préfrontal (Deiber et al., 1990; Petrides, Alivisatos, Evans, & Meyer, 1993). L’implication du cortex préfrontal est souvent considérée comme un contrôle d’ordre supérieur des fonctions exécutives et de l’attention (Luppino & Rizzolatti, 2000). Une séparation a été proposée dans le circuit fronto-pariétal, suggérant que le cortex intrapariétal et le cortex frontal supérieur sont impliqués dans la préparation et le contrôle descendant de la sélection des stimuli, tandis que le cortex temporopariétal et frontal inférieur sont impliqués dans la détection des stimuli exogènes (Corbetta & Shulman, 2002).

Le cortex postérieur pariétal (CPP) joue un rôle primordial dans la transformation visuomotrice, surtout dans la génération des mouvements de la portée du bras. Ceci est démontré par des études lésionnelles impliquant le CPP, notamment dans des cas de lésions bilatérales menant à l’incapacité de générer des mouvements visuellement guidés précis. Une des premières études identifiant l’implication directe du CPP dans les mouvements de la portée du bras visuellement guidés a été menée par Rezső Bálint en 1909. Le syndrome nommé en son nom, le syndrome de Balint, est une triade de symptômes qui inclut notamment l’ataxie optique, une dysfonction des mouvements visuellement guidés. Les patients présentant ce symptôme présentent des difficultés d’exécution d’un mouvement du bras vers une cible visuelle, sans aucun autre déficit aux niveaux moteur, sensoriel, perceptuel, ou d’acuité visuelle, soulignant le CPP comme étant la structuré clé impliquée dans ce type de mouvements.

En plus d'être impliqué dans l'attention visuelle, le CPP est également impliqué dans les mouvements oculaires (Andersen, 1989). Une des sous-divisions importantes du lobule inférieur du CPP, la région latérale intrapariétale (LIP), est particulièrement importante dans la génération des saccades, tel que démontré dans une étude de stimulation électrique cérébrale chez le singe (Shibutani, Sakata, & Hyvärinen, 1984). De plus, les patients ayant une lésion au niveau du CPP démontrent des déficits dans la planification des saccades (Gaveau et al., 2008). Les efférences du LIP vers les COF et le colliculus supérieur, deux régions tout autant impliquées dans l'exécution des saccades, en font un pôle majeur pour l'activité saccadique.

Une autre structure indispensable aux mouvements saccadiques est le colliculus supérieur. Le colliculus supérieur (CS) est une structure laminée à plusieurs couches de cellules présentant des différences anatomiques et fonctionnelles. Par exemple, les couches supérieures semblent répondre majoritairement à des entrées sensorielles directement de la rétine, et indirectement du cortex visuel, tandis que les couches plus profondes semblent avoir des fonctions sensorielles et motrices, et contribuent de façon importante à la génération des saccades. Le CS est la structure principale dans l'exécution des saccades réflexives et volontaires, dû à la présence de neurones d'accumulation (« build-up neurons ») et de décharge (« burst neurons ») dans celui-ci (Dorris et al., 1997; Everling, Dorris, Klein, & Munoz, 1999; Munoz and Wurtz, 1993, 1995).

Les efférences et afférences du CS à des structures corticales clés affectant différents aspects de l'attention visuelle et des caractéristiques des saccades en fait une structure primordiale dans la préparation des saccades. Par exemple, les champs oculaires frontaux sont une des régions du cortex frontal qui présentent des connexions afférentes vers le CS et contiennent des neurones répondant non seulement à des stimulations visuelles, mais aussi à la préparation des saccades

(Bruce & Goldberg, 1985; Khayat, Pooresmaeili, & Roelfsema, 2009; Schall & Thompson, 1999). De plus, les champs oculaires frontaux ont été liés à un déplacement attentionnel (Kim & Cave, 1995; Schall & Thompson, 1999), particulièrement durant une tâche de recherche visuelle (Bichot et al., 1999; Monosov et al, 2008; Murthy et al., 2001).

Bien que les neurones dans les couches intermédiaires et profondes du CS répondent de façon majoritaire durant l'exécution des saccades, une certaine sous-population de ces neurones a été démontrée comme étant active lors des mouvements des bras, suggérant leur implication dans le contrôle moteur des membres supérieurs (Song & McPeek, 2014; Werner, 1993; Werner, Dannenberg, & Hoffman, 1997; Werner, Hoffman, & Dannenberg, 1997). La présence des neurones répondant aux mouvements des bras aux côtés des neurones répondant aux saccades pourrait potentiellement expliquer une activation parallèle de ces deux systèmes moteurs distincts, et se traduirait même par une potentialisation des temps de réaction de ces mouvements (Snyder, Calton, Dickinson, & Lawrence, 2002). En effet, un changement dans la séquence principale – la relation entre l'amplitude et la pointe de la vélocité – des saccades était démontré quand celles-ci étaient combinées avec des mouvements de la portée du bras (Snyder, Calton, Dickinson, & Lawrence, 2002).

1.4. Interactions entre l’attention visuelle et les mouvements visuellement guidés

Il est possible de mesurer les effets de la modulation attentionnelle induite par les indices endogènes et exogènes sur différentes caractéristiques des mouvements des yeux. Un des effets rapportés par l’utilisation de l’indiçage attentionnel, surtout dans le cas des indices exogènes, est une baisse du temps de réaction d’un mouvement vers un stimulus indicé, en comparaison à un stimulus non-indicé. Il a été démontré que la présentation d’un indice à la position d’une cible avant son apparition permettait d’améliorer la performance à une tâche de temps de réaction motrice. Cette facilitation du temps de réaction dépend cependant de l’intervalle de temps entre l’indice et la cible (Klein, 2000; Milliken et al., 2003). En effet, si l’intervalle de temps entre ces deux évènements est plus court que 30 ms (Corbetta & Schulman, 2002) ou plus long que 220 ms (Li et al., 2017), la facilitation potentielle permise par l’indice attentionnel ne semble plus faire effet sur les caractéristiques temporelles des mouvements. Qui plus est, un ralentissement du temps de réaction est même rapporté suite à la présentation d’un indice attentionnel aux alentours de 300 à 500 ms, allant jusqu’à 1000 ms, avant la présentation d’une cible (Briand, Larrison, & Sereno, 2000; Hayward & Ristic, 2013; Posner and Cohen, 1984). Ce phénomène, nommé inhibition du retour, a été suggéré comme étant un mécanisme de suppression du traitement des stimuli qui ont été récemment parcourus, ayant pour but de favoriser l’exploration d’autres endroits de l’environnement visuel (Itti & Koch, 2001; Klein, 1988). L’inhibition du retour a initialement été soulignée dans le contexte des saccades et du système oculomoteur, mais ses effets peuvent aussi être perçus lors des mouvements de la main, par exemple lors des tâches de temps de réaction par appui d’une touche (Briand, Larrison, & Sereno, 2000; Hunt & Kingstone, 2003; Taylor & Klein, 2000). Les effets de l’inhibition du retour sur les mouvements de la main sont généralement similaires à ceux vus dans les saccades, et se résument à un ralentissement du temps de réaction vers des cibles précédées de cibles induisant l'inhibition du retour comparativement aux indices présentés hors du décours temporel de celui-ci (Briand, Larrison, & Sereno, 2000; Cowper-Smith & Westwood, 2013; Taylor & Klein, 2000). Cependant, une certaine nuance a été soulignée dans la distribution temporelle de l'effet de l'inhibition du retour entre les deux effecteurs en question. En effet, l'intervalle de temps durant lequel l'inhibition du retour est active semble être plus petit lors des saccades (MacInnes, Krüger, & Hunt, 2015) par rapport aux mouvements de la main, et ce, d'environ une seconde (Samuel & Kat, 2003).

Les mouvements saccadiques sont affectés par une facilitation temporelle suite à la présentation d'un stimulus exogène présenté à l'endroit d'une cible, peu avant celle-ci (entre 20 et 200 ms) (Fecteau et al., 2004; Fecteau & Munoz, 2005). De plus, nous avons rapporté un phénomène se rapportant aux temps de réactions saccadiques indicés sur une étendue spatiale (Section 3. Article 1). Durant une tâche attentionnelle où des indices étaient présentés à plusieurs endroits de l'environnement visuel, les mouvements saccadiques produits vers une cible étaient globalement affectés par la facilitation attentionnelle, mais la diminution du temps de réaction s'estompait quand l'indice était présenté de plus en plus loin de la cible (Khan et al., 2010, 2016). Il a été démontré que cet effet n'est pas toujours présent et que, sous certaines conditions, la présentation des indices attentionnels avait l'effet contraire, c'est-à-dire un ralentissement du temps de réaction des saccades (Bompas & Sumner, 2009). En plus d'affecter le temps de réaction des saccades et de produire une facilitation temporelle, l'indiçage attentionnel semble aussi avoir un effet considérable sur les caractéristiques spatiales des saccades, tel que leurs amplitudes et trajectoires (Cavegn, 1996; Crawford & Muller, 1992; Godijn & Theeuwes, 2002).

Les effets de l'indiçage attentionnel ont aussi été démontrés dans les mouvements de la portée du bras, sur différentes caractéristiques temporelles et spatiales (Briand et al., 2000; Chang & Ro, 2003; Hilchey, Klein, & Satel, 2014). Généralement, les mouvements du bras sont influencés par les indices exogènes de façon inhibitrice. Un exemple rapporté dans plusieurs études est l'effet de l'indiçage attentionnel sur la trajectoire d'un mouvement de la portée du bras (Soechting & Lacquaniti, 1983; Georgopoulos, Kalaska, & Massey, 1981; Welsh, Elliott, & Weeks, 1999; Howard & Tipper, 1997; Tipper, Howard, & Jackson, 1997). La présentation d'un indice exogène lors d'un mouvement de pointage du doigt ou de la portée du bras mènerait à une déviation de la trajectoire du mouvement, s'éloignant ou se rapprochant de l'indice. De plus, cette déviation causerait un ralentissement du temps d'exécution du mouvement dû à la correction nécessaire pour terminer la motion vers une cible. Une interaction à deux sens a été démontrée entre les systèmes attentionnels et moteurs, ce qui signifie que les positions et les mouvements du bras (Festman, Adam, Pratt, & Fischer, 2013; Perry, Sergio, Crawford, & Fallah, 2015) et des saccades (Belopolsky & Theeuwes, 2009) influencent aussi l'orientation et la modulation de l'attention visuelle.

Lors des mouvements combinés de la portée du bras et des saccades, l'œil a été démontré comme l'effecteur principal dans le contrôle du déploiement de l'attention, même si les mouvements des yeux et des bras étaient produits vers des cibles différentes (Khan, Song, & McPeek, 2011). L'addition du mouvement du bras lors des saccades ne semble pas affecter l'allocation de l'attention (Khan et al., 2011) et a même été suggéré de produire un déploiement attentionnel parallèle pour le bras, séparé de celui de l'œil (Jonikaitis & Deubel, 2011). Plusieurs études neurophysiologiques ont démontré que les systèmes saccadiques et des mouvements de la portée du bras étaient distincts lors des premières étapes de la préparation motrice (Calton, Dickinson,

& Snyder, 2002; Dickinson, Calton, & Snyder, 2003; Snyder, Batista, & Andersen, 1997). Inversement, des études psychophysiques et d'imagerie fonctionnelle suggèrent plutôt qu'un seul système unitaire est impliqué dans la sélection des mouvements des yeux et des bras, théorie qui prend source dans le chevauchement des systèmes oculomoteurs et moteurs de la portée du bras, surtout dans les cortex pariétal et frontal (Bekkering, Adam, van den Aarssen, Kingma, & Whiting, 1995; Beurze, de Lange, Toni, & Medendorp, 2009; Levy, Schluppeck, Heeger, & Glimcher, 2007; Neggers & Bekkering, 2000; Song & McPeek, 2009).

Dans leur ensemble, les résultats des études sur les effets de l'indiçage attentionnel soulignent des effets similaires sur les saccades et les mouvements de la portée du bras, mais présentent certaines différences lors de conditions expérimentales spécifiques. Cela dénote une possibilité de plusieurs mécanismes attentionnels impliqués en parallèle lors de la préparation des mouvements des yeux et des bras. Dans la section « Discussion » de ce mémoire, nous proposerons un modèle attentionnel de la préparation motrice à deux étapes appuyé par notre recherche, ainsi que par la littérature courante.

2. Objectifs de recherche

Les mécanismes de l'attention visuelle fonctionnent en sélectionnant et accentuant un espace ou un objet parmi d'autres pour prioriser le traitement visuel. Nous présumons que cette sélection attentionnelle mène ultimement à une action telle qu'un mouvement des yeux (une saccade) pour placer l'objet au centre de la vision en vue d'un traitement additionnel qui conduit à une meilleure reconnaissance de celui-ci, à un mouvement de la portée du bras pour pouvoir saisir l'objet, ou aux mouvements conjoints des yeux et du bras pour pouvoir saisir l'objet avec une précision accrue. Or, les mécanismes de sélection attentionnelle menant à une planification des mouvements des yeux ou du bras ne sont pas encore complètement connus. D'une part, la sélection attentionnelle a été proposée d'agir lors d'un niveau de traitement précoce, avant même que la planification de mouvement se produise. Cela impliquerait qu'un mécanisme attentionnel commun serait employé pour planifier les mouvements des yeux et du bras. D'autre part, la sélection attentionnelle pourrait se produire à un niveau de traitement sensorimoteur ultérieur, c'est-à-dire après ou durant la planification du mouvement, et par conséquent être spécifique à l'effecteur (yeux ou bras) utilisé. Notre projet de recherche a comme objectif à distinguer entre ces deux hypothèses en utilisant un paradigme de double-tâche combinant la réalisation d'une tâche visuo-attentionnelle à la production d'un mouvement des yeux ou du bras. Nous avons mesuré les temps de réaction et les amplitudes des saccades et des mouvements de la portée du bras, combinés ou seuls, pour quantifier et qualifier l'effet de l'attention visuelle exogène sur la planification de ceux-ci. De plus, nous avons utilisé une tâche d'adaptation visuomotrice qui séparait le mouvement planifié de l'objectif du mouvement, ce qui nous a permis de dissocier le mouvement perçu du mouvement réel. En somme, nous voulons discerner le ou les niveaux de traitement attentionnel durant lesquels se produit la planification des saccades et de la portée du bras. Ce projet de recherche approfondit la compréhension des mécanismes opérationnels de l’attention exogène sur les mouvements des yeux et des mains, ainsi que de l’interaction entre les systèmes sensoriels et moteurs, menant à une meilleure compréhension des fonctions fondamentales du cerveau.

3. Article 1

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Contrasting effects of exogenous cueing on saccades and reaches

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3.1. Abstract

Previous studies have shown that eye and arm movements tend to be intrinsically coupled in their behavior. There is however no consensus on whether planning of eye and arm movements is based on shared or independent representations. One way to gain insight into these processes is to compare how exogenous attentional modulation influences the temporal and spatial characteristics of the eye and the arm during single or combined movements. Thirteen participants (M = 22.8, SD = 1.5) performed single or combined movements to an eccentric target. A behaviourally irrelevant cue flashed just before the target at different locations. There was no effect of the cue on the saccade or reach amplitudes, whether they were performed alone or together. We found no differences in overall reaction times between single and combined movements. With respect to the effect of the cue, both saccades and reaches followed a similar pattern with the shortest reaction times when the cue was closest to the target, which we propose reflects effector-independent processes. Compared to when no cue was presented before the target, saccade reaction times were generally inhibited by the irrelevant cue with increasing cue-target distance. In contrast, reach reaction times showed strong facilitation at the target location and less facilitation at farther distances. We propose that this reflects the presence of effector-dependent processes. The similarities and differences in reaction times between the saccades and reaches are consistent with effector-dependent and -independent processes working in parallel.

Keywords: exogenous attention, eye movements, reach movements, hand-eye coordination

3.2. Introduction

In our daily life, we are constantly making coordinated eye and arm movements, e.g. pointing to an object that we are looking at. Numerous studies have demonstrated that simultaneous eye and arm movements are coordinated both spatially and temporally, suggesting a shared representation for planning movements of the eyes and the arms (Carey, 2000; Crawford, Medendorp & Marotta, 2004; Dean, Marti, Tsui, Rinzel, & Pesaran, 2011; Frens & Erkelens, 1991; Fischer & Rogal, 1986; Fisk & Goodale, 1985; Gribble, Everling, Ford, & Mattar, 2002; Herman, Herman, & Maulucci, 1981; Jeannerod, 1988; Land & Hayhoe, 2001; Neggers & Bekkering, 2002; Prablanc, Echallier, Komilis & Jeannerod, 1979; Sailer, Eggert, Ditterich & Straube, 2000; Song & McPeek, 2009). The shared representation implies that motor commands for the eyes can also influence the arm, and vice versa (Lee, Poizner, Corcos & Henriques, 2014; Sailer, Eggert, Ditterich, & Straube, 2002a; Sailer, Eggert, & Straube, 2002b; Soechting, Engel & Flanders, 2001; Vazquez, Federici & Pesaran, 2017). There are other studies that show little or no correlations between the timings (onsets) of the eye and arm movements, suggesting independent representations for the different effectors (Guitton & Volle, 1987; Tweed, Glenn, & Vilis, 1995; Vercher, Magenes, Prablanc, & Gauthier, 1994). Studies utilizing decoupled eye and arm movements also argue for independent representations of the effectors, with decoupling occurring in tasks where targets for the two effectors are spatially separated (Jonikaitis & Deubel, 2011), or when expectations are violated for learned visuomotor behaviors (Foerster, 2016). Moreover, combined eye and hand movements appear to be planned differently compared to single-effector movements, implying perhaps an additional and separate representation for combined movements (Lee et al., 2014; Nissens & Fiehler, 2018; Sailer et al., 2002a). In sum, the underlying processes for eye and arm coupling still remain poorly understood.

One way to gain insight into these processes is to compare how attentional modulation influences the temporal and spatial characteristics of eye, arm or combined eye-arm movements. Attention plays a major role in movement planning and can be either disruptive or beneficial (Gray, 2011; Wulf & Prinz, 2001). Exogenous attentional stimuli (e.g. a flash of lightning) have been shown to influence movement parameters for the eye (Fecteau, Bell, & Munoz, 2004; Khan, Blohm, McPeek, & Lefevre, 2009; Khan, Heinen, & McPeek, 2010; Khan, Munoz, Takahashi, Blohm, & McPeek, 2016; Maylor & Hockey, 1985; Posner & Cohen, 1984; Walker, Kentridge, & Findlay, 1995). Exogenous stimuli also influence arm movements in a specific and consistent manner (Galletti et al., 2010; Riggio & Kirsner, 1997). Moreover, exogenous attentional effects were also observed in cases where saccades and reaches were investigated separately (Briand, Larrison, & Sereno, 2000) or in combination with each other (Hilchey, Klein, & Satel, 2014). The effect of the exogenous stimuli on movement characteristics (timing and amplitude) can be exploited to test for independent versus shared movement planning representations. For instance, when a behaviourally irrelevant exogenous cue is presented at the same location slightly before the target (20 ms to 200 ms), saccadic reaction times are decreased (Fecteau et al., 2004; Fecteau & Munoz, 2005; Khan et al., 2010, 2016). This decrease in reaction times to cued targets is commonly known as attentional facilitation or capture (Jonides & Irwin, 1981; Klein, 2000; Theeuwes, Kramer, Hahn, Irwin, & Zelinsky, 1999). In contrast, there are also conditions under which cues tend to increase saccade reaction times (Bompas & Sumner, 2009). We have previously shown that behaviourally irrelevant cues flashed at various locations just before a target resulted in a specific pattern of saccade reaction times: a gradual decrease in RT as the cue approached the target (Khan et al., 2010, 2016).

In addition to the well documented effects of attention on RT, there is also evidence for attentional capture effects on saccade amplitudes and trajectory (Cavegn, 1996; Crawford & Muller, 1992; Godijn & Theeuwes, 2002). Fewer studies have demonstrated exogenous attentional effects on reach movement parameters (Briand et al., 2000; Chang & Ro, 2003; Hilchey, Klein, & Satel, 2014). In summary, it has been shown that a cue preceding the target (presented during the early stages of movement planning) influences saccade and reach movement parameters in a specific manner. What remains unknown, is whether the effect on saccades and reach movements are the same even when the movements are performed separately. To our knowledge, there have not yet been any studies using a pre-cue to compare the influence of irrelevant attentional cues on eye and arm movements performed either together (requiring hand-eye coordination), or separately. This comparison would aid in understanding the underlying independent or dependent mechanisms for eye and arm planning.

Here, we presented exogenous cues at different locations just prior to the target (Khan et al., 2010; 2016), to investigate how attentional mechanisms affect eye and hand reaction times and amplitudes when performed separately or together. On the one hand, if movement planning of the eyes or the hand are based on a shared representation of the movement target's location relative to the visual environment, we should observe similar spatial and temporal attentional cue effects on both effector movements. On the other hand, if movement planning of the effectors are based on independent representations, we should observe different patterns of reaction times and amplitudes in response to the exogenous cue. Additionally, different patterns during combined movements compared to single effector movements would suggest a separate representation for combined movements.

3.3. Materials and Methods

3.3.1. Participants

We recruited 13 participants (ages: M = 22.79, SD = 1.45, 10 females) to participate in the experiment. All participants except one (author AM) were naive to the goal of the experiment. The experimental protocol was preapproved by the University of Montreal Health Research Ethics Committee (CERES). All participants had normal or corrected to normal vision and were right-handed.

3.3.2. Apparatus

Participants were seated in a well-lit room at a distance of 35 cm from a 24-inch VIEWPixx 3D monitor (2.73 min arc/pixel, VPixx Technologies, Montreal, Canada) with a refresh rate of 60 Hz. The monitor background was dark gray (mean luminance of 2.07 cd/m2). Stimuli were presented using Eyelink Experiment Builder software (SR Research, Mississauga, Canada). Eye movement data were recorded from the participant's right eye at 1000 Hz using an EyeLink 1000 Plus Tower Mount (SR Research), an infrared video-based eye tracker. A vertically adjustable chinrest and a forehead rest maintained the viewing distance and stabilized the head for accurate eye tracking. A half-reflecting mirror was fixed in front of the participant's face at a 37.5° to 47.5° angle (**Fig. 1A**). The focus of the lens of the camera and the angle of the mirror were adjusted so that a clear and unobstructed corneal reflection and pupil image could be obtained for each participant.

Hand movement data were collected with a 3D Investigator motion tracking system, First Principles motion capture software and markers (Northern Digital Inc., Waterloo, Canada) recording at 200 Hz with a 0.01 mm spatial resolution. The 3D motion tracking system was factory calibrated and did not require additional calibration before or during testing to collect positional data. The markers were fixed with clear tape to the participant's right index finger and outer edge of the palm. Two markers were used to minimize spatial data loss in case one of the two was obstructed during testing.

3.3.3. Procedure

Participants performed the experiment in three pairing conditions, 1) only eye movements, 2) only hand movements and 3) combined eye and hand movements. There were 12 blocks of each of the three movement conditions, half of which were movements towards the right, and the other half to the left, in a completely randomized order. Within each block, only one movement condition, and only one movement direction were used to minimize delays and errors associated with task-switching (see Kiesel et al., 2010, for a review). During testing, participants were instructed to keep their right finger slightly below the fixation point to allow an unobstructed view of the target.

Before each block of trials, gaze position was calibrated and validated with a standard five-point fixation sequence. The trial sequence (**Fig. 1B**) was as follows: participants fixated on a white checkered cross subtending 1° of visual angle, presented at 5° to either the left or right from the center of the screen, for an interval of 700–1300 ms (randomly selected from a uniform distribution of 100 ms intervals). After fixation, a cue (light gray square of 0.5° diameter) was presented for 17 ms at 1 of 7 possible positions at -15°, -10°, -5°, 0°, 5°, 10°, 15° relative to the center of the screen, offset vertically by 5° above the horizontal meridian (**Fig. 1C**). After the cue disappeared, a dark gray blank screen was presented for 33 ms. Next, a target (white square of 0.5° diameter) appeared at the mirror position from the fixation point (i.e. at -5° if the latter appeared at 5° or vice versa). The stimulus-onset asynchrony (SOA), defined as the time period between the onset of the cue and the onset of the target, was 50 ms. Participants were instructed to make a movement from the fixation point to the target, as soon as the target appeared. The inter-trial interval was 700 ms, during which there was a dark gray blank screen. The location of the cue was randomized within each block. As a control, there was also a no-cue condition in which the cue was not presented, with otherwise the same timings.

Participants completed a minimum of 36 blocks (3 pairing conditions × 2 directions × 6 repetitions) with 56 trials each (8 possible cue positions × 7 repetitions), for a total of 2,016 trials per participant. A block was repeated if a considerable amount of eye tracking and/or motion tracking data was missing due to tracking problems, such as an obstructed marker. Due to the repetition, average number of blocks per participant was 38.15, SD = 7.34. There was a 1-2 minute break between the blocks. Participants performed the entire experiment in one session lasting approximately 3 hours.

3.3.4. Pre-processing

A total of 27,776 trials were collected. All data were analyzed off-line using custom-written software on MATLAB 9.1 (The MathWorks, Inc., Natick, MA, United States). Eye velocity was obtained through digital differentiation of the eye position signals and filtered to reduce noise (2-pole Butterworth filter, cut-off = 110 Hz). Saccade onsets and offsets were detected using acceleration and decceleration thresholds of $1000°/s^2$. Reach onsets and offsets were determined using a velocity threshold of 1 cm/s. (Luciw, Jarocka & Edin, 2014; Mason, Gomez & Ebner, 2001; Messier & Kalaska, 1999). Two measures of interest were assessed for the movements: reaction time and amplitude. Reaction time was defined as the time interval between the appearance of the target and the start of the effector's movement. Amplitudes were calculated by subtracting the horizontal end position value from the start position value; only horizontal position values were of interest.

To account for the overall differences in RTs and to investigate specifically the effect of cue position, we calculated normalized RTs (Khan et al., 2010). For each cue position and each participant, we subtracted each RT from the mean of the no-cue trials within each single and combined effector conditions. Saccades reaction times (SRTs) were normalized by subtracting the mean SRT of the participants' cued trials from their respective no-cue trial means. Normalized reach reaction times (RRTs) and amplitudes were calculated in the same way.

Individual trials were manually removed when any of the following occurred: a blink before or during a saccade, if the participant moved either the hand or the eyes or blinked within 100 ms of the cue, if saccade amplitude was less than 5° (half of the target amplitude), if data from both markers were missing simultaneously, if a saccade occurred during a reach-only trial, or if one of the two movements did not take place during a combined saccade and reach condition. Across all participants and conditions, we removed all trials with saccade or reach onsets under 80 ms or over 500 ms (Bartz, 1962; Fischer & Ramsperger, 1984; Smeets, Hayhoe & Ballard, 1996; White, Eason & Bartlett, 1962). These criteria removed 5,977 trials (21.52%). Next, trials were excluded if either saccade or reach start positions fell outside of an elliptic filter. The two centers of the ellipses, one for each direction, was defined as the mean starting position of the effectors within each participant, and the diameter of the ellipses were defined by 5 and 4 standard deviations for saccade and reach starting positions respectively. This resulted in a rejection of 1047 trials (4.8%). There remained 20,529 trials (74.27% of collected trials). Preliminary sorting and filtering of data was done with Matlab 9.1 (The MathWorks, Inc., Natick, MA, United States).

3.3.5. Statistical analysis

Repeated-measures three-way ANOVAs were conducted with the following independent variables: effector (saccade and reach), pairing condition (single and combined) and cue position (position 1 to 7). In the case of a significant interaction, this was followed up with repeated-measures two-way ANOVAs for each pairing condition, with effector and cue position as the independent variables. Significant effects were followed up with t-tests if there were only 2 levels, or a one-way ANOVAs for more than 2 levels. Greenhouse-Geisser corrected values are reported when Mauchly's test revealed that the sphericity assumption was violated. Further, one-sample t-tests comparing the baseline-normalized values to 0 (no-cue trials) were used to demonstrate any inhibition or facilitation related to the cue at each position. All p-values were Bonferroni corrected for multiple comparisons. To assess the relationship between reach times and saccade times, we used a general linear model assuming an independent covariance matrix. In addition to the independent participant variable, within-subject independent variables included cue position, and pairing condition (single vs. combined). The dependent variable was the average saccadic reaction time for each participant, for each cue position, for each pairing condition. Predictors were reach response times, and condition. Computations were carried out with SPSS Statistics, version 24 (IBM SPSS, Chicago, IL, United States).

3.4. Results

3.4.1. Single subject overall results

The RTs for a typical subject are plotted in **Figure 2** for saccades (gray lines) and reaches (black lines) for single effector (**Fig. 2A**) and combined effector (**Fig. 2B**) pairing conditions. RTs are plotted as a function of cue position (1-7). In addition, the baseline RTs are also plotted for the trials in which no cue was presented. A number of observations can be made. First, it can be seen that SRTs were overall lower than RRTs, as expected. Second, it appears that SRTs and RRTs might change depending when they were performed by themselves (single condition) compared to when the two movements are combined. Third, cued SRTs tend to be the same or longer compared to the no-cue trials, whereas cued RRTs are sometimes faster than the un-cued trials. Finally, there appears to be a systematic effect of cue position. We quantified these observations across all participants in the next section.

3.4.2. Overall reaction times of effector and pairing conditions

We first investigated overall reaction times. As can be seen in **Figure 3**, SRTs were shorter overall than RRTs. This was confirmed with a two-way ANOVA with effector and pairing condition as factors, which revealed a main effect of effector (F(1,12) = 6.894, p = .022, ηp2 = .365; overall SRTs: M = 162.53, SD = 20.98; overall RRTs: M = 178.15, SD = 29.35). Although there is a slight tendency towards increased SRTs and decreased RRTs in the combined condition, relative to the single condition, as has been previously reported (Sailer et al., 2002a), we did not find a main effect of pairing condition (F(1,12) = .696, p = .421, ηp2 = .055) nor an interaction between factors (F(1,12) = 3.994, p = .069, ηp2 = .250).

3.4.3. The effect of cue position, effector and pairing of effectors on reaction times

Next, we investigated the effect of cue position across the different conditions on reaction times. In **Figure 4**, we plotted the normalized mean RTs of saccades and reaches in single and combined conditions at different cue positions across all participants. The three-way ANOVA revealed a significant three-way interaction effect (F(6,72) = 3.1, p = .009, ηp2 = .205). To understand this interaction, we followed up with two-way ANOVAs separately for the single and combined conditions with effector and cue position (7 positions) as factors. In the single condition (**Fig. 4A**) two-way ANOVA, there was a main effect of effector (F(1,12) = 44.018, p > .001, ηp2 = .786). There was also a main effect of cue position (F(6,72) = 25.147, p > .001, ηp2 = .677), affecting both SRTs and RRTs. The interaction effect was not significant (p>0.05), indicating similar changes in RTs as a function of cue position for both saccades and reaches. To investigate patterns of facilitation and inhibition, we performed one-sample t-tests separately for saccades and reaches. Detailed results are reported in Table 1. For saccades: SRTs at positions 1, 2 (opposite hemifield from target) 3 (fixation position) and 7 (farther away from target) were significantly slower than the no-cue trials (position 1: t(12) = 5.403, p = .001; position 2: t(12) = 5.546, p > .001; position 3: t(12) = 3.825, p = .017; position 7: t(12) = 3.805, p = .018). These results demonstrated that the cue caused significant inhibition of SRTs at these locations. The cue did not cause any facilitation of SRTs, relative to no-cue, even when it was presented close to or at the target location. For reaches: we found the opposite pattern, with positions 4 to 7 (close, or at the target location) showing significant facilitation compared to no-cue (position 4: t(12) = -4.329, p = .007; position 5: t(12) = -6.776, p = .000; position 6: t(12) = -6.031, p = .000; position 7: t(12) = -3.329, p = .042), and no inhibition for cues that were presented farther from the target.

The pattern of results was similar for the combined effector condition (**Fig. 4B**). A two-way ANOVA revealed a main effect of effector (F(1,12) = 39.545, p > .001, ηp2 = .767), a main effect of cue position (F(6,72) = 8.303, p > .001, ηp2 = .409), and an interaction between the two (F(6,72) = 4.553, p = .001, ηp2 = .275). To tease apart the interaction, we followed up with two one-way ANOVAs, which revealed that combined reaches varied significantly with cue position (F(6,72) = 11.848, p > .001, ηp2 = .497), while combined saccades did not (although there was a trend, F(6,72) = 2.517, p = .071). One sample t-tests at each cue position showed similar results for the combined condition as for the single condition. For SRTs that were performed at the same time as reaches, there were significant delays at positions 1, 2 (opposite hemifield), 3 (fixation) and 6 (farther from target), compared to no-cue (position 1: t(12) = 4.271, p = .008; position 2: t(12) = 3.799, p = .018; position 3: t(12) = 3.329, p = .042; position 6: t(12) = 4.325, p = .007). In contrast, for RRTs that were performed at the same time as saccades, there was significant facilitation at positions 4 and 5 (close or at the target location), compared to no-cue (position 4: t(12) = -4.537, p = .005; position 5: t(12) = -4.147, p = .009). In summary, saccades in both the single and combined conditions generally demonstrated an inhibition when the cue was presented far from the target's position, in either direction, but no facilitation when the cue was presented at the target location. In contrast, reaches were generally facilitated by the cue when it appeared close to or at the target position, with no inhibition for cues that were presented far from the target's position. There are also similarities in the changes in RTs as a function of cue position for saccades and reaches; the fastest normalized RT invariably occurred when the cue was presented at the target position, and the slowest normalized RT occurred when the cue was presented in the opposite hemifield from the target.

We directly compared the pattern of normalized RTs for saccades and reaches. In **Figure 5** we have plotted normalized SRTs against normalized RRTs (7 data points per participant = 7 cue positions) for the single (open squares) and the combined (filled squares). Using generalized linear models to assess the relationship between SRT and RRTs, we found a significant relationship between SRTs and RRTs (χ^2(1, N=12) = 7.5, p=.006). The relationship between SRT and RRT appears to be somewhat stronger in the combined-effector condition (Pearson's r = .490, p < .001), compared to the single-effector condition (Pearson's r = .337, p = .001), but these linear models were not significantly different (χ^2(1, N=12) = 0.3, p=.584). These findings demonstrate that the changes in normalized RTs in response to the cue were very similar for the two effectors.

3.4.4. Overall amplitudes of effector and pairing conditions

For saccade and reach amplitude, we first analyzed overall amplitudes. As can be seen in **Figure 6**, saccade amplitudes were overall longer than reach amplitudes. This was confirmed with a two-way ANOVA with effector and pairing condition as factors, which revealed a main effect of effector ($F(1,12) = 5.564$, $p = .036$, $\eta_p^2 = .317$; overall saccade amplitudes: M = 10.00, SD = .53; overall reach amplitudes: M = 9.33, SD = .99) and a significant interaction between the two factors ($F(1,12) = 5.129$, $p = .043$, $\eta_p^2 = .299$). To tease apart this interaction, we followed up with t-tests, which revealed a significant difference between single and combined saccades ($t(12) = 2.635$, $p = .022$; single saccades: M = 10.06, SD = .55; saccades combined: M = 9.94, SD = .53), but not between single and combined reaches ($t(12) = 1.815$, $p = .095$; single reaches: M = 9.18, SD = 1.14; reaches combined: M = 9.48, SD = .84).

3.4.5. The effect of cue position, effector, and pairing of effectors on movement amplitudes

We investigated whether amplitudes changed as a function of cue position. To investigate the specific influence of the cue, we normalized saccade and reach amplitudes as described in the Methods. Normalized amplitudes for the single (**Fig. 7A**) and combined (**Fig. 7B**) conditions are plotted. As with RTs, we investigated the effects of cue position and condition on movement amplitudes. We conducted a three-way ANOVA with the same independent variables and levels as in the RT analysis, with cue position (7), effector (2) and pairing conditions (2). This analysis revealed a significant three-way interaction effect ($F(6,72) = 4.097$, $p = .001$, $\eta_p^2 = .255$).

Therefore, we conducted two-way repeated-measures ANOVAs on each pairing condition independently. We found no significant main effects for either the single or combined ANOVAs, but there was a significant interaction effect between effector (saccade or reach) and cue position in the single effector ANOVA ($F(6,72) = 3.32$, $p = .042$, $\eta_p^2 = .217$). We followed up this interaction effect with two one-way ANOVAs for each effector, to determine if the effect of cue varied the amplitude in the single reaches or the single saccades condition. However, neither ANOVA revealed a significant effect of cue (single saccades: $F(6,72) = 3.035$, $p = .074$, $\eta_p^2 = .202$; single reaches, $F(6,72) = 2.006$, $p = .131$, $\eta_p^2 = .143$). In summary, cue position did not reliably affect amplitudes in the single or combined conditions for saccades or reaches.

3.5. Discussion

We investigated how the reorienting of exogenous attention affects eye and arm movements when they are performed separately or together. While saccade amplitudes were larger than reach amplitudes, we did not find any effect of cue position on amplitude. For reaction times, we found no overall differences when movements were performed together compared to by themselves, regardless of cue presence. In addition, the pattern of relative changes in RTs as a function of cue position varied in a similar way across reaches and saccades. However, we also found differences in the patterns of facilitation and inhibition for saccades and reaches; reaches were facilitated when the cue was close to the target and were not inhibited by the cue at any position compared to the condition when a cue was not presented before the target. In contrast, saccades were not facilitated when the cue was presented close to the target, but were inhibited when the cue was presented away from the target in both directions. Taken together, our findings point towards a combination of effector-independent and -dependent processes in the initiation of goal-directed movements.

We did not find any differences in the overall RTs for either saccades or reaches when they were combined as opposed to when they moved alone; though we observed a slight tendency towards an increase in SRTs and a decrease in RRTs during combined movements (**Fig. 3**). Previous studies show a broad spectrum of changes for combined movements to the same target compared to when the effector moves independently, from no changes to either effector such as in our study (Bekkering, Adam, Aarssen, Kingma, Huson, & Whiting, 1994; Bekkering, Adam, Aarssen, Kingma, & Whiting, 1995; Neggers & Bekkering, 1999), to changes in SRTs but not RRTs (Jonikaitis & Deubel, 2011), and to changes in both SRTs and RRTs (Lünenburger, Kutz, & Hoffmann, 2000; Niechwiej-Szwedo, McIlroy, Green, & Verrier, 2005; Sailer et al., 2002). It may be that our task, which required reaching or making a saccade to the exact same target location on each trial, which may have become too automatic to demonstrate differences. Due to the fact that the movement target did not change over the trials, the participants had to generate an eye or arm movement to the same exact position on the screen for the complete duration of the task. It is possible that the repetitive nature of the movements of the eyes and the arm to the movement target could have induced the formation of a motor memory in the time frame of the experiment (Bütefisch et al., 2000, 2002; Classen, Liepert, Wise, Hallett, & Cohen, 1998; Flöel et al., 2005). The motor memory would have facilitated both the saccades and the reaches in a similar fashion, as both of the effectors produced the same stereotypical movements to the movement target, causing the reaction times of the eyes and the arms to become shorter as the experiment progressed. Consistent with this hypothesis, overall RTs for both saccades and reaches were indeed shorter than reported in other studies (Sailer et al., 2000; Lee et al., 2014).

In response to the exogenous cue, we found similar changes in RTs as a function of cue position for both saccades and reaches, but there was also an overall shift of RTs (with saccades not demonstrating the facilitation observed in the reaches when the cue was near the target). These findings are consistent with previous research suggesting both effector-dependent and -independent movement planning processes. As mentioned in the introduction, a number of studies have shown strong correlations between initiation times of the eye and the hand, consistent with a shared movement planning stage (Biguer, Jeannerod & Prablanc, 1982; Bekkering et al., 1995; Gopal & Murthy, 2015; Lee et al., 2014; Neggers & Bekkering, 1999; Sailer et al., 2000; Suzuki, Izawa, Takahashi & Yamazaki, 2008; Tao, Khan & Blohm, 2018). An effector independent stage reflecting shared outcomes for different effectors has been suggested previously in terms of a shared target selection stage for both the eye and the hand (Song & McPeek, 2009). Target selection has been proposed to occur through a priority map directed by visual attention (Fecteau & Munoz, 2006; Zelinsky & Bisley, 2015), which combines bottom-up inputs, i.e., the physical distinctiveness of objects in the scene, and top-down inputs, comprised of the goals and motivations of the observer (Bisley & Goldberg, 2010; Fecteau & Munoz, 2006; Serences, Yantis, Culberson, & Awh, 2004). When combined, these two types of inputs are used to create an integrated map (Itti & Koch, 2001; Treue, 2003), which is presumably used to select objects of interest for saccades and reach movements. In addition, we and others also show evidence for effector specific planning processes that result in different behavioural outcomes for the different motor systems. In our study, we observed that SRTs were mostly inhibited, while reaches were mostly facilitated. Previous studies have also proposed differential processing of eye and arm movement initiation (Briand et al., 2000; Sailer et al., 2000, 2002). Differences have also been shown in the allocation of attention to eye and arm goal locations during movement planning, presumably reflecting a later effector independent stage (Deubel & Schneider, 2003; Jonikaitis & Deubel, 2011; Khan, Song, & McPeek, 2011). Shared attentional resources during coordinated reaches and saccades were shown to be mainly guided by the eye, potentially as a synergistic mechanism to alleviate attentional demands, which in turn reduced the reaction times of the effectors (Khan et al., 2011; Pelz, Hayhoe & Loeber, 2001). This suggested effector-independent process of beneficial coordination can be disrupted by task-specific constraints (Pelz et al., 2001), suggesting that the hand and the eye relies, at least in part, on effector-specific processes when coordination is irrelevant or not possible.

A lack of attentional facilitation for SRTs in the presence of nearby exogenous cues, relative to the no-cue condition, has been reported before and is likely specific to the saccadic system (Crawford & Muller, 1992; Horowitz, Fine, Fencsik, Yurgenson, & Wolfe., 2007; Khan et al., 2016; Lubbe, Vogel & Postma, 2005; Walker et al., 1995). One possible explanation is that eye movements involve a gating mechanism where omnipause neurons inhibit brain stem saccade generators from producing a saccade in response to activity in the SC reflecting the visual cue (Corneil, Munoz, Chapman, Admans, & Cushing, 2008; Everling, Pare, & Dorris, 1998; Scudder, Kaneko & Fuchs, 2002). This is in contrast to other motor systems such as head or reach movements that do not have such a gating mechanism (Corneil et al., 2008; Kaufman et al., 2010; Kaufman, Churchland & Shenoy, 2013). Consistent with this finding, Corneil et al. (2008) found neck muscle activation during cue presentation consistent with covert orienting, i.e. with no eye movement towards the cue. Thus, it could be that arm movements are more easily facilitated by nearby cues because their activity is not limited by a gating mechanism, whereas eye movement activity is downregulated by the saccadic gating mechanism.

An alternate interpretation of the differences seen between the reaction times of effectors used alone versus in combination can be based on a tethered mechanism of information-sharing between the two effectors. While Fig. 4 shows relatively small overall differences between single and combined movements with a vaguely similar pattern, there is a convergence in normalized reaction times of the two effectors during the combined movements. We posit that this is due to an interaction between the two independent processes of motor selection, one for saccades and one for reaches. However, due to the small size of the observed effect, we cannot confidently infer the presence of the suggested interaction.

In terms of neuronal correlates, there are many neurophysiological studies showing evidence for target selection and movement planning processes that are both effector independent and dependent. It is well established that there are separate networks for eye vs. arm movement planning, consistent with effector dependent processing. Specifically, regions within the posterior parietal cortex (PPC), the frontal eye fields (FEF), the superior colliculus (SC) and brainstem areas are involved in eye movement planning (Bruce and Goldberg 1985; Goldberg and Bushnell, 1981; Schall, 1991; Schiller & Tehovnik, 2005; Sparks & Barton, 1993) while different regions of the PPC, the pre-motor, and motor cortices have been shown to be primarily involved in reach planning (Battaglia-Mayer, Caminiti, Lacquaniti & Zago, 2003; Buneo & Andersen, 2006). However, in line with a target selection effector independent stage, neurons in areas in the PPC such as the lateral intraparietal area (LIP) and in the frontal cortex, such as FEF, have been shown to respond to both eye and reach movements (LIP: Buneo & Andersen, 2006; Lawrence & Snyder, 2006; Oristaglio, Schneider, Balan, & Gottlieb, 2006; FEF: Lawrence & Snyder, 2006; Levy, Schluppeck, Heeger, & Glimcher, 2007; Thura, Hadj-Bouziane, Meunier, & Boussaoud, 2008). Indeed these are two of the areas that have been proposed to represent a priority map (Bisley & Goldberg, 2010; Goldberg, Bisley, Powell, & Gottlieb, 2006; Keller and McPeek, 2002; Liu, Yttri & Snyder, 2010; Thompson & Bichot, 2005). Moreover, the SC has also been demonstrated to be involved in target selection and covert attention for both eye and arm movements (Gandhi & Katnani, 2011; Krauzlis, Lovejoy, Zénon, 2013; Khan et al., 2016; Lünenburger, Kleiser, Stuphorn, Miller & Hoffman, 2001) and thus also proposed to be a candidate for a priority map (Fecteau & Munoz, 2006; Boehnke & Munoz, 2008; Song, Rafal & McPeek, 2011). Interestingly, LIP was recently shown to be involved in eye hand coordination, with inactivation of the region impairing combined saccades and reaches (Yttri, Liu & Snyder, 2013).

The exogenous cues did not seem to affect amplitudes in the same way it did RTs in that there was no effect of cue. This is in contrast to Sailer et al. (2002a), who showed an amplitude difference between effectors depending on cue's distance; when the cue was presented closer to the fixation point than the target, only saccade amplitudes decreased, whereas when it was presented farther than the target, both effectors' amplitudes increased. Moreover, while we found a systematic influence of cue position on RTs, Sailer et al. (2002a) did not. We believe the difference lies in the timing of the cue and the target. A number of studies have investigated how cues appearing at the same time or after the target influence eye, arm and combined movements. Studies comparing single effector movements of the eyes and arms have demonstrated that saccades are consistently influenced by late cues (Bompas, Hedge & Sumner, 2017; Buonocore, 2010; Sailer et al., 2002a, 2002b). While the amplitudes of reach movements were similarly affected by cues, the latencies were either not affected, or affected by a smaller amount (Sailer et al., 2002b; Bompas et al., 2017; Buonocore, 2010). Sailer et al. (2002) tested combined movements in addition to single effector movements and again found relatively unchanged patterns of responses to cues compared to single effector movements. In our study, we presented the cue before target onset, whereas in their study, they presented the cue and the target at the same time. It may be that the different timings affect different processes (e.g. attentional) in a different manner, where pre-target cues influence RTs more whereas post or simultaneously presented cues influence kinematics to a greater degree compared to initiation (Sailer et al., 2002b; McPeek, Han & Keller, 2003; Theeuwes & Godijn, 2004; McSorley, Haggard, Walker, 2005, 2006). It remains unclear whether the simultaneous presentation of a cue involves attentional mechanisms to the same degree as attentional capture, as their influence on eye movements appears to be different (Bompas & Sumner, 2009; Walker, Kentridge & Findlay, 1995), and simultaneous presentations appear to influence amplitudes more than reaction times (Sailer et al., 2002).

It is essential to note that during the pre-processing of the data, about 22% of total trials were removed due to a variety of reasons previously stated in section 3.3.4. This included trials with the presence of blinks or anticipatory movements of the eyes or arms. An important consideration would be to ensure that the removal of these trials did not introduce any kind of bias into the data. For example, it is possible that the presentation of an exogenous cue induced blinks during a number of trials. This could bias towards a retention of trials where the cue was not perceived by the participant, effectively skewing the results by underrepresenting the true effects of exogenous cueing. However, we had no means of verifying the nature of the blinks and, therefore, we could not completely eliminate the potential bias caused by the removal of trials which included them. In the case of anticipatory saccades, we removed all trials with a reaction time below 80 ms. The choice of this latency as a lower bound filter was based on a number of papers demonstrating the near-impossibility of producing accurate and voluntary saccades in response to a stimulus under this latency (Bartz, 1962; Fischer & Ramsperger, 1984; Gezeck, Fischer, & Timmer, 1997; Smeets, Hayhoe & Ballard, 1996; White, Eason & Bartlett, 1962).

To conclude, we found changes in RTs in reaches and saccades in response to an exogenous cue at different locations relative to the target. Our findings are in line with other research that has shown that oculomotor and reaching systems share certain attentional mechanisms (Sailer et al., 2000, 2002; Briand et al., 2000), but are also independently driven (Deubel & Schneider, 2003; Jonikaitis & Deubel, 2011; Khan et al., 2011). Taken together, our results provide evidence for both shared and independent movement planning processes of the movement target in respect to the visual environment driving reaches and saccades.

3.6. Acknowledgements

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3.7. Tables

3.7.1. Table 1

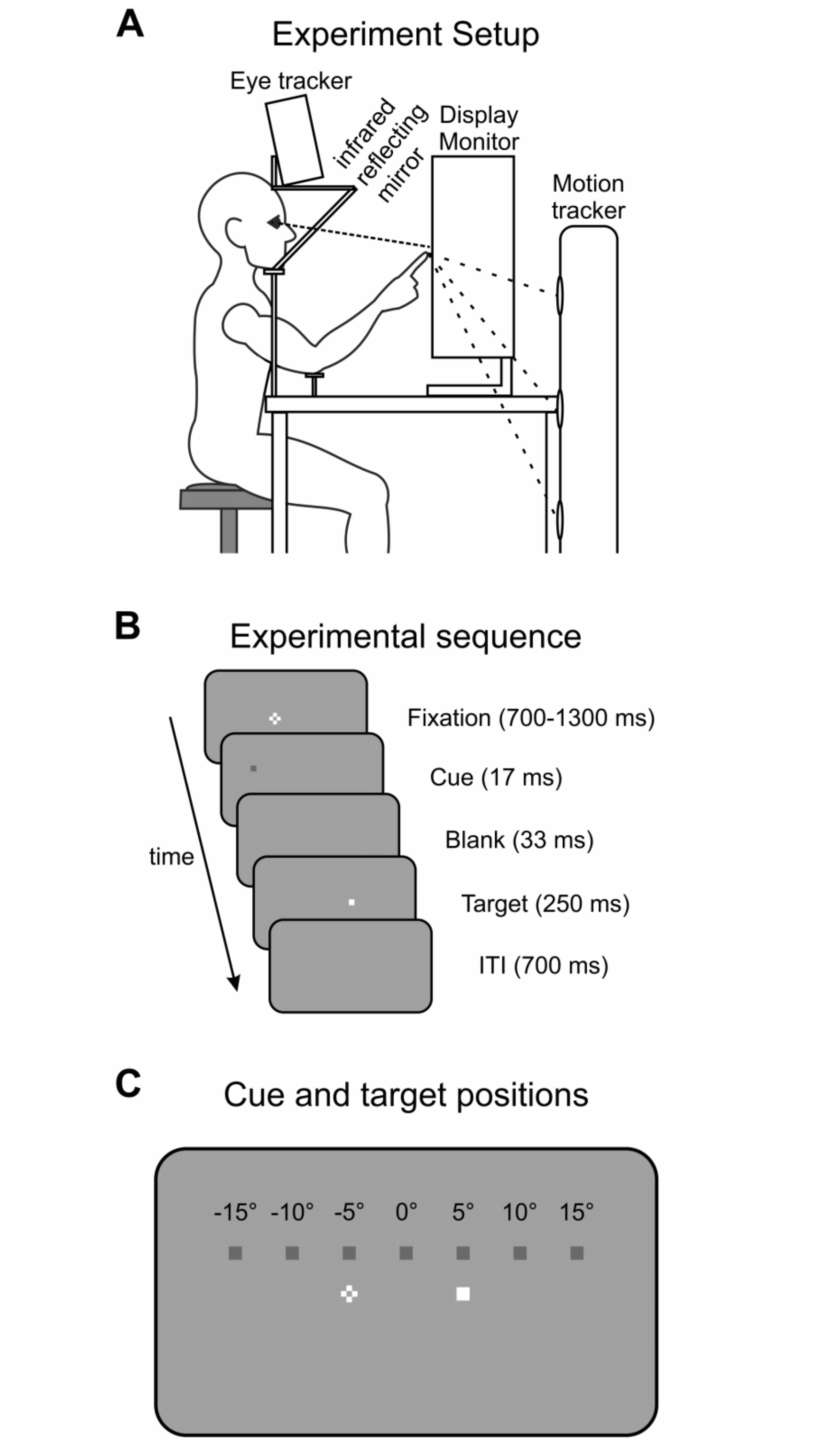
Normalized reaction times (ms)

Effector x Pairing	Cue Position	Mean	SEM	*t*-value	*p*-value and significance	
Single saccades						
	1	**12.2**	**2.3**	**5.403**	**0.001**	**
	2	**16.7**	**3.0**	**5.546**	**0.001**	***
	3	**10.9**	**2.9**	**3.825**	**0.017**	*
	4	5.8	2.5	2.302	0.280	NS
	5	1.3	2.3	0.560	>.999	NS
	6	3.9	2.5	1.585	0.972	NS
	7	**7.8**	**2.1**	**3.805**	**0.018**	*
Combined saccades						
	1	**10.7**	**2.5**	**4.271**	**0.008**	**
	2	**11.3**	**3.0**	**3.799**	**0.018**	*
	3	**9.2**	**2.8**	**3.329**	**0.042**	*
	4	5.0	2.4	2.105	0.400	NS
	5	3.4	1.6	2.138	0.377	NS
	6	**9.5**	**2.2**	**4.325**	**0.007**	**
	7	8.3	3.2	2.579	0.169	NS
Single reaches						
	1	0.1	2.1	0.051	>.999	NS
	2	0.9	1.9	0.487	>.999	NS
	3	-6.4	2.0	-3.175	0.056	NS
	4	**-8.1**	**1.9**	**-4.329**	**0.007**	**
	5	**-12.6**	**1.9**	**-6.776**	**<.001**	***
	6	**-10.6**	**1.7**	**-6.031**	**<.001**	***
	7	**-8.4**	**2.5**	**-3.329**	**0.042**	*
Combined reaches						
	1	3.7	3.1	1.198	>.999	NS
	2	3.7	2.8	1.326	>.999	NS
	3	2.1	1.3	1.570	0.997	NS
	4	**-8.1**	**1.8**	**-4.537**	**0.005**	**
	5	**-11.3**	**2.7**	**-4.147**	**0.009**	**
	6	-5.5	1.8	-3.005	0.077	NS
	7	-8.8	2.8	-3.138	0.060	NS

*p < .05; **p < .01; ***p < .001, Bonferroni-corrected

3.8 Figures

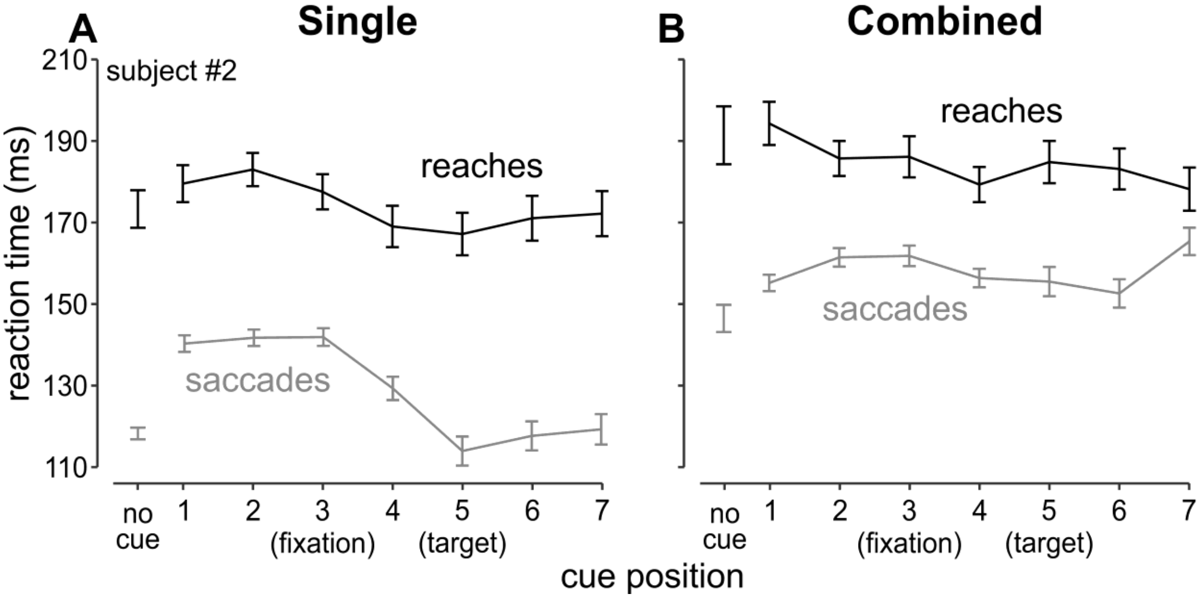
3.8.1. Figure 1



3.8.1.1. Figure 1 Legend

Figure 1. (A) Experimental setup. Participants sat in front of a computer display monitor on which stimuli were presented. An infrared-based eye-tracker was used to measure the position of the right eye. A transparent infrared reflecting mirror (labelled mirror in the figure) was used to reflect infrared light from the eye tracker camera to the eyes, to enable eye position recordings. A motion tracker system recorded the 3D positions of the markers placed on the right hand (dotted lines). **(B) Experimental sequence**. Each trial began with a fixation point at 5° to the left or right of the center of the screen (left demonstrated in the figure) for a random duration between 700 and 1300 ms distributed at 100 ms intervals. A cue appeared at 1 of 7 possible positions for 17 ms (leftmost position demonstrated). A blank screen followed for 33 ms after which a target was presented at the mirror position of the fixation point (distance of 10° between them) for 250 ms. The inter-trial interval (ITI) lasted 700 ms. **(C) Cue positions**. The cue was presented at -15°, -10°, -5°, 0°, 5°, 10° or 15° relative to the center of the screen, offset vertically by 5° above the horizontal meridian. For reference, the fixation point and target are also shown, but during a trial they would not be seen together.

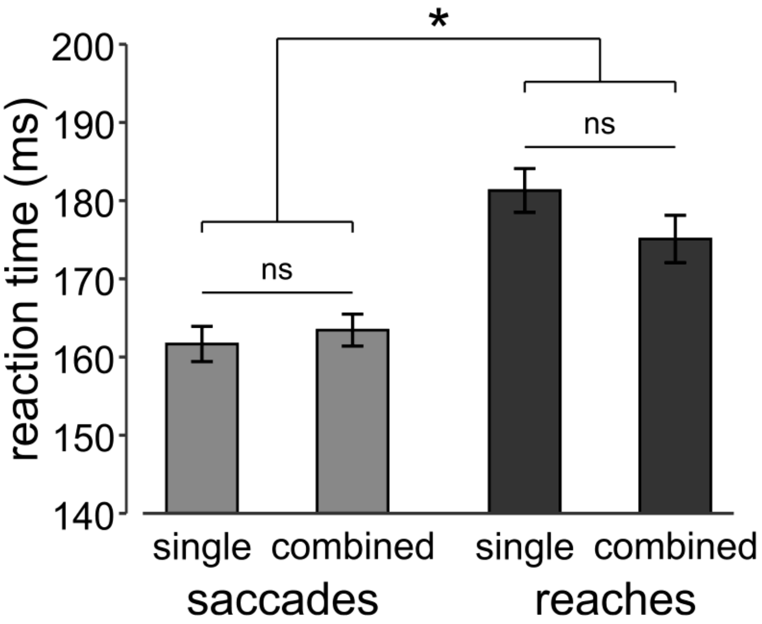
3.8.2. Figure 2



3.8.2.1. Figure 2 Legend

Figure 2. Representative participant reaction times. The light-gray bars represent saccades and the dark-gray bars represent reaches. Error bars represent SEM (standard error of the mean). **(A)** shows data from trials where movement was only performed with a single effector. **(B)** shows data from trials where eye and arm movements were combined. On the x-axis is cue position, where 1 is the cue farthest on the left and 7 is the cue position on the far right. Although the fixation point was either on the left or the right, for ease of graphical representation all data have been flipped so that the fixation point is always on the left (directly below cue position 3). Thus, cue position 1 and 2 were to the left of the fixation point, and cues 4-7 were to the right of the fixation point. Cue 5 was directly above the target. There are 5° between each cue position.

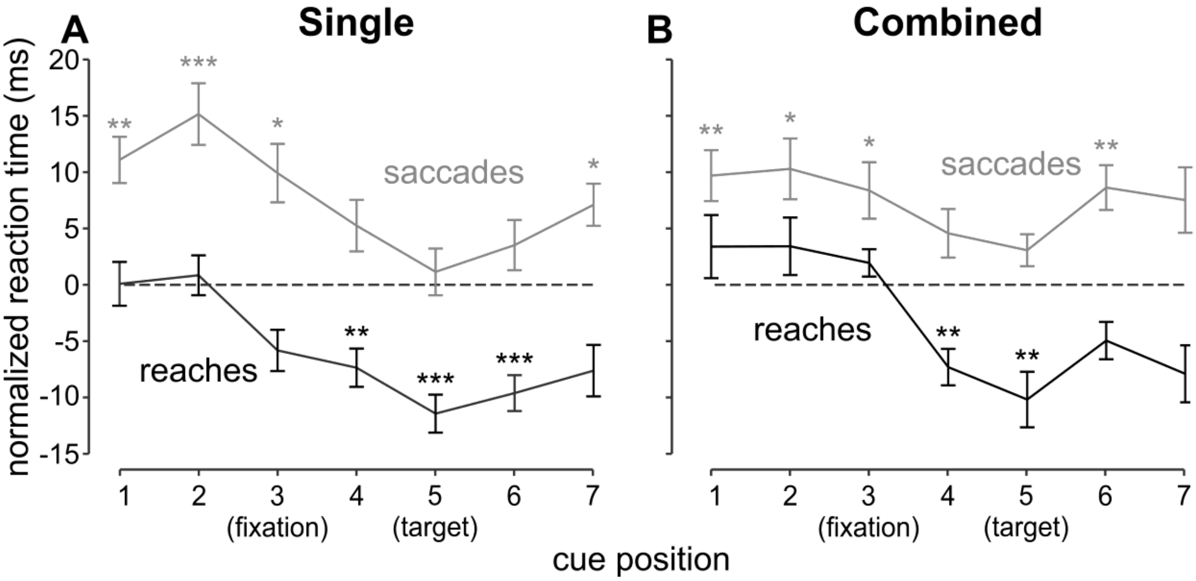
3.8.3. Figure 3



3.8.3.1. Figure 3 Legend

Figure 3. Overall mean reaction times. The light-gray bars represent saccades and the dark-gray bars represent reaches. The mean reaction time data are plotted for the single condition (where a single effector moved to the target), and the combined condition (where both effectors moved together to the target). Error bars represent SEM (standard error of the mean across participants). * indicates p<.05.

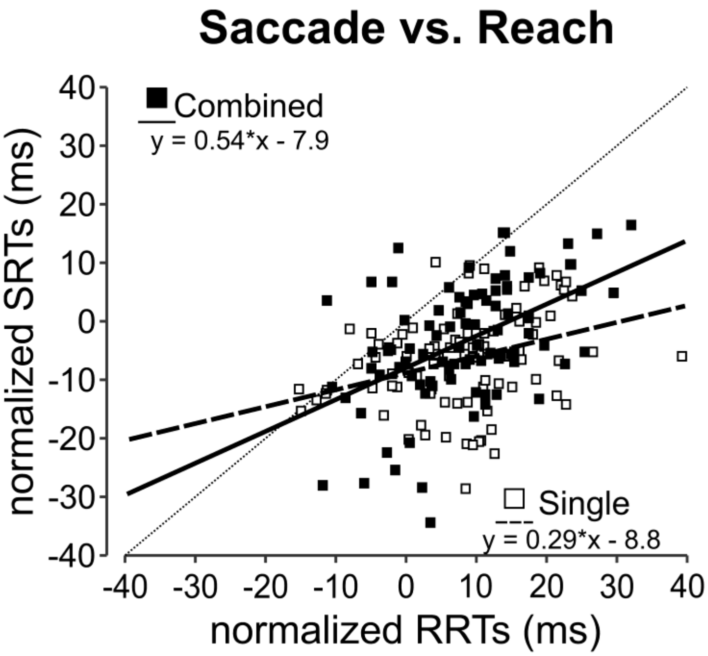
3.8.4. Figure 4



3.8.4.1. Figure 4 Legend

Figure 4. Mean reaction times as a function of cue position. The light gray lines represent saccades and the dark gray lines represent reaches. (A) shows data from trials where movement was only performed with a single effector. (B) shows data from trials where eye and arm movements were combined. On the x-axis is cue position, where 1 is the cue farthest on the left and 7 is the cue position on the far right (conventions as in Figure 2). Thus, cue position 1 and 2 were to the left of the fixation point, and cues 4-7 were to the right of the fixation point. Cue 5 was directly above the target. On the y-axis is the normalised reaction time, the difference between reaction time for each cue position trial and the reaction time for the no-cue trials. The dashed reference line at zero reflects reactions times in the no-cue trials. Negative normalized reaction times are those that were faster than the no-cue trials, whereas positive indicates reaction times slower than no-cue trials. Error bars represent SEM (standard error of the mean). * indicates $p<.05$, ** indicates $p<.01$, *** indicates $p<.001$.

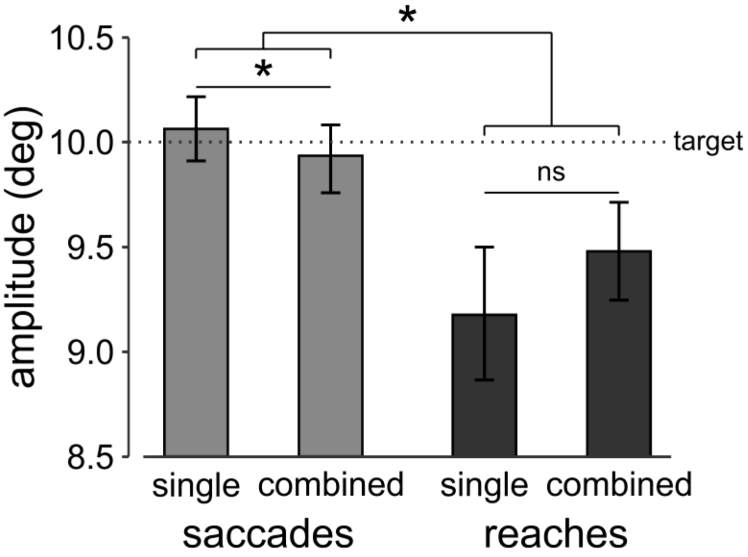
3.8.5. Figure 5



3.8.5.1. Figure 5 Legend

Figure 5. Correlations for SRTs and RRTs. Normalised SRTs are plotted as a function of normalised RRTs. The line of unity is drawn as a reference (grey dotted line). Empty squares represent the single effector pairing condition (dashed black line of best fit), where combined reaches and saccades are represented by filled squares (solid black line of best fit). Each participant has 7 points, corresponding to the 7 cue positions. The similar slopes and intercepts between SRTs and RRTs demonstrate that the changes in normalized RTs in response to the cue followed the same pattern for the two effectors.

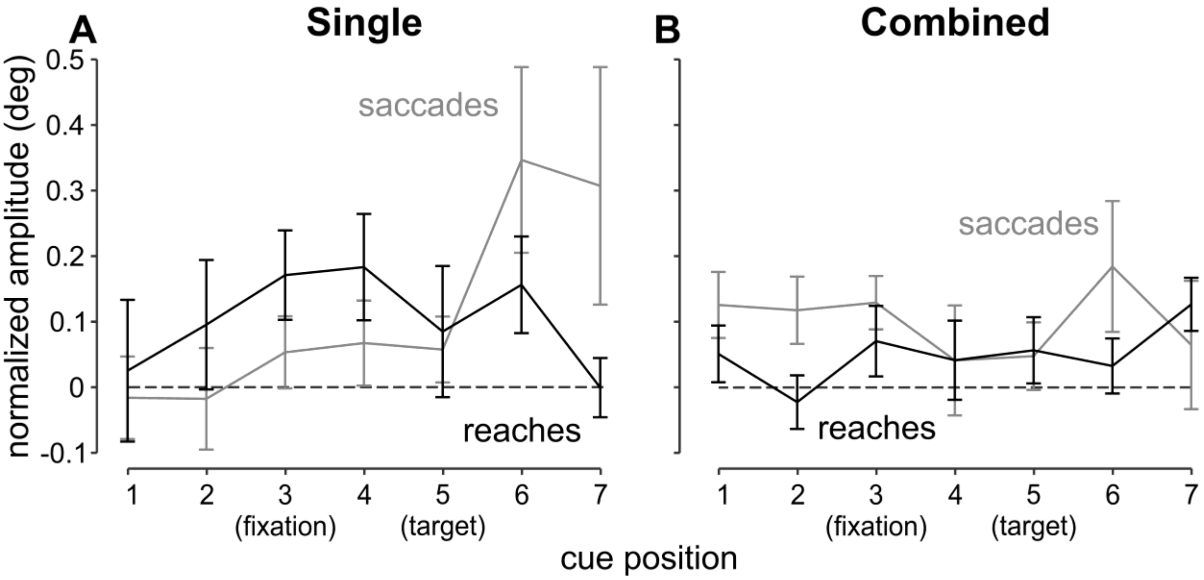
3.8.6. Figure 6



3.8.6.1. Figure 6 Legend

Figure 6. **Overall amplitudes**. The light-gray bars represent saccades and the dark-gray bars represent reaches. The mean amplitude data are plotted for the single condition (where a single effector moved to the target), and the combined condition (where both effectors moved together to the target). Error bars represent SEM (standard error of the mean across participants). * indicates p<.05.

3.8.7. Figure 7



3.8.7.1. Figure 7 Legend

Figure 7. Mean normalized amplitudes as a function of cue position. The light-gray bars represent saccades and the dark-gray bars represent reaches. Error bars represent SEM (standard error of the mean). **(A)** shows data from trials where movement was performed with a single effector. **(B)** shows data from trials where eye and arm movements were combined. On the x-axis is cue position and on the y-axis is the normalised amplitude in degrees, which is the difference between the amplitude in a cue trial and the mean amplitude in the no-cue trials. The dashed reference line represents the amplitude for the no-cue trials. Negative numbers reflect amplitudes smaller than the no-cue trials whereas positive numbers reflect amplitudes larger than the no-cue trials.

4. Article 2

Article en préparation :

Malienko, A. & Khan, A. Z. (2018). Temporal effects of exogenous attentional cueing during visuomotor adaptation. Article en préparation.

Temporal effects of exogenous attentional cueing during visuomotor adaptation

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Running title: Exogenous cues in visuomotor adaptation

4.1. Abstract

Exogenous cues were presented during a visuomotor adaptation task to investigate the influence of attentional modulation on reaches during different stages of motor planning. More precisely, we wanted to test whether attentional modulation occurs early in motor planning, where only the vector between the visual target and the start position has been computed, or later, after the motor plan has been generated. In two experiments, a total of twenty-four participants (*M* = 24.63, *SD* = 7.2) performed a visuomotor adaptation task where they needed to reach to a target while the visual feedback of their movements were shifted through an amplitude gain change during the adapted phase. A behaviourally irrelevant cue flashed just before the target at different locations. We found that there were no differences in the influence of the attentional cues when comparing the pre-adapted stage to the adapted stage, suggesting that attention influences reach planning at an early visual stage in motor planning and not at a later motor stage. When taking into consideration previous findings of attentional influence on saccades during the motor stage, our results emphasize the independence of planning between eye and arm movements.

Keywords: visuomotor adaptation, reaching, motor planning, exogenous cueing, attention

4.2. Introduction

Reaching movements are performed a countless number of times daily to interact with the physical world around us. Visually guided reaches result from an interaction between the visual system, with visuospatial information about the hand in reference to a target as input, and the motor system, with appropriate commands to control the arm as output (Buch, Young & Contreras-Vidal, 2003; Caminiti, Ferraina & Mayer, 1998). Due to the complex nature of this visuomotor transformation, it requires the involvement and interaction of several brain areas, notably the visual, parietal and premotor cortices (Buneo, Jarvis, Batista & Andersen, 2002; Lacquaniti & Caminiti, 1998; Jeannerod, Arbib, Rizzolatti & Sakata, 1995).

Visual attention is an intrinsic part of visually guided reaches and can influence various reach characteristics through the processing of behaviorally irrelevant, exogenous distractors. Several studies, including our previous work, have shown that exogenous cueing has differential effects on reach reaction times to a target (Malienko, Harrar & Khan, 2018; Song and Nakayama, 2006; 2008; McSorley et al., 2006). Other studies demonstrated effects of visual cues on the kinematics of reaches, such as the trajectory, precision, and accuracy of movements (Chapman et al., 2010; Chang and Abrams, 2004, Lee, 1999, Sailer, Eggert, Ditterich, & Straube, 2002; Song and Nakayama, 2008; Tipper, Howard, & Jackson, 1997; Tipper, Lortie, & Baylis, 1992). However, it remains unknown whether exogenous attention influences reach planning at the visual or the motor level.

Neurophysiology studies show that attentional mechanisms were implicated in several brain regions during reach planning. The parietal reach region (PRR) region within the posterior parietal cortex (PPC) (Medendorp, Goltz, Vilis, & Crawford, 2003), as well as the premotor and motor cortices have been shown to be implicated in early-stage processing (Battaglia-Mayer, Caminiti, Lacquaniti, & Zago, 2003; Buneo & Andersen, 2006). Additionally, reach planning has been shown to recruit parts of the prefrontal cortex, suggesting that additional processing occurs at a later stage of movement preparation (Beurze, de Lange, Toni, & Medendorp, 2007). Thus, it remains unclear whether exogenous attention influences reach planning at early compared to late stages of processing. We previously demonstrated that for eye movements, an exogenous cue flashed at the saccade goal rather than at the target location facilitated reaction times for adapted saccades (Khan, Heinen & McPeek, 2010). This finding indicates that the exogenous cue facilitates the planning of the actual saccade movement rather than the visual processing of the target, implying a close linkage between saccade planning and exogenous attentional mechanisms.

Here we investigated the stage of processing at which exogenous attentional cues influenced reach planning to determine whether, like saccades, the attentional cues play a more important role at later motor planning stages or unlike saccades, at earlier stages, i.e. at the stage at which only the visual-target vector has been determined. There are arguments for both possibilities.

On the one hand, there are significant differences between the saccadic and reaching systems. First, eye movements and reach movements have different functional goals (Foulsham, 2015, Khan, Song & McPeek, 2011; Liu, Whitall & Kepple, 2013). While they have no direct means of interacting with the environment, eye movements can acquire information from the visual field and accurately direct and guide the limbs which are able to interact with objects in their surroundings (Land & Hayhoe, 2001; Land, Mennie & Rusted, 1999). Due to these differences in the functions of these movements, it is suggested that different attentional mechanisms are in play during eye and reach movements. Second, the neural pathways and the processes involved in reach planning are much more complex than saccade planning, for which the pathways are well-known and thoroughly studied (Bruce & Goldberg 1985; Ghahghaei & Verghese, 2015; Khan et al., 2009; Kopecz & Schöner, 1995). Depending on the complexity of the movement, reaches might require additional motor planning stages to correctly execute abstract kinematics representations, which aren't necessary for saccades as they are point-to-point movements (Desmurget, Pélisson, Rossetti & Prablanc, 1998; Wong, Haith & Krakauer, 2015; Wong, Goldsmith & Krakauer, 2016). Our definition of a motor plan is based on the review conducted by Wong et al. (2015). They suggest that motor planning is a pathway of processes including abstract kinematics, action selection and movement specification, which, together, define how a movement towards a motor goal is attained. The tridimensionality of space adds an additional complexity layer for reach movement planning, as it needs to take into account any obstacle in the way of the hand and arm trajectory, unlike in saccade planning (Batista, Buneo, Snyder, & Andersen, 1999; Sabes & Jordan, 1997). Third, neurophysiological studies have identified regions in the PPC that respond strongly to either reaches or saccades, suggesting separate neurological pathways for the movement planning of each effector. The PRR responds nearly exclusively to reach planning, while the lateral intraparietal area (LIP) responds predominantly to saccade planning (Lawrence & Snyder, 2006; Dickinson, Carlton, & Snyder, 2003), but is not as effector-specific as the PRR (Christopoulos, Kagan & Andersen, 2018).

On the other hand, there are also numerous similarities between the saccadic and reaching motor systems. During coordinated movement, saccade and reach reaction times are strongly correlated on a trial-by-trial basis (Dean, et al., 2011; Fischer & Rogal, 1986; Gribble, Everling, Ford, & Mattar, 2002; Lünenburger, Kutz, & Hoffmann, 2000) suggesting that the eyes and arms share a common core in their movement planning processes (Malienko et al., 2018).

Moreover, brain imaging studies have demonstrated various levels of overlapping activation in regions implicated in the generation of saccades and reach movements, specifically in parts of the PPC, such as the aforementioned LIP (Christopoulos, Kagan & Andersen, 2018), and the frontal cortex, including the frontal eye fields (FEF) (Astafiev et al., 2003; Beurze, de Lange, Toni, & Medendorp, 2009; Connolly et al., 2000; Levy, Schluppeck, Heeger, & Glimcher, 2007; Medendorp et al., 2005). The LIP has been demonstrated to play a part in more global processes such as attention, which might explain why its neuronal activity is not fully effector-specific to saccades and can be seen during reach movements, which require attentional engagement (Bisley & Goldberg, 2003; Liu, Yttri, & Snyder, 2010).

In order to differentiate between early versus late planning stages, we utilized visuomotor adaptation to separate the actual hand reach (i.e. the motor plan) from the visual-target vector. Reach movement planning has been shown to actively adapt to changes in the visual environment (Buch, et al., 2003; Haar, Donchin & Dinstein, 2015; Hinder, Tresilian, Riek & Carson, 2008). This active adaptation can be observed in visuomotor adaptation tasks, during which the visual feedback of movement is distorted through various means, often by rotation or scaling of the movements (Contreras-Vidal & Kerick, 2004), or by using a prism to shift (Gaveau et al., 2018; Melamed, Beckett & Halay, 1979; Pisella et al., 2006). Adaptation to visuomotor distortion is achieved through either a gradual or a sudden adaptation, called step adaptation (Ingram et al., 2000; Kagerer, Contreras-Vidal, & Stelmach, 1997). By using gradual adaptation over step adaptation, the slow onset of imperceptible visual distortions leads the participants to be unaware of the distortions and the implicit correction of their movements (Buch et al., 2003). This offers a clear benefit over step adaptation, as it prevents the participants from using intentional cognitive strategies to correct their movements (Gaveau, Prablanc, Laurent, Rossetti, & Priot, 2014; Michel, Pisella, Prablanc, Rode, & Rossetti, 2007).

Here, we used a gradual visuomotor adaptation reaching task to dissociate the actual reaching movement from the perceived movement towards a visual target, and measured the influence of exogenous cues on reach reaction times and amplitudes. The exogenous cues were presented at different locations just prior to the target (Khan et al., 2010, 2016; Malienko et al., 2018) to investigate how the spatial spread of attentional mechanisms affect reach reaction times. In a previous study, we found that the exogenous cue presented around the position of the visual target had the greatest facilitatory effect on reaches, whereas there was no facilitatory effect of the exogenous cue away from or far past the movement target (Malienko et al., 2018). The present study aims to investigate the influence of exogenous cueing during visuomotor adaptation in reaches and to identify the processing level at which it occurs.

If attention influences reach planning at early processing, we expect the exogenous cues to facilitate reach reaction times in all conditions, with the peak of the facilitation occurring at the visual target position during baseline, at the adapted target position during the adaptation period, and between both of these targets during the post-adaptation period. This would suggest that motor planning relies not only on visual representations of the movement goal to efficiently generate the movement, but that it can also be affected by adapted motor behaviors. On the other hand, if attention influences reach planning at a later stage, we expect the effects of the exogenous cue to be unaffected by the visuomotor adaptation, thereby allowing the peak of the facilitation to happen at the visual target position during all conditions.

4.3. Experiment 1 – Materials and Methods

4.3.1. Participants

We recruited 15 participants (ages: M = 25.07, SD = 6.49, 8 females). All participants except two (authors AM and AK) were naive to the purpose of the experiment. The experimental protocol and recruitment was approved by the University of Montreal Health Research Ethics Committee (CERES) under the certificate #16-103-CERES-D(1). All participants had normal or corrected-to-normal vision and were right-handed.

4.3.2. Apparatus

The experiment took place in a dark room. Participants were seated in front of a custom-built three-leveled augmented reality setup (**Fig. 1A**). On the top level, above the head, was a downward-facing 55" OLED television (OLED55B7P, LG Electronics, Seoul, South Korea) running at a resolution of 1920x1080 (2.99 min arc/pixel) and a refresh rate of 60 Hz. The screen's background color was black throughout the experiment with a mean luminance of 0.027 cd/m^2. On the middle level was an adjustable chinrest maintained the viewing distance and a half-reflecting mirror which reflected the image of the screen towards the participant, but prevented the participants from viewing their hand. On the bottom level of the setup, there was a solid platform which was used as an armrest and allowed comfortable freedom of movement of the arm during the experiment. All three levels were angled at 15° to the horizontal plane and separated by a distance of 40 cm.

Stimuli were programmed and generated using the Psychophysics Toolbox Version 3.0.11 (Brainard, 1997) for MATLAB (The MathWorks, Inc., Natick, MA, United States).

Hand movement data were collected with a 3D Investigator motion tracking system and infrared markers recording at 500 Hz with a spatial resolution of 0.01 mm (Northern Digital Inc., Waterloo, Canada) and controlled by a custom MATLAB extension. The markers were fixed with clear medical tape to the tip of the participant's right index finger. During the experiment, the participant had no vision of their hand or finger due to the low-light experimental setting, and instead saw a dynamic green cursor that represented their finger during the trials.

4.3.3. Procedure

The experimental design was, in part, based on the findings of our previous study (Malienko et al., 2018). The trial sequence (**Fig. 1B**) was as follows: participants aligned their index finger, whose position was represented on the screen by a green dot (cursor) that moved with the finger, on a white start position dot with a diameter subtending 1° of visual angle presented at 5° to the left from the center of the screen for a random interval between 900-1500 ms. After the participant placed their finger on the start position dot, a cue with the same characteristics as the start position dot was presented for 33.3 ms (2 frames) at 1 of 7 possible positions at -15°, -10°, -5°, 0°, 5°, 10°, 15° relative to the center of the screen, offset vertically by 2° above the height of the start position dot (**Fig. 1C**). After the cue disappeared, a blank screen was presented for 66.7 ms (4 frames). This was followed by the presentation of a target (red dot with a diameter of 1° of visual angle) at 5° to the right from the center of the screen. Participants were instructed to reach towards the target with their hand as rapidly and accurately as possible as soon as it appeared. The target remained on the screen for 1.1 seconds after reach movement initiation, which corresponded to the end of the trial. When the next trial's fixation position reappeared, participants were asked to return their finger to the start position. Participants were not given any explicit eye movement instructions.

The location of the cue was randomized and balanced throughout the trials, with an equal number of presentations at every position. As a control, there were also no-cue trials during which no cue were presented, but which were instead replaced by a blank screen to maintain the same timings as the cued trials.

Participants completed two blocks of 464 trials each (8 possible cue positions × 16 repetitions during pre-, post- and adaptation trials, and 8 possible cue positions × 5 repetitions during adaptation onset and offset), for a total of 928 trials per participant. There was a 5-10 minute break between the blocks. Participants performed the entire experiment in one session lasting approximately one hour.

4.3.4. Adaptation

Each block was identical and was separated into five periods of adaptation: (1) baseline, (2) gradual onset, (3) adapted, (4) gradual offset and (5) post-adaptation.

(1) There were 128 baseline pre-adaptation trials. (2) Over the next 40 trials, participants were subjected a gradual adaptation onset, during which the gain of the visible cursor changed with respect to the actual hand position. The adaptation was based on the following formula:

$$(Gain \times \ [Finger\ Position - Fixation\ Position] + Fixation\ Position)$$

The gain increased from 1 (baseline trials) to 2 by steps of 0.0256. A gain of 2 resulted in the cursor's horizontal amplitude moving twice as further than the actual position of the hand. Thus, the participants had to produce movements with a horizontal amplitude 50% smaller than in the baseline trials to correctly align the cursor with the movement target. (3) The gain was maintained at 2 for 128 trials. (4) Following adaptation trials, the amplitude gain gradually returned to 1 over 40 trials. (5) The block concluded with 128 post-adaptation trials.

4.3.5. Data Analysis

We collected a total of 13,920 trials. Offline analyses were performed using MATLAB (The MathWorks, Inc., Natick, MA, United States). Hand velocity was obtained through digital differentiation of the hand position signals and filtered to reduce noise (2-pole Butterworth filter, cut-off = 50 Hz). Hand movement onset and offset were identified using a velocity threshold of 2°/s (Donchin, Gribova, Steinberg, Bergman & Vaadia, 1998; Roby-Brami, Bennis, Mokhtari & Baraduc, 2000; Jonikaitis, Schubert & Deubel, 2010; Malienko et al., 2018).

When marker position data were missing during the reach movement, the data were linearly interpolated across the missing region. Linear interpolation was required in 6.05% of trials. Individual trials were visually inspected and manually removed if any of the following occurred: the participant initiated a reach movement before the target appeared, no movement was initiated during the trial and/or there were more than one continuous movement of the arm during the trial. These criteria lead to a manual removal of 16.75% of total trials across all participants.

The first measure of interest of the reach movements was reaction time. Reach reaction times (RRT) were calculated by subtracting the time of movement onset from the time of target onset. We removed all trials with RRTs under 80 ms or over 500 ms (Bompas & Sumner, 2009; Smeets, Hayhoe & Ballard, 1996; Song & Nakayama, 2008). This led to the removal of 6.38% of total trials. Next, we removed trials that were 3 SD above or below each participant's mean reaction time (0.71% of total trials removed).

The second measure of interest of the reach movements was amplitude. For the hand's reach amplitude, we subtracted the marker's horizontal position 30 ms after the end of the reach movement from 30 ms before its starting position. The 30 ms buffer allowed to collect the hand's static position data, before movement initiation and after movement completion. For the cursor's position, we subtracted the cursor's horizontal end position from its start position with the same 30 ms buffer before and after the reach movement. Trials were removed if the amplitude was less than 4° or more than 12° (0.77% of total trials removed) and if the amplitude were more than 3 SD above or below the participant's mean start position (1.98% of total trials removed). For analysis, we selected trials where the cursor's end position was inside a 3° horizontal window around the target (1.5° in each direction), which removed 0.75% of total trials. After all filtering and trial selection, there remained 10,115 trials which were used for analysis (72.67% of total trials).

4.3.6. Normalization

In order to account for the overall differences between participants and to singularize the effect of cue position before, during and after adaptation, we normalized the values by subtracting participant's mean value of each cue position and each adaptation period from the mean values of their respective no-cue trials (Khan et al., 2010; Malienko et al., 2018).

4.3.7. Statistical analysis

Repeated-measures one-way ANOVAs were conducted with adaptation period as the independent variable (three levels: baseline, adaptation, and post-adaptation) on amplitudes and reaction times. Greenhouse-Geisser corrected values are reported when Mauchly's test revealed that the sphericity assumption was violated. Further, pairwise comparisons were used to demonstrate differences between each pair of adaptation periods. All reported p-values were Bonferroni-corrected for multiple comparisons. All statistical computations were carried out with SPSS Statistics, version 25 (IBM SPSS, Chicago, IL, United States).

4.4. Experiment 1 – Results

4.4.1. Typical participant's hand and cursor amplitudes

Figure 2 shows a single participant's hand and cursor horizontal reach amplitudes over the course of the experiment. An 11-trial moving average (black line) was plotted over the hand (open and filled circles) and cursor individual trials to discern the general trend of amplitude changes due to the different adaptation periods. In **Figure 2A**, we can see the hand's amplitudes during baseline trials (light gray) reaching the actual target position of 10° until the gradual horizontal gain change (dotted-line circles to the left). As the trials progressed, the hand's amplitudes gradually reached the adapted target position of an amplitude of 5° and remained at this amplitude during the adaptation period (medium gray). Afterwards, the return-to-normal-gain trials (dotted-line circles to the right) show that the reaches gradually went from the adapted target at 5° back to the actual target amplitude at 10° over 40 trials. Lastly, the post-adaptation trials (dark gray) show that the hand's amplitudes were slightly below the target amplitude of 10°, possibly due to a residual effect of adaptation during the preceding trials. When looking at the cursor's movements, in **Figure 2B**, we can see that the baseline (light gray) and post-adaptation (dark gray) trials are exactly the same as the hand's movements, as the horizontal amplitude gain change only affected trials during the gradual change and adaptation periods. As the experiment progressed towards a gradual change of horizontal gain (dotted-line circles to the left), the cursor's movements diverged from the hand's movements, and their amplitudes were larger by about 1° at the beginning of the gradual change, but approached the target's 10° amplitude by the end of the gain change. During adaptation trials (medium gray), even though the cursor's movements were at the peak of the gain change, their amplitudes were near the target amplitude of 10°, but had a larger variability when compared to the baseline trials. This can be explained by the fact that the participants were at the peak of the changed horizontal gain, leading to the largest perturbations between visual and proprioceptive inputs. The cursor's amplitudes during the return-to-normal-gain trials (dotted-line circles to the right) show a gradual decrease of amplitudes compared to baseline and adaptation periods. Lastly, during the post-adaptation trials (dark gray), we can observe a trend of lowered amplitudes compared to previous periods, with the moving average staying under the target amplitude of 10°. We quantified these observations across all participants in the next section.

4.4.2. Overall amplitudes of adaptation periods

We looked at overall reach amplitudes during the different adaptation periods (baseline, adaptation, post-adaptation) to see whether an adaptation effect was present. In **Figure 3**, we plotted each participant's mean amplitudes with the overall mean of each adaptation period. A repeated-measures one-way ANOVA revealed an effect of adaptation ($F(2,28) = 13728.703$, $p < .001$, $\eta_p^2 = .999$). Post hoc comparisons with Bonferroni correction between each pair was conducted to tease apart and to quantify the differences. We observed significant differences between all pairs: between baseline (M = 9.98, SD = .12) and adaptation (M = 5.05, SD = .14) with p < .001, baseline and post-adaptation (M = 9.83, SD = .17) with $p = .002$, and between adaptation and post-adaptation with $p < .001$. These results suggest that the participants successfully adapted their reaches, as the amplitudes produced during the adaptation period were reaching the adapted target position at 5°. The baseline amplitudes were the closest to the target amplitude of 10°, showing that the participants produced the most precise movements before any amplitude gain perturbations. Additionally, the difference between baseline and post-adaptation demonstrates that, while the gain was unaffected during these periods, the participants still incurred residual amplitude effects from the adaptation period which in turn resulted in reaches of smaller amplitude.

4.4.3. Overall reach reaction times of adaptation periods

We then looked at overall RRT during the different adaptation periods (baseline, adaptation, post-adaptation) to see whether this amplitude adaptation had an effect on RRT. In **Figure 4**, we plotted the participants' mean RRT with the overall mean of each adaptation period. A repeated-measures one-way ANOVA did not reveal an effect of adaptation period on RRT ($F(2,28) = 2.101$, $p = .141$, $\eta_p^2 = .130$). These results demonstrated that, in overall, RRT of baseline, adapted and post-adapted movements were not different from each other.

4.4.4. Effect of cue position and adaptation period on normalized reaction times

Next, we investigated the effect of cue position across the different adaptation periods on normalized RRT. In **Figure 6**, we plotted the normalized mean RRTs of each adaptation period across all participants. We conducted a two-way ANOVA with adaptation period (3 levels: baseline, adaptation, post-adaptation) and cues (7 positions) as factors. We observed a main effect of cue ($F(6,84) = 49.761$, $p < .001$, $\eta_p^2 = .780$), but no main effect of adaptation period ($p = .307$). The ANOVA also revealed an interaction effect, ($F(12,168) = 2.178$, $p = .015$, $\eta p^2 = .135$). First, these results suggest that all three adaptation periods have overall similar patterns of RRT as a function of cue positions, and, second, the main effect of cue suggests that there is a significant downtrend of RRT (faster RRT) as the cue was presented closer towards the right extremity, past the target positions. The interaction effect suggests that, even though the adaptation periods have similar patterns of RRT as a function of cue positions, different cue positions depending on the adaptation period might lead to significantly different outcomes in terms of RRT.

Further, we used one-sample t-tests to compare each cue position of each adaptation period with 0, representing the respective no-cue trials of each adaptation period. These t-tests revealed that all of the cue positions, except cue positions 1 and 2 in both baseline and post-adaptation periods, were significantly different from 0. This suggests that the presence of the cue, in most part, facilitated RRTs.

To tease out the effect of the cue positions in each adaptation period (baseline, adaptation and post-adaptation), we performed repeated-measures one-way ANOVAs with cue positions (7 positions) as the factor. Bonferroni-corrected pairwise comparisons were used to identify significant differences between each cue position inside of every adaptation period.

The one-way ANOVA for the baseline period revealed a significant main effect of cue position on RRT ($F(6,84) = 34.539$, $p < .001$, $\eta_p^2 = .712$). The pairwise comparisons revealed that cue positions 1 to 3 were all significantly different from cue positions 4 to 7. We can also observe that cue positions 2 and 3 were significantly different from all cue positions except cue position 1, and that cue positions 5 and 6 were significantly different from each other, with the largest facilitation occurring at cue position 6. In summary, this demonstrates that cues presented at or to the left of the fixation position (cue positions 1 to 3) facilitate the reaches in terms of RRT, but that the cues appearing towards the target (cue positions 4 to 7) allow a significantly larger facilitation.

Next, we conducted a one-way ANOVA for the adaptation period. There was a main effect of cue on RRT ($F(6,84) = 15.849$, $p < .001$, $\eta_p^2 = .531$). We followed this up with pairwise comparisons between each cue condition. Similar findings to the baseline period were revealed with slight differences during the adaptation period. First, cue positions 1 and 2 were all significantly different from cue positions 4 to 7. The significantly different degrees of facilitation between cue positions 1 and 2 versus 4 to 7 were maintained during the adaptation period, compared to baseline. The main difference from the baseline period was that cue position 3 was now only different from cue position 5, which was the position with the largest facilitation.

We then conducted a one-way ANOVA on the post-adaptation period, and revealed a main effect of cue position on RRT ($F(6,84) = 16.624$, $p < .001$, $\eta_p^2 = .543$). The pairwise comparisons revealed once again an unequivocal trend of cues presented at or to the left of the fixation position to be significantly different from cues presented to the right of the fixation position. Cue positions 1 to 3 were all statistically different from cue positions 4 to 7. Comparatively to baseline and adaptation, post-adaptation did not have a cue position with a distinctively larger facilitation, but instead showed a relatively similar facilitation at all cues past the fixation position.

Lastly, through paired t-tests in each adaptation period, we compared RRTs when the cue was presented at the actual target (position 5) versus those at the adapted target (position 4) to discern the position at which the cue induced the strongest facilitation. The baseline and post-adaptation periods did not reveal a difference in RRTs between positions 4 and 5 (both $p > 0.05$), while the adaptation period revealed a significant difference between them (position 4: M = -40.1, SD = 15.2; position 5: M = -48.7, SD = 13.8, $t(14) = 2.750$, $p = .016$), with a greater facilitation occurring at position 5.

4.5. Experiment 1 – Discussion

We investigated the effects of exogenous attentional mechanisms on motor planning and execution during a visuomotor adaptation task. All of the participants demonstrated a successful adaptation throughout the experiment. However, even though the motor goal and visual target goal were dissociated during the adaptation period, we found no difference overall between the adaptation periods in terms of reaction times. Additionally, there were also no differences between adaptation periods in terms of normalized reaction times as a function of cue position. Considering that the visual goal was unchanged during the experiment, and that the motor goal was shifted during the adaptation period, these findings suggest that the attentional mechanisms implicated during motor planning rely mainly on the visual goal to prepare the movement, instead of the correctly adapted motor goal.

First, we can observe a warning effect of the cue, which induced facilitation in terms of RRTs in most cued conditions when compared to the neutral, no-cue condition. This replicates our previous work on exogenous cueing during reaches and saccades (Malienko et al., 2018) and is in concordance with the current body of research on the facilitatory effect of distractors during reach movements (Briand, Larrison, & Sereno, 2000; Fischer & Adam, 2001; Maylor, 1985; Maylor & Hockey, 1987; Tassinari, et al., 1993).

Our hypothesis on the attentional facilitation occurring at the later motor goal stage was unsupported by our findings. We expected the adapted period to be facilitated by the cue at the adapted target (position 4), and the baseline and post-adaptation periods to be facilitated the most at the actual target (position 5). We did not find a greater facilitation at position 5 versus position 4 in baseline or post-adaptation periods. However, we observed a significant difference between positions 4 and 5 in the adapted period and position, but in the opposite direction that was hypothesized.

4.6. Experiment 2 – Introduction

The first experiment demonstrated indeterminate findings about the effect of exogenous cues on reaction times during all periods of the visuomotor adaptation task. This may be due to a few factors. First, the specificity of the timings of the cue and the SOA may not have been optimal to give rise to a global effect of cue on reaction times, as was demonstrated in our previous paper. By shortening the cue duration from 33.3 ms to 16.6 ms, this second experiment aims to increase the facilitative effect of the exogenous cue on RTs. Second, differences in amplitudes between baseline and adapted reach movement as well as between the cues may have been insufficient to generate the full extent of a reaching movement; some participants reported using rotational movements of the wrist to complete the movement during the adaptation period. By increasing the amplitudes between cues and targets, and offsetting the target from the start position by one position, participants now move their arm 12° and 18° during adapted and non-adapted periods respectively, instead of 5° and 10°. Third, the presentation of cues at positions away from the target (positions 1 and 2 in the first experiment) showed typical inhibitory effects (relative to the no cue condition) and the effect of distant cues are not entirely relevant to the question asked in this work. Therefore, we reduced the number of cues and only presented cues at positions between fixation and the target position.

4.7. Experiment 2 – Methods and Materials

4.7.1. Participants

We recruited 15 participants (ages: M = 25, SD = 8.3, 9 females). 6 of the participants, including author AM, also took part in the first experiment.

4.7.2. Procedure

The experimental procedure was similar to the first experiment, with the differences being that the start position was at 6° to the left from the center of the screen, the target position was at 12° to the right from the center of the screen, and the cue was presented for 16.6 ms (1 frame) at 1 of 4 possible positions at 0°, 6°, 12°, 18° relative to the center of the screen, offset vertically by 1° above the height of the start position dot (**Fig. 7**). No cue was presented at the start position.

Participants performed two blocks of trials in the second experiment in the same manner as the first experiment. Baseline, adapted and post-adaptation periods were 75 trials long, and gradual onset and offset were 40 trials long. The adaptation in this experiment was based on the same formula as the first experiment. A gain ratio of 1.5 was reached at adaptation period by steps of 0.0128. During adapted trials, participants had to produce movements with a horizontal amplitude 33% smaller than in the baseline trials to correctly align the cursor with the movement target.

Participants completed two blocks of 305 trials each (5 possible cue positions × 15 repetitions during pre-, post- and adaptation trials, and 5 possible cue positions × 8 repetitions during adaptation onset and offset), for a total of 610 trials per participant. There was a 5-10 minute break between the blocks. Participants performed the entire experiment in one session lasting approximately 45 minutes.

4.7.3. Data analysis

We collected a total of 9,150 trials. Offline analyses were performed using MATLAB (The MathWorks, Inc., Natick, MA, United States). The hand movement data was filtered in the same manner as the first experiment. Linear interpolation was required in 9.11% of trials. We first manually removed all faulty trials (20.13% of total trials). Next we removed all trials with reach reaction times under 80 ms and over 500 ms (2.21% of total trials), then all trials with reaction times outside 3 standard deviations of each participant's mean reaction time (0.93% of total trials), trials with amplitudes of less than 10° and more than 20° (5.94% of total trials), trials with start positions outside 3 standard deviations of each participant's mean start position (0.5% of total trials) and trials outside of 1.5° of the unadapted and adapted target amplitudes depending on the experimental period (0.35% of total trials). There remained 6400 trials which were used for analysis (69.95% of total trials).

4.8. Experiment 2 – Results

4.8.1. Typical participant's hand and cursor amplitudes

In **Figure 8**, we illustrate a single participant's hand and cursor amplitudes over the course of the second experiment. As in Figure 2, we plotted an 11-trial moving average (black line) over the hand and cursor trials to highlight the general trend of amplitude changes caused by the different adaptation periods. The general observations for the typical participant amplitudes from the first experiment are in great part reproduced in the second experiment, with a change in the hand reach amplitude during the adaptation period and the post-adaptation period. We further examined the effects of the adaptation periods on amplitudes across all participants in the next section.

4.8.2. Overall amplitudes of adaptation periods

We began by confirming that adaptation effect was present, by looking at overall reach amplitudes during the different adaptation periods (baseline, adaptation, post-adaptation). In **Figure 9**, we plotted each participant's mean amplitudes with the overall mean of each adaptation period. A repeated-measures one-way ANOVA revealed an effect of adaptation ($F(2,28) = 21700.814$, $p < .001$, $\eta_p^2 = .999$). This was followed with Bonferroni-corrected post hoc comparisons between each pair. We observed significant differences between all pairs: between baseline (M = 17.94, SD = .11) and adaptation (M = 12.05, SD = .16) with p < .001; baseline and post-adaptation (M = 17.81, SD = .14) with *p* < .001; adaptation and post-adaptation with *p* < .001. In sum, all participants adapted appropriately during the adaptation period. Because we observed a small but significant difference between baseline and post-adaptation, we compared to see if the amplitudes were different from the target amplitudes in each of the periods. We thus performed one-way t-tests for each period on the difference between the observed amplitude and the corresponding target amplitude. We found a significant difference between post-adaptation amplitudes and the target amplitude, at 18° (*t*(14) = 5.236, *p* > .001), but no difference between baseline amplitudes and the target amplitude (*t*(14) = 2.003, *p* = .065) and between the adapted amplitudes and the adapted target amplitude, at 12° (*t*(14) = 1.241, *p* = .235).

4.8.3. Overall reach reaction times of adaptation periods

We then looked at overall RRT during the different adaptation periods (baseline, adaptation, post-adaptation) to see whether this amplitude adaptation had an effect on RRT. In **Figure 10**, we plotted the participants' mean RRT with the overall mean of each adaptation period. While a repeated-measures one-way ANOVA revealed an effect of adaptation period on RRT (*F*(2,28) = 4.758, *p* = .017, η_p^2 = .254), the post hoc comparisons with Bonferroni corrections did not demonstrate differences between any pair: baseline (M = 191.82, SD = 33.31) and adaptation (M = 201.73, SD = 39.95) with *p* = .073, baseline and post-adaptation (M = 202.29, SD = 35.88) with *p* = .082 and adaptation versus post-adaptation with *p* = .999.

4.8.4. Effect of cue position and adaptation period on normalized reaction times

Next, we investigated the effect of cue position across the different adaptation periods on RT. We only looked at normalized RT, as the facilitation effect of the cue in all conditions was already demonstrated in the first experiment. In **Figure 11**, we plotted the normalized mean RRTs of each adaptation period across all participants. We conducted a two-way ANOVA with adaptation period (3 levels: baseline, adaptation, post-adaptation) and cues (4 positions) as factors. The analyses did not reveal any significance for either main or interaction effects.

We compared RRTs of the cue presented at the actual target (position 3) with those presented at the adapted target (2) with paired t-tests in each adaptation period to discern the position at which the cue caused the largest facilitation. The adapted and post-adaptation periods did not reveal a difference in RRTs between positions 2 and 3 (both $p > 0.05$), while the baseline period revealed a significant difference between them (position 2: M = -21.12, SD = 11.39; position 3: M = -26.32, SD = 16.49, $t(14) = 2.454$, $p = .028$), with a greater facilitation occurring at the actual target (position 3).

4.9. Experiment 2 – Discussion

We studied exogenous attentional mechanisms at the locations most proximate to the target and the adapted location to reduce the scope of the effects of the cue and to clearly differentiate between the motor goal and the visual target during visuomotor adaptation. While all participants successfully adapted during the task, we found no difference in reaction time between the adaptation periods, nor between the cue positions in overall. However, when comparing the normalized reaction times of the cues at the positions of the motor goal and the visual target, we found a difference in the baseline condition, but none in the adapted or post-adaptation conditions, suggesting that the attentional mechanisms during reach planning rely on the visual target more than they do on the motor goal. However, as the visuomotor adaptation starts, progresses, and washes out, the visual target position is no longer different from the motor goal position in terms of facilitation, suggesting interference from the now-dissociated motor goal.

This experiment successfully replicates results from the first experiment, reiterating the general lack of differences in reaction times between adaptation periods or cue positions. However, while a general trend of faster reactions times towards the cued targets was seen in the first experiment, replicating results from our previous research (Malienko et al., 2018), this effect is indiscernible in the second experiment. This could be due to the fact attentional influences, especially exogenous attention, happen on a low spatial frequency (Carretié, Rios, Perianez, Kessel, & Alvarez-Linera, 2012), and that by only looking at a select few positions in the second experiment compared to first experiment, as well to our previous study, the effect washes out and is no longer perceptible due to a large overlap of the coarse spatial resolution of exogenous capture.

4.10. Concluding Discussion

Visuomotor adaptation is a form of learning comprised of both sensory and motor components, which makes it a prime candidate to study the attentional components in play during reach planning. In our experiments, we examined reach movements towards a target while gradually manipulating the visual feedback received by the participants, causing them to correct for perceived perturbations. Concomitantly, we flashed a behaviourally irrelevant cue right before the reach movement occurred. The presentation of a cue before a reach is known to modify its latency (Lee, 1999; McSorley et al., 2006; Sailer et al., 2002; Song and Nakayama, 2006, 2008; Tipper et al., 1997). Our experiments allowed us to discern between attention influences on reach planning at the visual or the motor level by dissociating the actual reaching movement from the visual target, and by measuring the influence of exogenous cues on reach reaction times.

Saccadic adaptation is another form of visuomotor adaptation during which participants adjust their saccade parameters in order to adapt to an artificial shift in either direction or size of movement. Previous studies on saccadic eye movements support a stronger role of exogenous attention at the motor level. It has also been previously shown that exogenous cues flashed at the saccade goal rather than at the target location affected saccade latencies for adapted saccades where the saccade goal and the target location were dissociated. However, our findings were not consistent with previous findings in terms of attentional effects on adapted movements. Indeed, while our participants were able to successfully adapt to visuomotor gain changes during both experiments, they did not show facilitated reach reaction times at the motor goal versus the target location.

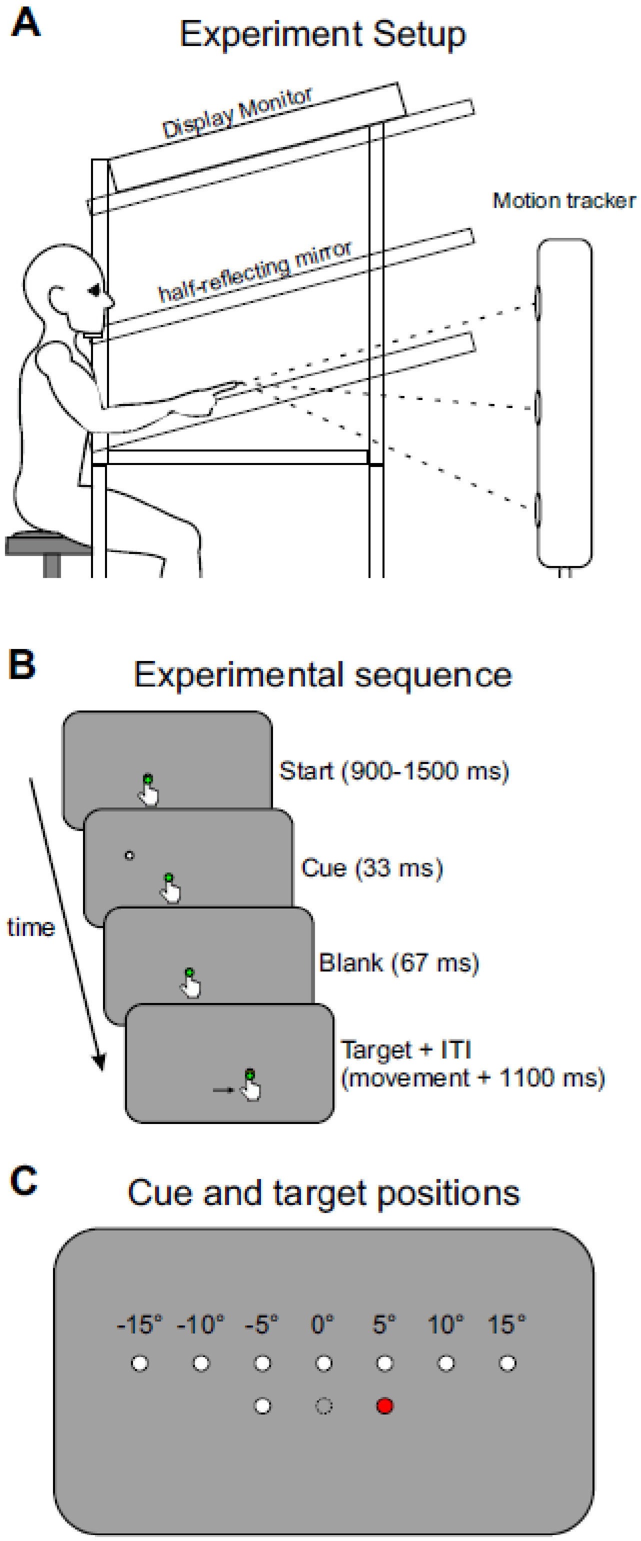
Exogenous attentional influences on saccades and reaches are one of the multiple behavioral differences between saccadic and arm motor systems. One possible explanation for the differences between these two motor systems is that attention influences each of them at different processing stages in the visual to motor transformation. Reaches seem to be affected at an early visual stage of planning, while saccades are affected at a later motor planning stage. Consistent with this, attentional mechanisms in reaches, such as target selection, have been demonstrated at the level of the posterior parietal cortex (PPC) (Corbetta and Shulman 2002; Corbetta et al. 2008), more precisely in the parietal reach region (PRR) (Scherberger & Andersen, 2007). The PRR reflects activity during reach preparation and has been suggested to only indirectly influence the movement initiation through a bottleneck mechanism, versus being a region which directly exerts influence capable of changing the movement output (Day & Lyon, 2000), i.e. motor set (Evarts et al., 1984).

4.11. Acknowledgements

The authors would like to thank the participants for their time and efforts in this experiment, Romain Fournet for his technical assistance, and the student members of the VISATTAC laboratory for the stimulating discussions that helped improve this paper. AM received support from an MSc excellence and mobility scholarship from Faculté des Études Supérieures et Postdoctorales et l'École d'Optométrie de l'Université de Montréal (FESP-ÉOUM). AZK was funded by the Natural Sciences and Engineering Research Council of Canada (NSERC) and supported by the Canada Research Chair program.

4.12. Figures

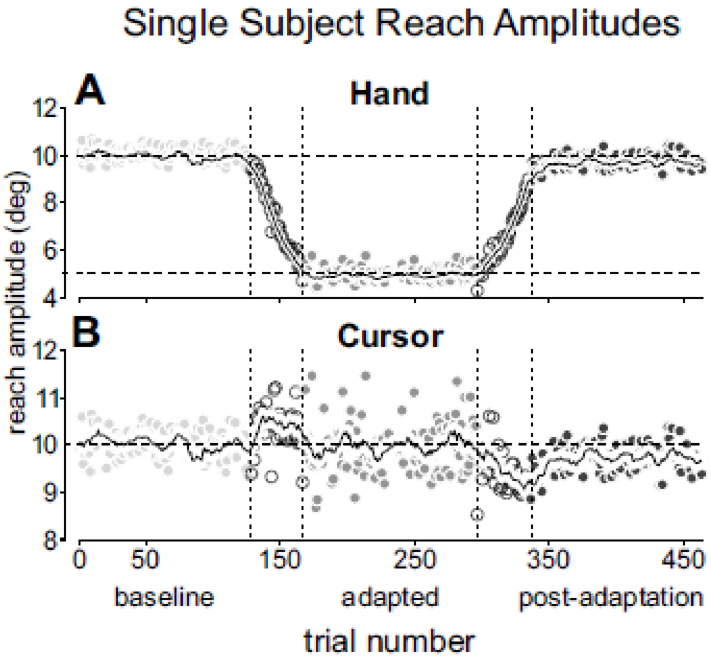
4.12.1. Figure 1



4.12.1.1. Figure 1 Legend

Figure 1. (A) Experimental setup. Participants were seated in front of a three-leveled augmented reality setup with a display monitor on the top level on which stimuli were presented, a half-reflecting mirror on the middle level, and a solid platform on the bottom level on which the participants moved their arm freely. A motion-tracking camera placed behind the setup recorded the 3D positions of the sensor placed on the index finger on the right hand of the participant (dotted lines). **(B) Experimental sequence.** Each trial began with participants aligning their index finger, seen as a green dot, on a white start position dot at 5° to the left from the center of the screen for a random interval between 900-1500 ms. Next, a cue appeared at 1 of 7 possible positions for 33 ms (leftmost position demonstrated). After the cue disappeared, a blank screen was presented for 67 ms. This was followed by the presentation of a target (red dot) at 5° to the right from the center of the screen. As soon as the target appeared, participants were instructed to reach towards the target with their hand. The inter-trial interval (ITI) lasted 700 ms after the reach movement was initiated. **(C) Cue and target positions.** The cue was presented at -15°, -10°, -5°, 0°, 5°, 10° or 15° relative to the center of the screen, offset vertically by 5° above the start and target positions. The start position and the target position were presented respectively at 5° to the left and to the right from the center of the screen. For reference, the adapted target position is shown at 0° from the center, but it was not physically represented during the experiment.

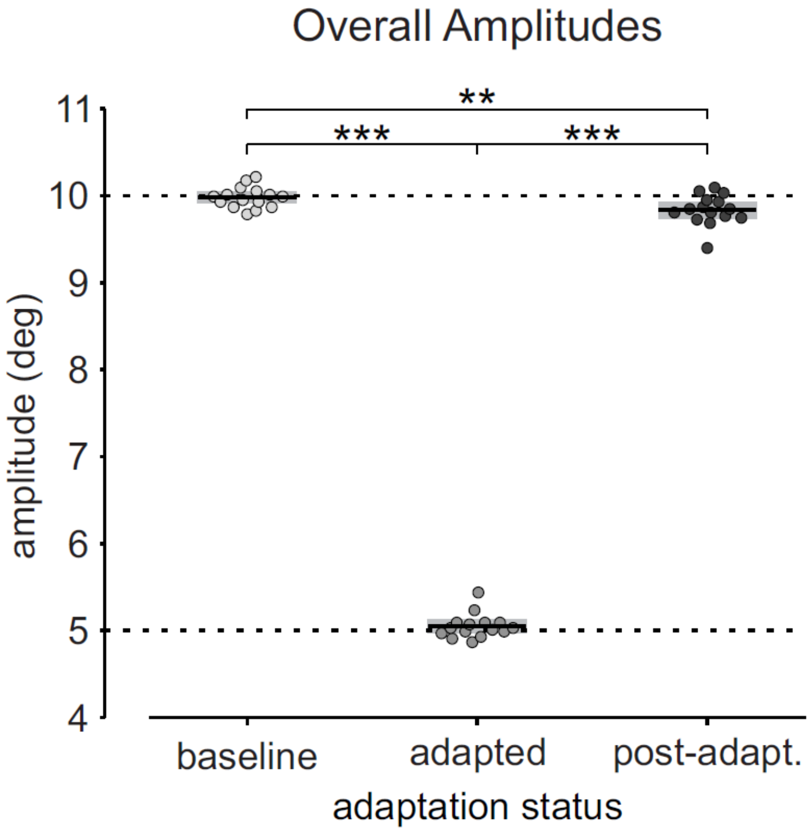
4.12.2. Figure 2



4.12.2.1. Figure 2 Legend

Figure 2. Representative participant reach amplitudes of hand and cursor of one block. The trials of one experiment block are shown on the x-axis, and the amplitude in visual degrees are shown on the y-axis. Each trial is represented by a circle. Trials 1 to 127 (light-gray) are baseline trials, trials 128 to 168 (empty circles) are adaptation onset trials, trials 169 to 296 are adapted trials (medium-gray), trials 297 to 336 are adaptation offset trials (empty circles), and trials 337 to 464 are post-adaptation trials (dark-gray). The vertical dotted lines represent a change in adaptation period. The horizontal dotted lines represent the actual target amplitude (10°) and the adapted target amplitude (5°). A moving average of 11 trials is represented as a black line over the individual trials. **(A)** shows hand amplitude data. **(B)** shows cursor amplitude data. The hand and cursor data are taken from the same participant during the same block, and trials are correlated one-to-one.

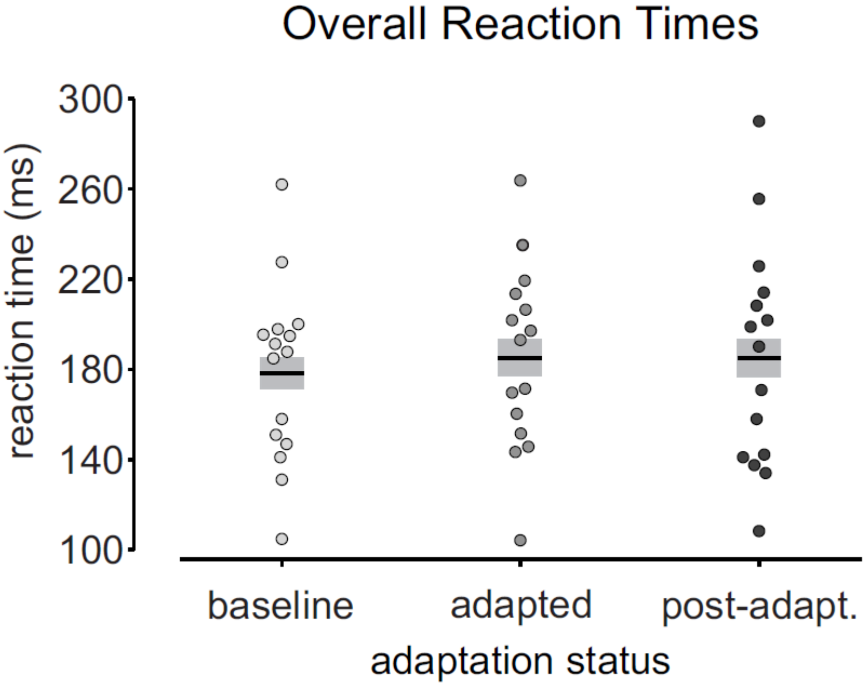
4.12.3. Figure 3



4.12.3.1. Figure 3 Legend

Figure 3. Overall amplitudes. The mean amplitude data are plotted for baseline, adapted and post-adaptation periods and are represented by a black bar. Each dot represents one participant. The light gray box behind the dots represents the 95% confidence interval (±1.96 standard error of the mean across participants). ** indicates p<.01, *** indicates p<.001.

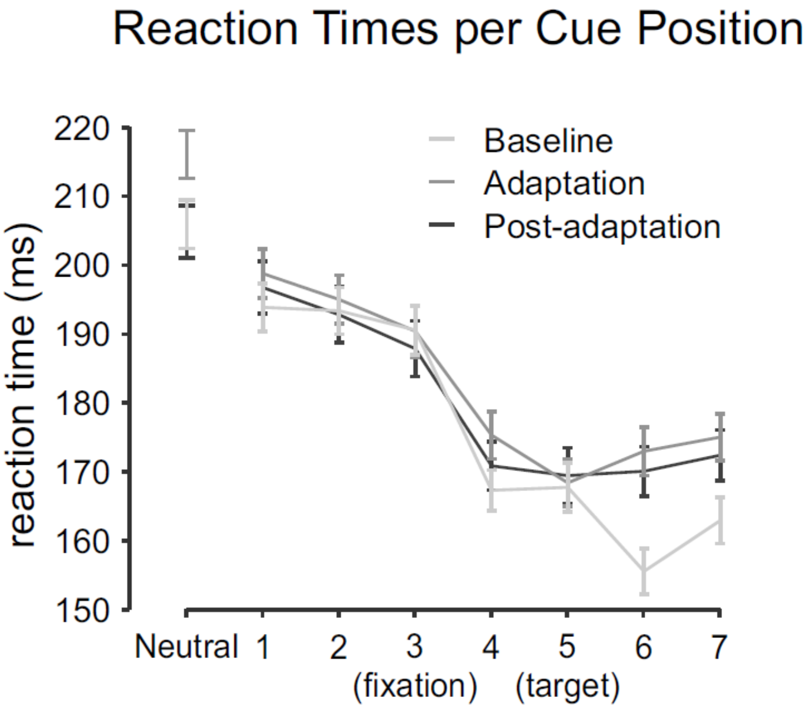
4.12.4. Figure 4



4.12.4.1. Figure 4 Legend

Figure 4. Overall reaction times. The mean reaction time data are plotted for baseline, adapted and post-adaptation periods and are represented by a black bar. Each dot represents one participant. The light gray box behind the dots represents the 95% confidence interval (±1.96 standard error of the mean across participants).

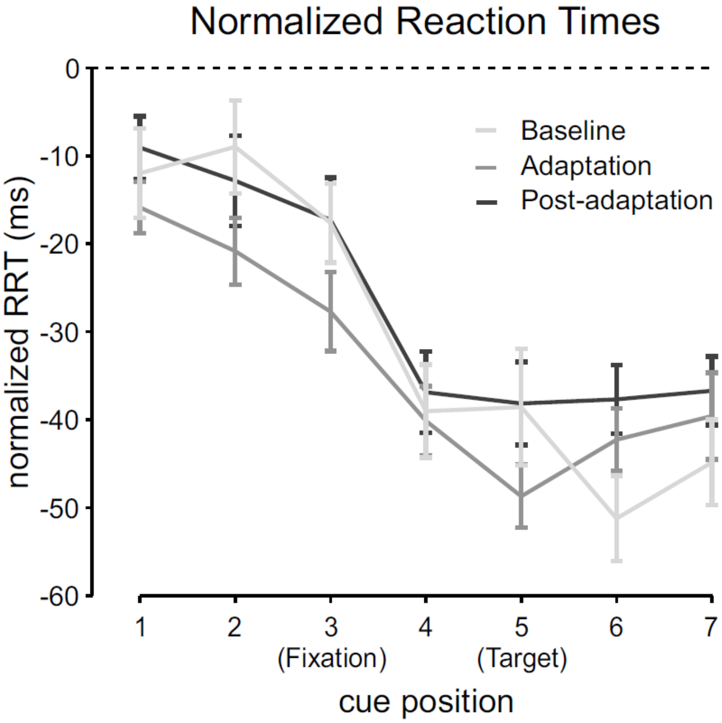
4.12.5. Figure 5



4.12.5.1. Figure 5 Legend

Figure 5. **Mean reaction times as a function of cue position.** The light-gray line represents the baseline period data, the medium-gray line represents the adapted period and the dark-gray line represents the post-adaptation period. On the x-axis is cue position and on the y-axis is the reaction time in milliseconds. Error bars represent SEM (standard error of the mean).

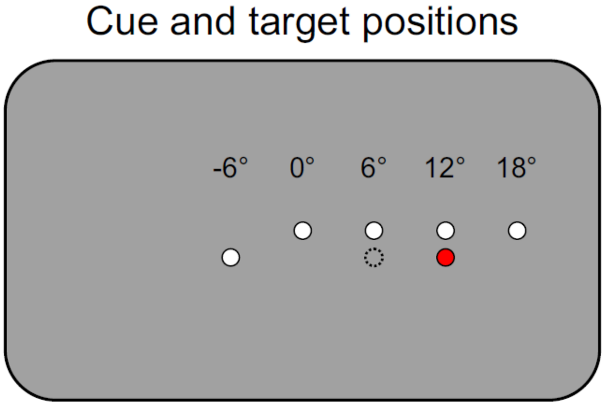
4.12.6. Figure 6



4.12.6.1. Figure 6 Legend

Figure 6. **Mean normalized reaction times as a function of cue position.** The light-gray line represents the baseline period data, the medium-gray line represents the adapted period and the dark-gray line represents the post-adaptation period. On the x-axis is cue position and on the y-axis is the normalized reaction time in milliseconds, which is the difference between the mean reaction time in a cue trial and the mean reaction time in the no-cue trials. Error bars represent SEM (standard error of the mean). The dotted reference line represents the reaction time for the no-cue trials. Negative normalized reaction times are those that were faster than the no-cue trials.

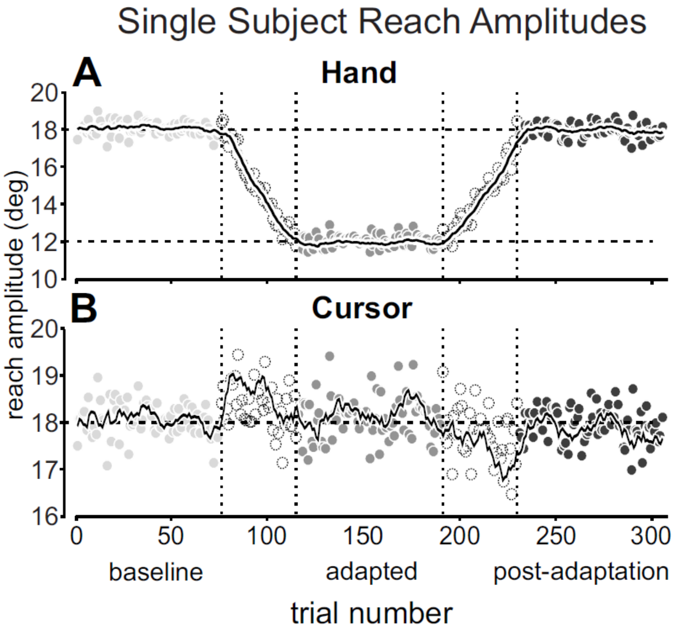
4.12.7. Figure 7



4.12.7.1. Figure 7 Legend

Figure 7. **Cue and target positions.** The cue was presented at -6°, -0°, 6°, 12° or 18° relative to the center of the screen, offset vertically by 1° above the start and target positions. The start position and the target position were presented respectively at -6° and 12° relative to the center of the screen. For reference, the adapted target position is shown at 6° to the right of the center, but it was not physically represented during the experiment.

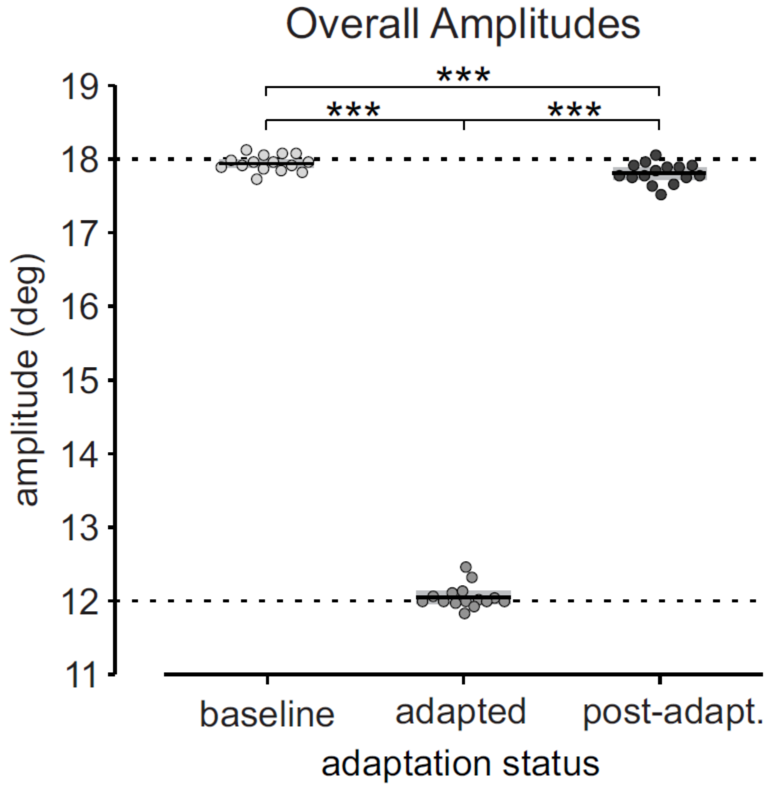
4.12.8. Figure 8



4.12.8.1. Figure 8 Legend

Figure 8. **Representative participant reach amplitudes of hand and cursor of one block.** The trials of one experiment block are shown on the x-axis, and the amplitude in visual degrees are shown on the y-axis. Each trial is represented by a circle. Trials 1 to 75 (light-gray) are baseline trials, trials 76 to 115 (empty circles) are adaptation onset trials, trials 116 to 190 are adapted trials (medium-gray), trials 191 to 230 are adaptation offset trials (empty circles), and trials 231 to 305 are post-adaptation trials (dark-gray). The vertical dotted lines represent a change in adaptation period. The horizontal dotted lines represent the actual target amplitude (18°) and the adapted target amplitude (12°). A moving average of 11 trials is represented as a black line over the individual trials. **(A)** shows hand amplitude data. **(B)** shows cursor amplitude data. The hand and cursor data are taken from the same participant during the same block, and trials are correlated one-to-one.

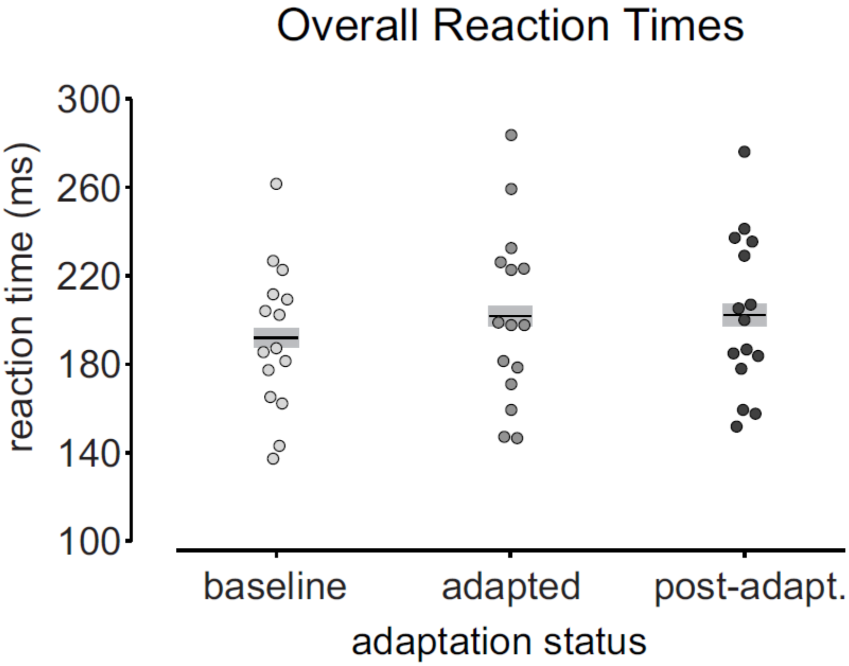
4.12.9. Figure 9



4.12.9.1. Figure 9 Legend

Figure 9. Overall amplitudes. The mean amplitude data are plotted for baseline, adapted and post-adaptation periods and are represented by a black bar. Each dot represents one participant. The light gray box behind the dots represents the 95% confidence interval (±1.96 standard error of the mean across participants). *** indicates p<.001.

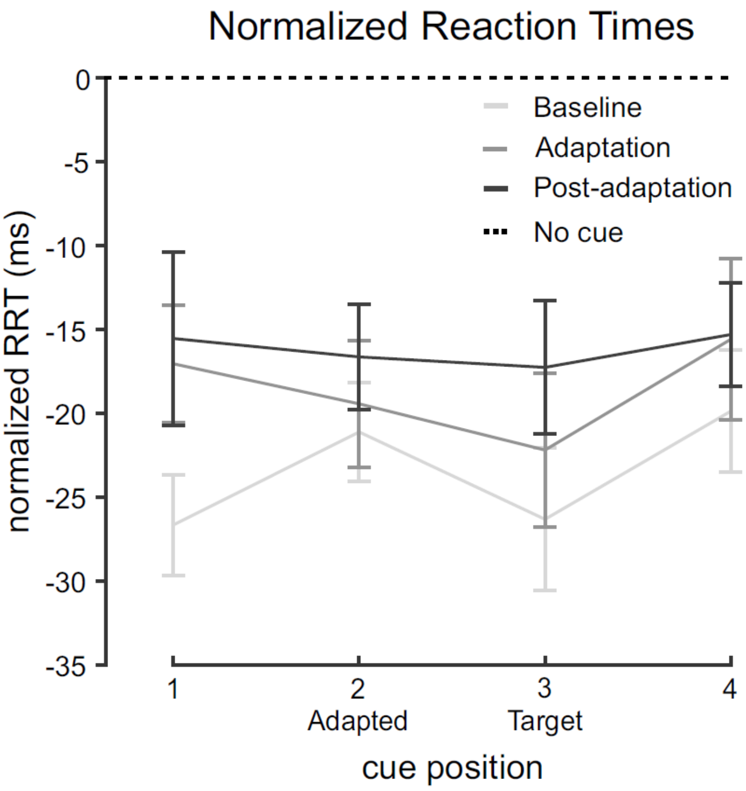
4.12.10. Figure 10



4.12.10.1. Figure 10 Legend

Figure 10. Overall reaction times. The mean reaction time data are plotted for baseline, adapted and post-adaptation periods and are represented by a black bar. Each dot represents one participant. The light gray box behind the dots represents the 95% confidence interval (±1.96 standard error of the mean across participants).

4.12.11. Figure 11



4.12.11.1. Figure 11 Legend

Figure 11. **Mean normalized reaction times as a function of cue position.** The light-gray line represents the baseline period data, the medium-gray line represents the adapted period and the dark-gray line represents the post-adaptation period. On the x-axis is cue position and on the y-axis is the normalized reaction time in milliseconds, which is the difference between the mean reaction time in a cue trial and the mean reaction time in the no-cue trials. Error bars represent SEM (standard error of the mean). The dotted reference line represents the reaction time for the no-cue trials. Negative normalized reaction times are those that were faster than the no-cue trials.

5. Discussion

La discussion abordée dans les paragraphes qui suivent permettra tout d'abord de réitérer de façon concise les résultats obtenus lors de nos études. Par la suite, les applications potentielles des études seront abordées sous différents angles d'approche, notamment la remédiation des déficits attentionnels par la présentation de stimuli visuels exogènes et par l'adaptation visuomotrice. Les limites de notre projet de recherche vont être également soulignées. Enfin, une synthèse globale des résultats suivie des directions sur les recherches futures va conclure la discussion.

5.1. Résumé des résultats

L'objectif principal de ce projet de recherche était d'étudier l'interaction entre la sélection attentionnelle et la planification du mouvement. Pour ce faire, nous avons conçu deux études aux paradigmes différents qui ont permis de mesurer les effets de la modulation de l'attention exogène sur les mouvements des yeux et des bras. Nos deux études proposent des résultats complémentaires.

La première étude présentait une tâche motrice simple qui impliquait une planification et une exécution des mouvements des yeux et/ou du bras vers une cible distante durant laquelle un indice attentionnel était présenté à des endroits prédéterminés afin de moduler l'attention lors du processus de planification motrice. Cette étude a montré une tendance globale similaire en termes de temps de réaction entre les saccades et les mouvements de la portée du bras en réponse à des stimuli exogènes. En effet, quand un stimulus était présenté dans les environs immédiats de la cible, ces deux effecteurs présentaient les temps de réaction les plus rapides, puis graduellement plus lents quand les stimuli étaient présentés vers les extrémités de la cible. De plus, nous avons observé une différence entre les mouvements des deux effecteurs en termes de temps de réaction dû à la présentation d’un stimulus exogène. Les temps de réaction des saccades étaient généralement inhibés, c’est-à-dire ralentis, lors de la présentation d’un stimulus exogène loin de la cible, tandis que ceux des mouvements de la portée du bras étaient généralement facilités, c’est-à-dire plus rapides, dû à la présence du stimulus, surtout en proximité de la cible. Cette tendance temporelle générale des mouvements des yeux et de la main suggère que la planification motrice ne dépend pas de l’effecteur utilisé, mais semble être partagée par l’ensemble des effecteurs.

Additionnellement, la première étude nous a permis de constater des résultats sur les différences entre les mouvements produits seuls ou en combinaison avec un deuxième effecteur. Bien que, globalement, nous n’avons pas pu démontrer de différence sur le plan temporel entre les mouvements produits seuls et les mouvements en combinaison, nous avons démontré qu’il y avait une différence en termes d’amplitude entre les saccades seules et celles combinées à un mouvement de la portée du bras vers la même cible. Ces résultats soulignent encore une fois l’idée d’une planification partagée des deux effecteurs comme démontré par la tendance similaire des amplitudes et temps de réaction des mouvements de la main et des yeux. Cependant, en montrant une différence entre les saccades produites seules et combinées, cela suggère une étape de planification du mouvement à part, une étape propre à l’effecteur utilisé.

La deuxième étude consistait d’une tâche d’adaptation visuomotrice durant laquelle était présenté un stimulus visuel exogène afin d’évaluer les effets de l’attention sur la planification de mouvements de la portée du bras vers une cible, tout en modifiant la rétroaction visuelle de la position du bras. Ceci nous a permis de séparer la planification motrice de la cible visuelle durant le point culminant de l’adaptation visuomotrice. En étudiant l’influence de la modulation attentionnelle lors de la préparation du mouvement dans un contexte d'adaptation visuomotrice, il était possible de tester si la modulation affectait la première phase de la planification motrice, où seul le vecteur de mouvement entre la position de départ et la cible était connu, ou si la modulation attentionnelle affectait une phase tardive de la planification, quand celle-ci était presque complétée. En d'autres mots, l'adaptation visuomotrice a permis de séparer le plan moteur du vecteur visuel. Cette étude a démontré, à travers deux expériences, qu'il n'y avait pas de différence entre les mouvements produits avant et pendant l'adaptation visuomotrice, suggérant que l'attention affecte les mouvements de la portée du bras dès la première phase de la planification motrice. Ces résultats vont dans le même sens que notre première étude, soulignant que la planification du mouvement est en partie indépendante de l'effecteur utilisé.

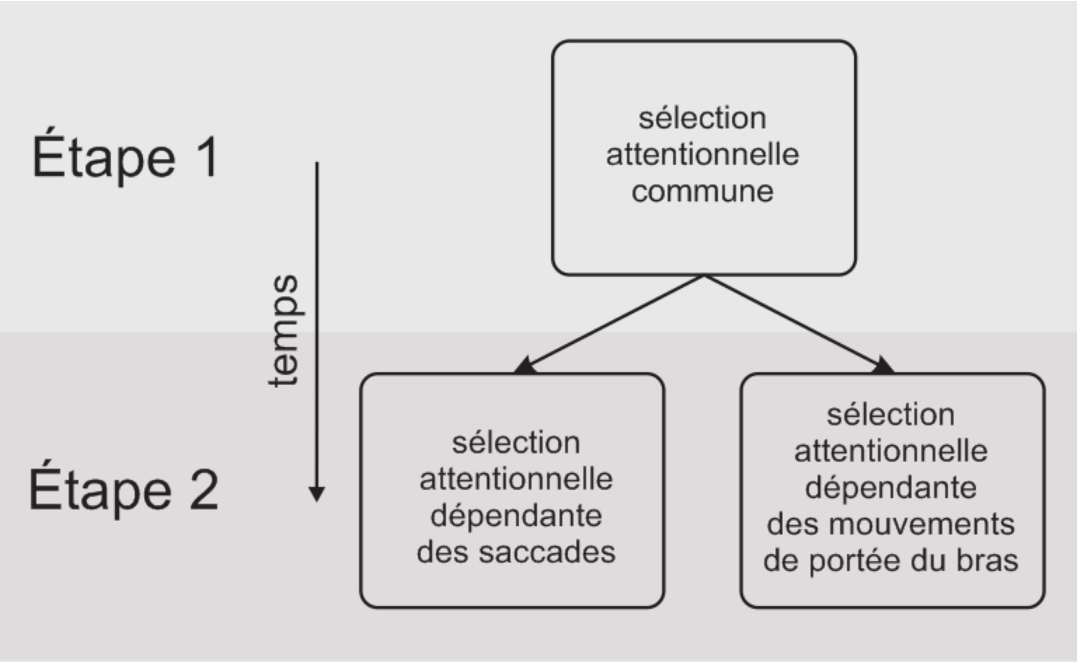
Ensemble, les similarités et les différences des caractéristiques temporelles et spatiales des saccades et des mouvements de la portée du bras causés par les indices attentionnels durant leurs planifications motrices suggèrent la présence de mécanismes attentionnels opérant sur deux niveaux distincts. Les deux niveaux, l'un global et l'autre dépendant de l'effecteur, peuvent être observés à travers les effets de la modulation exogène de l'attention sur le temps de réaction et l'amplitude des mouvements, et ce, dans le contexte de la préparation d'un mouvement simple ou combiné, ainsi que dans celui d'une adaptation à un changement visuomoteur.

Le modèle à deux étapes préposé dans ce projet de recherche vise à intégrer les connaissances actuelles sur le rôle des systèmes attentionnels dans la préparation du mouvement des yeux et des bras. La première étape consiste d'un traitement sensoriel global, indépendant des effecteurs utilisés, impliquant majoritairement le CPP et opérant plus tôt dans le processus de planification motrice. La deuxième étape, affectée par le traitement effectué lors de la première étape, génère ensuite des comportements moteurs spécifiques à l'effecteur utilisé. Cette deuxième étape, intervenant plus tard dans le processus de la planification motrice, impliquerait de façon séparée les parties liées aux effecteurs utilisés, notamment la partie médiane intrapariétale du CPP pour les mouvements de la portée du bras (Grefkes & Fink, 2005), puis les champs oculaires frontaux ainsi que la partie latérale intrapariétale du CPP pour les saccades. Récemment, il a été démontré que les régions du CPP, notamment le PLI et le PRR (parietal reach region) ne sont pas aussi spécifiques aux effecteurs qu'il a précédemment été établi. Les résultats de Mooshagian & Snyder (2018) dans une étude de coordination main-yeux démontrent que ni l'une ou l'autre de ces régions du CPP était systématiquement active avant une saccade vers le bras porté vers un objet quand le mouvement était bimanuel. Cela démontrait que la coordination de ces deux effecteurs se passe en effet à l'extérieur du CPP.

Nos études ont démontré premièrement que les saccades et les mouvements de la portée du bras sont tous les deux initialement affectés de façon globale par l'indiçage attentionnel, tel que souligné par les influences attentionnelles similaires dans le décours temporel des mouvements produits et, deuxièmement, que les mouvements de la portée du bras semblent être affectés plus tôt que les saccades quand nous contrastons nos données avec une étude précédente sur l'adaptation saccadique (Khan, Heinen, & McPeek, 2010). Dans l'ensemble, nos études et la recherche précédente semblent indiquer que l'indiçage attentionnel lors de la première étape du modèle attentionnel de la préparation du mouvement produit plusieurs des effets différents dépendant de l'effecteur.

Cela dit, une théorie alternative pourrait expliquer nos résultats. Les différences dans les tendances des temps de réaction des saccades et des mouvements de la portée du bras dans le premier article, puis les différences entre les influences de l'attention exogène sur les objectifs des mouvements des saccades (Khan et al., 2011) versus ceux des mains ne sont pas incohérentes avec un modèle de flux de traitements parallèles. Cependant, la notion d'une première étape de traitement partagée entre les deux effecteurs qui a pour résultat une tendance similaire des temps de réaction pour les mains et les yeux semble plus efficace et économique en terme de traitement requis en comparaison avec deux flux de traitements indépendants sur lesquels les processus attentionnels entrainent des influences temporelles presque identiques.

Figure 5.1.1 Modèle attentionnel à deux étapes de la planification des mouvements saccadiques et de portée du bras



5.2. Applications de l’étude

Notre proposition d’un modèle attentionnel à deux étapes de la planification des mouvements saccadiques et de portée du bras a été démontrée dans un contexte d’adaptation visuomotrice, ainsi que dans un contexte de coordination des yeux et de la main. Étant axé sur la recherche fondamentale, ce projet d’étude présente des applications concrètes actuellement limitées, mais permet d’accroître les connaissances dans le domaine de l’attention et l’action afin d’améliorer la pratique clinique. Nous allons donc nous concentrer sur une seule application qui découle de notre projet d’étude: l’utilisation de l’attention visuelle pour remédier aux déficits moteurs.

5.2.1. L’utilisation de l’attention visuelle pour la remédiation des déficits moteurs

Les dysfonctions attentionnelles sont l’un des déficits cognitifs les plus communs résultants d’un traumatisme crânio-cérébral (TCC) (van Donkelaar et al., 2005) ou d’un accident vasculaire cérébral (AVC) (Loetscher & Lincoln, 2013), affectant plus de 10 000 Canadiens par année (Colantonio et al., 2010; Faul & Coronado, 2015) et plus de 80% de tous les patients ayant des atteintes cérébrales diverses (Leclercq & Sturm, 2002). Un nombre de recherches a démontré qu’une population de patients présentant des déficits attentionnels suite à un AVC ou un TCC pourrait bénéficier d’une rééducation ou réadaptation attentionnelle (Gray & Robertson, 1989; Sturm et al., 2002; Sturm, Wilmes, Orgass, & Hartje, 1997), menant ultimement à une amélioration de certains aspects attentionnels tels que la sélection, la vigilance, l’alerte, et l’attention divisée. D’autres recherches ont aussi démontré que les bienfaits d’une réadaptation de l’attention avaient des retombées positives sur d’autres fonctions cognitives, notamment la mémoire (Strache, 1987; Sturme et al., 1997), et amélioraient généralement la qualité de vie des patients (Ben-Yishay, Silver, Piasetsky, & Rattok, 1987; Sohlberg & Mateer, 1989).

Une des autres majeures conséquences des AVC et TCC sont les déficits moteurs qui affectent le cortex moteur et les mouvements des bras dans l'hémicorps controlatéral de la lésion. Parmi les déficits les plus rapportés sont une faiblesse des mouvements et des problèmes d'exécution motrice, tels que les mouvements de la portée du bras et le pointage du doigt. Un effort important a été consacré à la recherche dans le domaine de la réadaptation motrice des membres supérieurs suite à des lésions cérébrales causées par des TCC ou des AVC. Une des avenues de recherche est l'efficacité des thérapies ayant pour but d'améliorer l'exécution de ces mouvements à l'aide. Une technique couramment utilisée est un entrainement répétitif d'un mouvement isolé du membre atteint afin d'induire des changements dans le cortex cérébral favorisant une récupération des comportements moteurs (Bütefisch, Hummelsheim, Denzler, & Mauritz, 1995; Cirstea & Levin, 2007; Fisher & Sullivan, 2001; Timmermans, Seelen, Willmann, & Kingma, 2009; Wade, 2000; Woldag & Hummelsheim, 2002).

Nous proposons que l'utilisation de l'attention exogène en combinaison de ces thérapies puisse s'avérer bénéfique au réapprentissage et à une meilleure réadaptation des mouvements du bras chez les patients affectés par les AVC. L'attention visuelle a été étudiée dans des contextes de réadaptation des patients atteints d'un AVC dans plusieurs contextes différents, notamment durant une tâche de conduite simulée (Mazer, Sofer, Korner-Bitensky, Gelinas, Hanley, & Wood-Dauphinee, 2003), et durant une tâche de recherche visuelle (Robertson, Ridgeway, Greenfield, & Parr, 1997). Cependant, l'utilisation des stimuli exogènes comme outil principal pour la réadaptation motrice n'a pas auparavant été explorée. L'utilisation d'une tâche impliquant des stimuli exogènes et des mouvements spécifiques aux dysfonctions de chaque patient permettrait de mieux cibler un regain des comportements moteurs causés par la lésion.

De plus, nos études ont démontré la présence d'une étape commune de la préparation motrice affectant les yeux et les bras de façon globale et similaire. Dans les cas des patients ayant une vision inaffectée, il serait possible d'utilisation ces deux effecteurs en combinaison dans une tâche de réadaptation afin de mener à des améliorations au niveau du regain d'un contrôle accru des mouvements du bras. La tâche consisterait à exécuter des mouvements systématiques simultanés des yeux et des bras vers une même cible, aidés par la présence d'indices exogènes. Bien qu'il semble que les patients, dans leur vie de tous les jours, bougent souvent leurs bras et leurs yeux vers des endroits similaires de façon simultanée, l'addition d'indices exogènes jumelée à une répétition accrue des mouvements produits occasionnerait potentiellement des meilleurs bénéfices, et ce, plus rapidement. Étant donné l'intersection importante entre les réseaux neuronaux impliqués dans la préparation du mouvement des yeux et des bras, et basé sur nos résultats sur une étape commune de la préparation motrice, nous proposons même que l'utilisation seule des saccades puisse s'avérer comme étant une option pour commencer la réadaptation chez les patients ayant perdu toute ou la majeure partie de la motricité du bras de l'hémicorps controlatéral de la lésion.

5.3. Limites

Certaines limites aux études présentées demandent à être considérées. Premièrement, la portée de nos études est limitée à étudier les effets de la modulation attentionnelle sur les caractéristiques temporelles et spatiales des saccades et les mouvements de la portée du bras. Plus précisément, les tâches utilisées durant les études étaient conçues de manière à cibler les effets de l'attention exogène. Cependant, l'attention exogène ne représente qu'une moitié du contrôle attentionnel. L'attention endogène, l'autre moitié indispensable au contrôle attentionnel, n'a pas été étudiée lors de nos études. Deuxièmement, les effets étudiés de l'attention exogène sur les mouvements des yeux et du bras étaient restreints au temps de réaction et à l'amplitude des mouvements. Bien que nous voulions étudier les saccades et les mouvements de la portée du bras sur un plan temporel et spatial, les caractéristiques étudiées ne représentent pas pleinement la complexité cinématique et la dynamique de ces mouvements.

5.3.1 L'attention endogène

Le découpage conceptuel de l'attention en deux moyens d'orientation, endogène et exogène, est basé sur des différences au niveau du traitement, du décours temporel et de leur relation avec la mémoire de travail (Pinto, van der Leij, Sligte, Lamme, & Scholte, 2013; van Zoest, Donk, & Theeuwes, 2004). En effet, l'attention endogène est considérablement différente de l'attention exogène, puisqu'elle est déployée de façon majoritairement volontaire, mais requiert plus de temps pour entrer en action, versus l'attention exogène qui a un décours plus rapide et majoritairement automatique (Mayer, Dorflinger, Rao, & Seidenberg, 2004; Santangelo & Spence, 2008; Theeuwes, 1991). Cela dit, l'intégration de ces deux types d'attention est fondamentale à la sélection et au contrôle attentionnel.

L’attention endogène présente quelques avantages par rapport à l’attention exogène, notamment par rapport au traitement perceptuel lors des conditions de faible sensibilité, p. ex. des tâches de contraste (MacLean et al., 2009). Cependant, les effets de l’attention endogène sur la préparation du mouvement n’ont pas été, à notre connaissance, directement étudiés. Nous spéculons que l’attention endogène joue un rôle complémentaire à l’attention exogène durant les étapes de la préparation motrice, et qu’en permettant un meilleur traitement perceptuel des stimuli visuels, elle réduirait la variabilité de l’amplitude et du temps de réaction des mouvements des bras et des yeux produits vers une cible donnée.

5.3.2 La cinématique et dynamique des saccades et des mouvements de la portée du bras

Nous avons étudié les effets de l’attention exogène sur la planification des saccades yeux et de portée de la main par l’entremise du temps de réaction et de l’amplitude des mouvements. Cependant, ces deux caractéristiques des mouvements ne dressent qu’un portrait partiel des saccades et des mouvements de la portée du bras. Pour avoir un profil cinématique et dynamique complet des mouvements étudiés, il nous aurait fallu analyser plusieurs autres caractéristiques, tels la trajectoire, la précision et l’exactitude.

L’influence de l’attention sur la préparation des saccades et des mouvements de la main a été démontrée à travers les effets de l’indiçage attentionnel sur les trajectoires des mouvements. Un grand nombre d’études sur les trajectoires des saccades (McSorley, Haggard, & Walker, 2004; Sheliga, Riggio, & Rizzolatti, 1994, 1995; Van der Stigchel & Theeuwes, 2005, 2008; McPeek, Han, & Keller, 2003; McPeek & Keller, 2001), des mouvements de la main (Howard & Tipper, 1997; Song & Nakayama, 2006, 2008; Tipper, Howard, & Jackson, 1997) ont dévoilé un effet systématique de déviation de la trajectoire lors de la présentation d’indices exogènes avant, ou lors des mouvements produits. Dans le même ordre d'idée, la précision et l'exactitude sont d'autres caractéristiques mesurables importantes dans le contexte de la préparation du mouvement saccadique et du bras, affectées de façon indépendante à la trajectoire. Ces deux caractéristiques spatiales des mouvements ont été liées au détournement de l'attention visuelle et jouent un rôle important dans l'identification perceptuelle des objets (Gersh, Kowler, Schnitzer, & Dosher, 2008; Kowler, Anderson, Dosher, & Blaser, 1995; Wilder, Kowler, Schnitzer, Gersch, & Dosher, 2009), démontrant des mécanismes attentionnels généralisables à des contextes de préparation motrice.

De plus, ayant des caméras du suivi de l'œil permettant une résolution spatiale et temporelle considérable, nous aurions pu étudier les microsaccades, des mouvements de fixation de l'œil. Les microsaccades sont des saccades de petite amplitude, d'environ 12 minutes d'arc (1/5^{e} d'un degré visuel), qui ont comme fonction de maintenir une vision des objets stationnaires de l'environnement visuel en stimulant les neurones visuels en réponse à ceux-ci (Martinez-Condez, Macknik, Troncoso, & Hubel, 2009; Rolfs, 2009). Sans ces mouvements involontaires, une personne devient fonctionnellement aveugle pour des objets stationnaires. Elles sont modulables par un indiçage attentionnel et sont influencées par la préparation des saccades et des mouvements de la main (Engbert & Kliegl, 2003; Hafed, Chen, & Tian, 2015; Pastukhov, Vonau, Stonkute, & Braun, 2013), suggérant des liens avec des mécanismes opératoires de l'attention visuelle couverte. L'étude des microsaccades s'avère une excellente opportunité d'étudier les influences de l'attention visuelle sur la préparation du mouvement.

5.4. Synthèse globale

Nos études avaient pour but de distinguer les niveaux de traitement attentionnel durant la planification du mouvement des yeux et de la portée du bras à travers le temps de réaction et l'amplitude des mouvements. Le but de nos études était de concilier les recherches antérieures présentant des conclusions divergentes au sujet du rôle de la sélection attentionnelle dans la préparation et la génération des mouvements de la main et des yeux. Nous avons exploré les effets de la présentation d'un stimulus exogène durant la planification de mouvements seuls ou combinés, dans un premier temps lors d'une tâche de mouvement simple, et dans un deuxième temps dans une tâche d'adaptation visuomotrice. Par l'intermédiaire des effets du stimulus sur les caractéristiques des mouvements, nos trouvailles reflètent des processus dépendants de l'effecteur, et d'autres processus globaux, indépendants de l'effecteur. Nous suggérons que ces deux processus attentionnels travaillent en parallèle pour planifier les mouvements. Dans leur ensemble, nos études approfondissent la compréhension des mécanismes opérationnels de l'attention exogène sur les mouvements des yeux et des mains, du processus de la planification du mouvement, ainsi que de l'interaction entre les systèmes sensoriels et moteurs.

5.5. Directions futures

L’objectif général de ce projet était d’élaborer sur les connaissances se rapportant aux mécanismes attentionnels lors de la planification des mouvements de saccade et de la portée du bras. Les réponses apportées par notre recherche étaient multiples et complexes, mais ne dressent qu’un portrait partiel des influences attentionnelles sur la préparation des mouvements. Nous suggérons trois potentielles voies d’investigation pour dresser un portrait plus complet de cette problématique et d’analyser davantage notre hypothèse d’un modèle attentionnel à deux étapes : l’étude de l’attention endogène lors de la planification des mouvements, l’étude des conséquences de lésions cérébrales dans les régions impliquées dans la préparation du mouvement et la neurostimulation non invasive lors de la planification des mouvements.

5.5.1. Étude de l’attention endogène lors de la planification des mouvements saccadiques et de la portée du bras

Pour pallier l’une des principales limites de nos présentes études, nous proposons d’étudier la planification des mouvements dans un contexte de modulation de l’attention endogène. Des études précédentes ont démontré l’implication de l’attention endogène lors des mouvements du bras (Bekkering & Neggers, 2002; Gutteling, Kenemans, & Neggers, 2011), suggérant que l’attention endogène pourrait jouer un rôle complémentaire à l’attention exogène dans la planification motrice (Perry & Fallah, 2017). L’étude de l’orientation spatiale de l’attention par l’entremise des processus endogènes dans un contexte de préparation de mouvement de la portée du bras et des saccades présenterait un complément considérable aux connaissances actuelles sur l’indiçage exogène, incluant les deux articles présentés dans ce mémoire. Une manière d’étudier l’impact de l’attention endogène sur la préparation des yeux et du bras est de créer un protocole de recherche qui utilise un indiçage endogène, p.ex. une flèche indiquant l’endroit vers lequel l’attention doit être déployée. L’orientation de l’attention endogène est un processus en majeure partie volontaire et conscient, contrairement à l'orientation par stimuli exogènes qui est un processus automatique. Il est donc plus difficile de contrôler avec précision un indiçage endogène et de s'assurer que les impacts mesurés sur les caractéristiques des mouvements sont bel et bien dus à ce phénomène. De plus, l'étude de l'attention visuelle à travers une combinaison d'indiçage endogène et exogène permettra d'avoir une image plus complète des processus attentionnels impliqués durant la planification motrice et pourrait nuancer notre modèle à deux étapes.

5.5.1. Étude des conséquences des lésions cérébrales impliquées dans la préparation du mouvement

Les études lésionnelles nous éclairent, depuis les débuts de la recherche en neuropsychologie, sur les interactions entre le cerveau et le comportement humain, et l'implication des différentes parties du cerveau dans les processus neurologiques, tels que l'attention visuelle et la préparation de mouvements. L'importance de l'attention visuelle dans la préparation motrice a été soulignée dans les études sur les patients cérébrolésés, notamment dans le trouble de l'ataxie optique, un trouble lié à une lésion dans le CPP et qui produit des dysfonctions au niveau de la coordination visuomotrice (Khan et al., 2005; Perenin & Vighetto, 1988; Pisella et al., 2009). Les lésions dans des parties du cerveau impliquant d'une part les mouvements de la portée du bras et des saccades, et d'une autre part l'attention visuelle, tels le CPP, la jonction pariéto-occipitale, et les champs oculaires frontaux, présentent une opportunité unique d'étudier les relations causales entre l'anatomie cérébrale et les comportements afin de mieux inférer les mécanismes fonctionnels qui en découlent. Cependant, dû à la complexité de l'architecture neuronale sous-tendant l'attention visuelle et la préparation des mouvements, il est important de souligner que toute différence individuelle potentielle ne reflète pas nécessairement un processus attentionnel spécifique. Les effets survenant lors de la manipulation de l'attention lors de la préparation des mouvements des yeux et du bras peuvent varier de façon importante en fonction de l'endroit, de la taille et l'âge de la survenue de la lésion. De plus, les potentielles corrélations entre les lésions et les déficiences encourues ne sont que spéculatives, puisque dans la grande majorité des cas, il est impossible de déterminer la performance d'un individu cérébrolésé avant lésion et que la performance aux tâches visuomotrices présente des différences interindividuelles considérables. Ceci dit, les études lésionnelles permettent néanmoins d'avoir une compréhension approfondie des structures neuronales impliquées, et permettent de dresser un portrait plus complet des influences attentionnelles sur la préparation du mouvement.

Durant une tâche attentionnelle et motrice similaire à celle présentée dans nos études, nous suggérons que des patients cérébrolésés présenteraient des déficits liés à la région cérébrale affectée par la lésion. En effet, dépendant de leurs lésions et des structures neurologiques touchées, nous postulons que les déficits aux niveaux comportemental et moteur diffèreraient de façon importante s'il y a atteinte au niveau du cortex pariétal versus une atteinte aux parties liées à chaque effecteur utilisé, c'est-à-dire les champs oculaires frontaux pour les saccades et le cortex prémoteur dorsal pour les mouvements de la portée du bras. La combinaison des différentes atteintes viendrait corroborer les deux niveaux distincts de notre modèle de sélection attentionnelle durant la planification motrice. Dans le cas d'une atteinte au cortex pariétal, nous posons l'hypothèse d'une atteinte globale des caractéristiques des mouvements produits, notamment des difficultés d'exécution, de précision et de temps de réaction des saccades et des mouvements de la portée de la main vers des cibles. Une lésion dans le cortex pariétal devrait se traduire par une affectation globale similaire des caractéristiques des mouvements des deux effecteurs lors d'une tâche attentionnelle. Ces résultats démontreront le premier niveau du modèle de sélection attentionnelle durant la préparation des mouvements. Dans le cas d'une atteinte au niveau des champs oculaires frontaux et du cortex préfrontal dorsal, nous postulons que les patients démontreraient des dysfonctions attentionnelles liées à la partie cérébrale touchée. Nous suggérons que la sélection attentionnelle lors de la préparation du mouvement dépendrait de façon importante de l'effecteur utilisé, ce qui serait traduit par des différences importantes dans les caractéristiques spatiales et temporelles entre les mouvements des saccades et ceux de la portée du bras lors de la tâche attentionnelle. Ceci confirmera le deuxième niveau de notre modèle proposé.

5.5.2. Étude de la connectivité neuronale lors de la planification du mouvement par neurostimulation non invasive

L'utilisation de techniques de neurostimulation non invasive (e.g. stimulation magnétique transcrânienne (SMT) ou à courant direct (tDCS)) permet de manipuler la connectivité neuronale et d'étudier les implications de parties spécifiques du cerveau dans certains processus neurologiques et comportements qui en découlent. La SMT est une technique non invasive qui permet d'étudier les processus neurologiques grâce à l'induction électromagnétique appliquée à des parties spécifiques du cerveau à travers le crâne. La tDCS est une technique similaire à la SMT, mais qui utilise un faible courant direct à travers des électrodes sur le scalp. Ces deux techniques permettent de contrôler les caractéristiques de la lésion virtuelle, telle que l'étendue de la lésion, contrairement aux études lésionnelles, dans lesquelles la variabilité interindividuelle est importante. La méthode principale utilisée avec ces techniques est l'induction d'une perturbation corticale temporaire, causant une lésion virtuelle temporaire (Reis et al., 2008; Siebner & Rothwell, 2003; Zheng, Alsop, & Schlaug, 2011). La SMT ou la tDCS sont des candidats de pointe pour étudier les processus attentionnels durant la planification du mouvement. En effet, en ciblant les parties cérébrales impliquées dans l’attention visuelle et la préparation motrice, telles que le CPP et le cortex frontal, il est possible de cerner les effets d’une modulation de l’activité dans ces structures anatomiques et d’en inférer les fonctions et mécanismes impliqués. De plus, afin d’avoir une meilleure compréhension temporelle de l’implication de ces parties du cerveau, il est possible de combiner la SMT et la tDCS avec des techniques d’imagerie cérébrale fonctionnelle, telles que l'imagerie par résonance magnétique fonctionnelle (IRMf) (Bohning, Pecheny, & Epstein, 1997; Bohning, Shastri, & McConnell, 1998) ou la tomographie par émission de positrons (TEP) (Paus et al., 1997), et ce, même dans le contexte de l’attention visuelle (Leitão, Thielscher, Tünnerhoff, & Noppeney, 2015). Cette approche multiméthodologique permet d’étudier et de comparer de façon précise, temporellement et spatialement, les effets des lésions spécifiques sur l’activité neuronale durant des tâches comportementales (Stewart, Ellison, Walsh, & Cowey, 2001). Nous suggérons que la neurostimulation utilisée de façon à renforcer l’activité cérébrale (stimulation anodale) au niveau du cortex frontal lors d’une tâche attentionnelle comme celle de nos études permettra d’améliorer la performance à celle-ci en termes de temps de réaction, notamment en augmentant la facilitation permise par l’indiçage attentionnel. Nous postulons qu’une neurostimulation inhibitrice (cathodale) au niveau du cortex pariétal causera des déficits sensorimoteurs similaires à ceux vus chez certains patients atteints d’une lésion à la même région cérébrale, menant à des problèmes d’exécution et de précision des mouvements visuellement guidés.

De façon similaire aux études lésionnelles proposées, l’utilisation des techniques de neurostimulation nous permettrait de localiser et de cerner de façon plus précise les parties cérébrales affectées lors de la préparation des mouvements des yeux et des bras. En effet, afin de séparer les deux niveaux de notre modèle attentionnel proposé, nous délimiterons dans un premier temps les affectations d’une lésion virtuelle du CPP pour mesurer si les caractéristiques des saccades et des mouvements de la portée du bras lors d’une tâche attentionnelle sont affectées de façon similaire, peu importe l’effecteur utilisé. Cela se rapporterait au premier niveau de notre modèle. Dans un deuxième temps, nous stimulerons séparément les parties cérébrales impliquées dans l’exécution des saccades et des mouvements de la portée du bras lors de la tâche attentionnelle pour vérifier si les conséquences sur les caractéristiques des mouvements varient de façon importante entre les effecteurs dans les différentes conditions de la tâche. Cela confirmerait la présence du deuxième niveau du modèle attentionnel se produisant plus tard lors de la préparation motrice.

6. Conclusion

Les études réalisées lors de ce mémoire présentent dans leur ensemble des résultats concordants avec un modèle attentionnel à deux étapes de la planification des mouvements de portée du bras et des saccades. Dans les contextes étudiés, c'est-à-dire lors des tâches visuomotrices, la modulation de l'attention exogène lors de la planification des mouvements des yeux et du bras a produit des effets sur les caractéristiques temporelles et spatiales de ceux-ci. Nos résultats suggèrent la présence de processus attentionnels sur deux niveaux principaux travaillant en parallèle: l'un affectant les caractéristiques spatiales et temporelles des saccades et des mouvements de la portée du bras lors de leur préparation de façon globale, peu importe l'effecteur utilisé, et l'autre affectant chaque effecteur de façon individuelle.

7. Références

Alvarez, G. A., & Cavanagh, P. (2004). The capacity of visual short-term memory is set both by visual information load and by number of objects. *Psychological Science, 15*(2), 106-111.

Anderson, B. A. (2013). A value-driven mechanism of attentional selection. *Journal of Vision, 13*(3), 1-7.

Andersen, R. A. (1989). Visual and eye movement functions of the posterior parietal cortex. *Annual Review of Neuroscience, 12*(1), 377-403.

Astafiev, S. V., Shulman, G. L., Stanley, C. M., Snyder, A. Z., Van Essen, D. C., & Corbetta, M. (2003). Functional organization of human intraparietal and frontal cortex for attending, looking, and pointing. *Journal of Neuroscience*, *23*(11), 4689-4699. doi: 10.1523/jneurosci.23-11-04689.2003

Bartz, A. E. (1962). Eye-movement latency, duration, and response time as a function of angular displacement. *Journal of Experimental Psychology, 64*(3), 318–324. doi: 10.1037/h0043475

Batista, A. P., Buneo, C. A., Snyder, L. H., & Andersen, R. A. (1999). Reach plans in eye-centered coordinates. *Science*, *285*(5425), 257-260.

Battaglia-Mayer, A., Caminiti, R., Lacquaniti, F.Z, & Zago M. (2003). Multiple levels of representation of reaching in the parieto-frontal network. *Cerebral Cortex, 13*(10), 1009–1022. doi: 10.1093/cercor/13.10.1009

Bekkering, H., Adam, J. J., Kingma, H., Huson, A., & Whiting, H.T.A. (1994). Reaction time latencies of eye and hand movements in single and dual-task conditions. *Experimental Brain Research, 97*(3), 471–476. doi: 10.1007/BF00241541

Bekkering, H., Adam, J. J., van den Aarssen, A., Kingma, H., & Whiting, H.T.A. (1995). Interference between saccadic eye and goal-directed hand movements. *Experimental Brain Research, 106*(3), 475–484. doi: 10.1007/BF00231070

Ben-Yishay, Y., Silver, S. M., Piasetsky, E., & Rattok, J. (1987). Relationship between employability and vocational outcome after intensive holistic cognitive rehabilitation. *The Journal of Head Trauma Rehabilitation*.

Berger, A., Henik, A., & Rafal, R. (2005). Competition between endogenous and exogenous orienting of visual attention. *Journal of Experimental Psychology: General, 134*(2), 207.

Beurze, S. M., De Lange, F. P., Toni, I., & Medendorp, W. P. (2009). Spatial and effector processing in the human parietofrontal network for reaches and saccades. *Journal of Neurophysiology, 101*(6), 3053-3062.

Beurze, S. M., De Lange, F. P., Toni, I., & Medendorp, W. P. (2009). Spatial and effector processing in the human parietofrontal network for reaches and saccades. *Journal of Neurophysiology, 101*(6), 3053-3062. doi: 10.1152/jn.91194.2008

Beurze, S. M., De Lange, F. P., Toni, I., & Medendorp, W. P. (2007). Integration of target and effector information in the human brain during reach planning. *Journal of neurophysiology, 97*(1), 188-199.

Biguer, B., Jeannerod, M., & Prablanc, C. (1982). The coordination of eye, head, and arm movements during reaching at a single visual target. *Experimental Brain Research, 46*(2), 301–304. doi: 10.1007/BF00237188

Bisley, J. W. & Goldberg, M. E. (2010). Attention, intention, and priority in the parietal lobe. *Annual Review of Neuroscience, 33*, 1–21. doi: 10.1146/annurev-neuro-060909-152823

Bisley, J. W., & Goldberg, M. E. (2003). Neuronal activity in the lateral intraparietal area and spatial attention. *Science, 299*(5603), 81-86.

Boch, R. A., & Goldberg, M. E. (1989). Participation of prefrontal neurons in the preparation of visually guided eye movements in the rhesus monkey. *Journal of Neurophysiology, 61*(5), 1064-1084.

Boehnke, S. E. & Munoz, D. P. (2008). On the importance of the transient visual response in the superior colliculus. *Current Opinion in Neurobiology, 18*(6), 544–551. doi: 10.1016/j.conb.2008.11.004

Bogler, C., Bode, S., & Haynes, J. D. (2011). Decoding successive computational stages of saliency processing. *Current Biology, 21*(19), 1667-1671.

Bompas, A. & Sumner, P. (2009). Temporal dynamics of saccadic distraction. *Journal of Vision, 9*(9):17, 1–14. doi: 10.1167/9.9.17

Bompas, A., Hedge, C., & Sumner, P. (2017). Speeded saccadic and manual visuo-motor decisions: Distinct processes but same principles. *Cognitive Psychology, 94*, 26–52. doi: 10.1016/j.cogpsych.2017.02.002

Brainard, D. H., & Vision, S. (1997). The psychophysics toolbox. *Spatial vision, 10*, 433-436. doi: 10.1163/156856897x00357

Briand, K. A., Larrison, A. L., & Sereno, A. B. (2000). Inhibition of return in manual and saccadic response systems. *Perception & Psychophysics, 62*(8), 1512-1524. doi: 10.3758/bf03212152

Bruce, C. J. & Goldberg, M. E. (1985). Primate frontal eye fields. I. Single neurons discharging before saccades. *Journal of Neurophysiology, 53*(3), 603–635. doi: 10.1152/jn.1985.53.3.603

Buch, E. R., Young, S., & Contreras-Vidal, J. L. (2003). Visuomotor adaptation in normal aging. *Learning & Memory, 10*(1), 55-63. doi: 10.1101/lm.50303

Buneo, C. A. & Andersen, R. A. (2006). The posterior parietal cortex: sensorimotor interface for the planning and online control of visually guided movements. *Neuropsychologia, 44*(13), 2594–2606. doi: 10.1016/j.neuropsychologia.2005.10.011

Buneo, C. A., Jarvis, M. R., Batista, A. P., & Andersen, R. A. (2002). Direct visuomotor transformations for reaching. *Nature, 416*(6881), 632.

Buonocore, A. (2010). Remote distractor effects in saccadic, manual and covert attention tasks (Doctoral dissertation). Retrieved from https://www.era.lib.ed.ac.uk/bitstream/handle/1842/5850/Buonocore2010.pdf

Bütefisch, C. M., Hummelsheim, H., Denzler, P., & Mauritz, K. H. (1995). Repetitive training of isolated movements improves the outcome of motor rehabilitation of the centrally paretic hand. *Journal of the Neurological Sciences, 130*(1), 59-68.

Bütefisch, C. M., Davis, B. C., Wise, S. P., Sawaki, L., Kopylev, L., Classen, J., & Cohen, L. G. (2000). Mechanisms of use-dependent plasticity in the human motor cortex. *Proceedings of the National Academy of Sciences, 97*(7), 3661-3665.

Bütefisch, C. M., Davis, B. C., Sawaki, L., Waldvogel, D., Classen, J., Kopylev, L., & Cohen, L. G. (2002). Modulation of use-dependent plasticity by d-amphetamine. *Annals of Neurology: Official Journal of the American Neurological Association and the Child Neurology Society, 51*(1), 59-68.

Calton, J. L., Dickinson, A. R., & Snyder, L. H. (2002). Non-spatial, motor-specific activation in posterior parietal cortex. *Nature neuroscience, 5*(6), 580.

Caminiti, R., Ferraina, S., & Mayer, A. B. (1998). Visuomotor transformations: early cortical mechanisms of reaching. *Current opinion in neurobiology, 8*(6), 753-761. doi: 10.1016/s0959-4388(98)80118-9

Carey, D. P. (2000). Eye–hand coordination: Eye to hand or hand to eye? *Current Biology, 10*(11), R416–419. doi: 10.1016/S0960-9822(00)00508-X

Carnahan, H., & Marteniuk, R. G. (1991). The temporal organization of hand, eye, and head movements during reaching and pointing. *Journal of Motor Behavior, 23*(2), 109-119. doi: 10.1080/00222895.1991.9942028

Carrasco, M., & McElree, B. (2001). Covert attention accelerates the rate of visual information processing. *Proceedings of the National Academy of Sciences, 98*(9), 5363-5367.

Carrasco, M., Giordano, A. M., & McElree, B. (2004). Temporal performance fields: Visual and attentional factors. *Vision Research, 44*(12), 1351-1365.

Carrasco, M., Giordano, A. M., & McElree, B. (2006). Attention speeds processing across eccentricity: Feature and conjunction searches. *Vision Research, 46*(13), 2028-2040.

Carrasco, M., Talgar, C. P., & Eckstein, M. (2000). Spatial covert attention increases contrast sensitivity across the CSF: support for signal enhancement. *Vision Research, 40*(10-12), 1203-1215.

Cavegn, D. (1996). Bilateral interactions in saccade programming. *Experimental Brain Research, 109*(2), 312–332. doi: 10.1007/BF00231790

Chang, E. & Ro, T. 2005. Inhibition of return in perception and action. *Visual Cognition, 12*(3), 443–472. doi: 10.1080/13506280444000391

Chang, S. W., & Abrams, R. A. (2004). Hand movements deviate toward distracters in the absence of response competition. *Journal of General Psychology, 131*(4), 328-344.

Chapman, C. S., Gallivan, J. P., Wood, D. K., Milne, J. L., Culham, J. C., & Goodale, M. A. (2010). Reaching for the unknown: multiple target encoding and real-time decision-making in a rapid reach task. *Cognition, 116*(2), 168-176.

Chica, A. B., Bartolomeo, P., & Lupiáñez, J. (2013). Two cognitive and neural systems for endogenous and exogenous spatial attention. *Behavioural brain research, 237*, 107-123.

Christopoulos, V. N., Kagan, I., & Andersen, R. A. (2018). Lateral intraparietal area (LIP) is largely effector-specific in free-choice decisions. *Scientific reports, 8*(1), 8611.

Cirstea, M. C., & Levin, M. F. (2007). Improvement of arm movement patterns and endpoint control depends on type of feedback during practice in stroke survivors. *Neurorehabilitation and neural repair, 21*(5), 398-411.

Cisek, P., & Kalaska, J. F. (2005). Neural correlates of reaching decisions in dorsal premotor cortex: specification of multiple direction choices and final selection of action. *Neuron, 45*(5), 801-814.

Classen, J., Liepert, J., Wise, S. P., Hallett, M., & Cohen, L. G. (1998). Rapid plasticity of human cortical movement representation induced by practice. Journal of Neurophysiology, 79(2), 1117-1123.

Colantonio, A., Saverino, C., Zagorski, B., Swaine, B., Lewko, J., Jaglal, S., & Vernich, L. (2010). Hospitalizations and emergency department visits for TBI in Ontario. *Canadian journal of neurological sciences, 37*(6), 783-790.

Connolly, J. D., Goodale, M. A., Desouza, J. F., Menon, R. S., Vilis, T., & Medical Research Council Group for Action and Perception. (2000). A comparison of frontoparietal fMRI activation during anti-saccades and anti-pointing. *Journal of neurophysiology, 84*(3), 1645-1655. doi: 10.1152/jn.2000.84.3.1645

Contreras-Vidal, J. L., & Kerick, S. E. (2004). Independent component analysis of dynamic brain responses during visuomotor adaptation. *Neuroimage, 21*(3), 936-945. doi: 10.1016/j.neuroimage.2003.10.037

Convento, S., Bolognini, N., Fusaro, M., Lollo, F., & Vallar, G. (2014). Neuromodulation of parietal and motor activity affects motor planning and execution. *Cortex, 57*, 51-59.

Corbetta, M., Patel, G., & Shulman, G. L. (2008). The reorienting system of the human brain: from environment to theory of mind. *Neuron, 58*(3), 306-324.

Corbetta, M., & Shulman, G. L. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nature reviews neuroscience, 3*(3), 201.

Corneil, B.D., Munoz, D.P., Chapman, B.B., Admans, T., & Cushing, S.L. (2008). Neuromuscular consequences of reflexive covert orienting. *Nature Neuroscience, 11*(1), 13–15. doi: 10.1038/nn2023

Coull, J. T., Frith, C. D., Büchel, C., & Nobre, A. C. (2000). Orienting attention in time: behavioural and neuroanatomical distinction between exogenous and endogenous shifts. *Neuropsychologia, 38*(6), 808-819.

Cowper-Smith, C. D., & Westwood, D. A. (2013). Motor IOR revealed for reaching. *Attention, Perception, & Psychophysics, 75*(8), 1914-1922.

Crammond, D. J., & Kalaska, J. F. (1996). Differential relation of discharge in primary motor cortex and premotor cortex to movements versus actively maintained postures during a reaching task. *Experimental brain research, 108*(1), 45-61.

Crawford, T. J. & Medendorp, W. P., & Marotta, J. J. (2004). Spatial transformations for eye-hand coordination. *Journal of Neurophysiology, 92*(1), 10–19. doi: 10.1152/jn.00117.2004

Crawford, T. J. & Muller, H. J. (1992). Spatial and temporal effects of spatial attention on human saccadic eye movements. *Vision Research, 32*(2), 293–304. doi: 10.1016/0042-6989(92)90140-E

Day, B. L., & Lyon, I. N. (2000). Voluntary modification of automatic arm movements evoked by motion of a visual target. Experimental Brain Research, 130(2), 159-168.

Dean, H. L., Marti, D., Tsui, E., Rinzel, J, & Pesaran, B. (2011). Reaction Time Correlations during Eye–Hand Coordination: Behavior and Modeling. *Journal of Neuroscience, 31*(7). 2399–2412. doi: 10.1523/ jneurosci.4591-10.2011

Deco, G., & Zihl, J. (2001). Top-down selective visual attention: A neurodynamical approach. *Visual Cognition, 8*(1), 118-139.

Deiber, M. P., Passingham, R. E., Colebatch, J. G., Friston, K. J., Nixon, P. D., & Frackowiak, R. S. J. (1991). Cortical areas and the selection of movement: a study with positron emission tomography. *Experimental brain research, 84*(2), 393-402.

Deiber, M. P., Wise, S. P., Honda, M., Catalan, M. J., Grafman, J., & Hallett, M. (1997). Frontal and parietal networks for conditional motor learning: a positron emission tomography study. *Journal of Neurophysiology, 78*(2), 977-991.

Desmurget, M., Pélisson, D., Rossetti, Y., & Prablanc, C. (1998). From eye to hand: planning goal-directed movements. *Neuroscience & Biobehavioral Reviews, 22*(6), 761-788. doi: 10.1016/s0149-7634(98)00004-9

Deubel, H. & Schneider, W. X. (2003). Delayed saccades, but not delayed manual aiming movements, require visual attention shifts. *Annals of the New York Academy of Sciences, 1004*(1), 289–296. doi: 10.1196/annals.1303.026

Dickinson, A. R., Calton, J. L., & Snyder, L. H. (2003). Nonspatial saccade-specific activation in area LIP of monkey parietal cortex. *Journal of neurophysiology, 90*(4), 2460-2464.

Donchin, O., Gribova, A., Steinberg, O., Bergman, H., & Vaadia, E. (1998). Primary motor cortex is involved in bimanual coordination. *Nature, 395*(6699), 274. doi: 10.1038/26220

Dorris, M. C., Pare, M., & Munoz, D. P. (1997). Neuronal activity in monkey superior colliculus related to the initiation of saccadic eye movements. *Journal of Neuroscience, 17*(21), 8566-8579.

Doubell, T. P., Skaliora, I., Baron, J., & King, A. J. (2003). Functional connectivity between the superficial and deeper layers of the superior colliculus: an anatomical substrate for sensorimotor integration. *Journal of Neuroscience, 23*(16), 6596-6607.

Egeth, H. E., & Yantis, S. (1997). Visual attention: Control, representation, and time course. *Annual review of psychology, 48*(1), 269-297.

Engbert, R., & Kliegl, R. (2003). Microsaccades uncover the orientation of covert attention. *Vision Research, 43*(9), 1035-1045.

Eriksen, C. W., & Yeh, Y. Y. (1985). Allocation of attention in the visual field. Journal of Experimental Psychology: *Human Perception and Performance, 11*(5), 583.

Evarts, E. V., Shinoda, Y., & Wise, S. P. (1984). Preparatory set and behavior. Neurophysiological approaches to higher brain function. John Wiley and Sons, New York, 7-20.

Everling, S., Dorris, M. C., Klein, R. M., & Munoz, D. P. (1999). Role of primate superior colliculus in preparation and execution of anti-saccades and pro-saccades. *Journal of Neuroscience, 19*(7), 2740-2754.

Everling, S., Pare, M., Dorris, M. C., & Munoz, D. P. (1998). Comparison of the Discharge Characteristics of Brain Stem Omnipause Neurons and Superior Colliculus Fixation Neurons in Monkey: Implications for Control of Fixation and Saccade Behavior. *Journal of Neurophysiology, 79*(2), 511–528. doi: 10.1152/jn.1998.79.2.511

Faul, M., & Coronado, V. (2015). Epidemiology of traumatic brain injury. In *Handbook of clinical neurology* (Vol. 127, pp. 3-13). Elsevier.

Fecteau, J. H. & Munoz, D. P. (2005). Correlates of Capture of Attention and Inhibition of Return across Stages of Visual Processing. *Journal of Cognitive Neuroscience, 17*(11), 1714–1727. doi: 10.1162/089892905774589235

Fecteau, J. H. & Munoz, D. P. (2006). Salience, relevance, and firing: a priority map for target selection. *Trends in Cognitive Sciences, 10*(8), 382–390. doi: 10.1016/j.tics.2006.06.011

Fecteau, J. H., Bell, A. H., & Munoz, D. P. (2004). Neural correlates of the automatic and goal-driven biases in orienting spatial attention. *Journal of Neurophysiology, 92*(3), 1728–1737. doi: 10.1152/jn.00184.2004

Festman, Y., Adam, J., Pratt, J., & Fischer, M. H. (2013). Both hand position and movement direction modulate visual attention. *Frontiers in psychology, 4*, 657.

Fischer, B. & Ramsperger, E. (1984). Human express saccades: extremely short reaction times of goal directed eye movements. *Experimental Brain Research, 57*(1), 191–195. doi.org/10.1007/BF00231145

Fischer, B. & Rogal, L. (1986). Eye-hand-coordination in man: A reaction time study. *Biological Cybernetics, 55*(4), 253–261. doi: 10.1007/BF00355600

Fischer, M. H., & Adam, J. J. (2001). Distractor effects on pointing: The role of spatial layout. *Experimental Brain Research, 136*(4), 507-513. doi: 10.1007/s002210000596

Fisher, B. E., & Sullivan, K. J. (2001). Activity-dependent factors affecting poststroke functional outcomes. *Topics in stroke rehabilitation, 8*(3), 31-44.

Fisk, J. D. & Goodale, M. A. (1985). The organization of eye and limb movements during unrestricted reaching to targets in contralateral and ipsilateral visual space. *Experimental Brain Research, 60*(1), 159–178. doi: 10.1007/BF00237028

Flöel, A., Breitenstein, C., Hummel, F., Celnik, P., Gingert, C., Sawaki, L., Knecht, S., & Cohen, L. G. (2005). Dopaminergic influences on formation of a motor memory. Annals of neurology, 58(1), 121-130.

Foerster, R. M. (2016). Task-irrelevant expectation violations in sequential manual actions: Evidence for a "check-after-surprise" mode of visual attention and eye-hand decoupling. *Frontiers in Psychology, 7*, 1-12. doi: 10.3389/fpsyg.2016.01845

Foulsham, T. (2015). Eye movements and their functions in everyday tasks. *Eye, 29*(2), 196. doi: 10.1038/eye.2014.275

Freedman, E. G. & Sparks, D. L. (2000). Coordination of the eyes and head: movement kinematics. *Experimental Brain Research, 131*(1), 22–32. doi: 10.1007/s002219900

Frens, M. A. & Erkelens, C. J. (1991). Coordination of hand movements and saccades: evidence for a common and a separate pathway. *Experimental Brain Research, 85*(3), 682–690. doi: 10.1007/BF00231754

Funes, M. J., Lupiáñez, J., & Milliken, B. (2007). Separate mechanisms recruited by exogenous and endogenous spatial cues: evidence from a spatial Stroop paradigm. *Journal of Experimental Psychology: Human Perception and Performance, 33*(2), 348.

Galletti, C., Breveglieri, R., Lappe, M., Bosco, A., Ciavarro, M., & Fattori, P. (2010). Covert shift of attention modulates the ongoing neural activity in a reaching area of the macaque dorsomedial visual stream. *PLoS One, 5*(11), e15078. doi: 10.1371/journal.pone.0015078

Gandhi, N. J. & Katnani, H. A. (2011). Motor functions of the superior colliculus. *Annual Review of Neuroscience, 34*, 205–231. doi: 10.1146/annurev-neuro-061010-113728

Gaveau, V., Pélisson, D., Blangero, A., Urquizar, C., Prablanc, C., Vighetto, A., & Pisella, L. (2008). Saccade control and eye–hand coordination in optic ataxia. *Neuropsychologia, 46*(2), 475-486.

Gaveau, V., Prablanc, C., Laurent, D., Rossetti, Y., & Priot, A. E. (2014). Visuomotor adaptation needs a validation of prediction error by feedback error. *Frontiers in human neuroscience*, 8, 880.

Gaveau, V., Priot, A. E., Pisella, L., Havé, L., Prablanc, C., & Rossetti, Y. (2018). Paradoxical adaptation of successful movements: The crucial role of internal error signals. *Consciousness and cognition, 64*, 135-145. doi: 10.1016/j.concog.2018.06.011

Gersch, T. M., Kowler, E., Schnitzer, B. S., & Dosher, B. A. (2008). Visual memory during pauses between successive saccades. *Journal of Vision, 8*(16), 15-15.

Gezeck, S., Fischer, B., & Timmer, J. (1997). Saccadic reaction times: a statistical analysis of multimodal distributions. *Vision Research, 37*(15), 2119-2131.

Ghahghaei, S., & Verghese, P. (2015). Efficient saccade planning requires time and clear choices. *Vision Research, 113*, 125-136. doi: 10.1016/j.visres.2015.05.006

Godijn, R. & Theeuwes, J. (2002). Oculomotor capture and inhibition of return: Evidence for an oculomotor suppression account of IOR. *Psychological Research, 66*(4), 234–246. doi: 10.1007/s00426-002-0098-1

Godijn, R., & Theeuwes, J. (2002). Programming of endogenous and exogenous saccades: evidence for a competitive integration model. *Journal of experimental psychology: human perception and performance, 28*(5), 1039.

Goldberg, M. E. & Bushnell, M. C. (1981). Behavioral enhancement of visual responses in monkey cerebral cortex. II. Modulation in frontal eye fields specifically related to saccades. *Journal of Neurophysiology, 46*(4), 773–787. doi: 10.1152/jn.1981.46.4.773

Goldberg, M. E. Bisley, J. W., Powell, K. D., & Gottlieb, J. (2006). Saccades, salience and attention: the role of the lateral intraparietal area in visual behavior. *Progress in Brain Research, 155*(B), 157–175. doi: 10.1016/S0079-6123(06)55010-1

Goodale, M. A., & Milner, A. D. (1992). Separate visual pathways for perception and action. *Trends in neurosciences, 15*(1), 20-25.

Gopal, A. & Murthy, A. (2015). Eye-hand coordination during a double-step task: evidence for a common stochastic accumulator. *Journal of Neurophysiology, 114*(3), 1438–1454. doi: 10.1152/jn.00276.2015

Gray, J. M., & Robertson, I. (1989). Remediation of attentional difficulties following brain injury: Three experimental single case studies. *Brain Injury, 3*(2), 163-170.

Gray, R. (2011). Links between attention, performance pressure, and movement in skilled motor action. *Current Directions in Psychological Science, 20*(5), 301–306. doi: 10.1177/0963721411416572

Grefkes, C., & Fink, G. R. (2005). The functional organization of the intraparietal sulcus in humans and monkeys. *Journal of Anatomy, 207*(1), 3-17.

Gribble, P. L, Everling, S., Ford, K., & Mattar, A. (2002). Hand-eye coordination for rapid pointing movements: Arm movement direction and distance are specified prior to saccade onset. *Experimental Brain Research, 145*, 372–382. doi: 10.1007/s00221-002-1122-9

Guitton, D. & Volle, M. (1987). Gaze control in humans: eye-head coordination during orienting movements to targets within and beyond the oculomotor range. *Journal of Neurophysiology, 58*(3), 427–459. doi: 10.1152/jn.1987.58.3.427

Haar, S., Donchin, O., & Dinstein, I. (2015). Dissociating visual and motor directional selectivity using visuomotor adaptation. *Journal of Neuroscience, 35*(17), 6813-6821. doi: 10.1523/jneurosci.0182-15.2015

Hafed, Z. M., Chen, C. Y., & Tian, X. (2015). Vision, perception, and attention through the lens of microsaccades: mechanisms and implications. *Frontiers in systems neuroscience, 9*, 167.

Herman, R., Herman, R., & Maulucci, R. (1981). Visually triggered eye-arm movements in man. *Experimental Brain Research, 42*(3-4), 392–398. doi: 10.1007/BF00237504

Hickey, C., McDonald, J. J., & Theeuwes, J. (2006). Electrophysiological evidence of the capture of visual attention. *Journal of cognitive neuroscience, 18*(4), 604-613.

Hilchey, M. D., Klein, R. M., & Satel, J. (2014). Returning to "inhibition of return" by dissociating long-term oculomotor IOR from short-term sensory adaptation and other nonoculomotor "inhibitory" cueing effects. *Journal of Experimental Psychology: Human Perception and Performance, 40*(4), 1603–1616. doi: 10.1037/a0036859

Hinder, M. R., Tresilian, J. R., Riek, S., & Carson, R. G. (2008). The contribution of visual feedback to visuomotor adaptation: how much and when? *Brain Research, 1197*, 123-134. doi: 10.1016/j.brainres.2007.12.067

Hopfinger, J. B., & West, V. M. (2006). Interactions between endogenous and exogenous attention on cortical visual processing. *NeuroImage, 31*(2), 774-789.

Horowitz, T. S., Fine, E. M., Fencsik, D. E., Yurgenson, S., & Wolfe, J. M. (2007). Fixational eye movements are not an index of covert attention. *Psychological Science, 18*(4), 356–363. doi: 10.1111/j.1467-9280.2007.01903.x

Howard, L. A., & Tipper, S. P. (1997). Hand deviations away from visual cues: indirect evidence for inhibition. *Experimental brain research, 113*(1), 144-152.

Hunt, A. R., & Kingstone, A. (2003). Inhibition of return: Dissociating attentional and oculomotor components. *Journal of Experimental Psychology: Human Perception and Performance, 29*(5), 1068.

Ingram, H. A., Van Donkelaar, P., Cole, J., Vercher, J. L., Gauthier, G. M., & Miall, R. C. (2000). The role of proprioception and attention in a visuomotor adaptation task. *Experimental Brain Research, 132*(1), 114-126.

Itti, L. & Koch, C. (2001). Computational modelling of visual attention. *Nature Reviews Neuroscience, 2*(3), 194–203. doi: 10.1038/35058500

Jeannerod, M. (1988). *Oxford psychology series, No. 15. The neural and behavioural organization of goal-directed movements*. New York, NY, US: Clarendon Press/Oxford University Press.

Jeannerod, M., Arbib, M. A., Rizzolatti, G., & Sakata, H. (1995). Grasping objects: the cortical mechanisms of visuomotor transformation. *Trends in neurosciences, 18*(7), 314-320.

Jonides, J. & Irwin, D. E. (1981). Capturing attention. *Cognition, 10*, 145–150.

Jonikaitis, D. & Deubel, H. (2011). Independent Allocation of Attention to Eye and Hand Targets in Coordinated Eye-Hand Movements. *Psychological Science, 22*(3), 339–347. doi: 10.1177/0956797610397666

Jonikaitis, D., & Deubel, H. (2011). Independent allocation of attention to eye and hand targets in coordinated eye-hand movements. *Psychological Science, 22*(3), 339-347.

Jonikaitis, D., Schubert, T., & Deubel, H. (2010). Preparing coordinated eye and hand movements: dual-task costs are not attentional. *Journal of Vision, 10*(14), 23-23. doi: 10.1167/10.14.23

Kagerer, F. A., Contreras-Vidal, J. L., & Stelmach, G. E. (1997). Adaptation to gradual as compared with sudden visuo-motor distortions. *Experimental brain research, 115*(3), 557-561.

Kalaska J.F. (2009) From Intention to Action: Motor Cortex and the Control of Reaching Movements. In: Sternad D. (eds) *Progress in Motor Control. Advances in Experimental Medicine and Biology*, vol 629. Springer, Boston, MA

Kamkar, S., Moghaddam, H. A., & Lashgari, R. (2018). Early visual processing of feature saliency tasks: A review of psychophysical experiments. *Frontiers in Systems Neuroscience, 12*.

Kaufman, M. T., Churchland, M. M., & Shenoy, K. V. (2013). The roles of monkey M1 neuron classes in movement preparation and execution. *Journal of Neurophysiology, 110*(4), 817–825. doi: 10.1152/jn.00892.2011

Kaufman, M. T., Churchland, M. M., Santhanam, G., Yu, B. M., Afshar, A., Ryu, S. I., & Shenoy, K. V. (2010). Roles of monkey premotor neuron classes in movement preparation and execution. *Journal of Neurophysiology, 104*(2), 799–810. doi: 10.1152/jn.00231.2009

Khan, A. Z., Blohm, G., McPeek, R. M., & Lefevre, P. (2009). Differential influence of attention on gaze and head movements. *Journal of neurophysiology, 101*(1), 198-206. doi: 10.1152/jn.90815.2008

Khan, A. Z., Heinen, S. J., & McPeek, R. M. (2010). Attentional Cueing at the Saccade Goal, Not at the Target Location, Facilitates Saccades. *Journal of Neuroscience, 30*(16), 5481–5488. doi: 10.1523/JNEUROSCI.4437-09.2010

Khan, A. Z., Munoz, D. P., Takahashi, N., Blohm, G., & McPeek, R. M. (2016). Effects of a pretarget distractor on saccade reaction times across space and time in monkeys and humans. *Journal of Vision*, 16(7), 5-5. doi: 10.1167/16.7.5

Khan, A. Z., Pisella, L., Vighetto, A., Cotton, F., Luaute, J., Boisson, D., Salemme, R., Crawford, J. D., & Rossetti, Y. (2005). Optic ataxia errors depend on remapped, not viewed, target location. *Nature neuroscience, 8*(4), 418.

Khan, A. Z., Song, J.-H., & McPeek, R. M. (2011). The eye dominates in guiding attention during simultaneous eye and hand movements. *Journal of Vision, 11*(1):9, 1–14. doi: 10.1167/11.1.9

Kiesel, A., Steinhauser, M., Wendt, M., Falkenstein, M., Jost, K., Philipp, A. M., & Koch, I. (2010). Control and interference in task switching—A review. *Psychological bulletin, 136*(5), 849–874. doi: 10.1037/a0019842

Klein, R. M. (2000). Inhibition of return. *Trends in Cognitive Sciences, 4*(4), 138–147. doi: 10.1016/S1364-6613(00)01452-2

Kopecz, K., & Schöner, G. (1995). Saccadic motor planning by integrating visual information and pre-information on neural dynamic fields. *Biological cybernetics, 73*(1), 49-60. doi: 10.1007/bf00199055

Kowler, E., Anderson, E., Dosher, B., & Blaser, E. (1995). The role of attention in the programming of saccades. *Vision Research*, *35*(13), 1897-1916.

Krauzlis, R. J., Lovejoy, L. P., & Zénon, A. (2013). Superior colliculus and visual spatial attention. *Annual Review of Neuroscience, 36*, 165–182.

Kustov, A. A., & Robinson, D. L. (1996). Shared neural control of attentional shifts and eye movements. *Nature, 384*(6604), 74.

Lacquaniti, F., & Caminiti, R. (1998). Visuo-motor transformations for arm reaching. *European Journal of Neuroscience, 10*, 195-203. doi: 10.1046/j.1460-9568.1998.00040.x

Land, M. F. & Hayhoe, M. (2001). In what ways do eye movements contribute to everyday activities? *Vision Research, 41*(25-26), 3559–3565. doi: 10.1016/S0042-6989(01)00102-X

Land, M. F., Mennie, N., & Rusted, J. (1999). The roles of vision and eye movements in the control of activities of daily living. *Perception, 28*(11), 1311-1328.

Lawrence, B. M. & Snyder, L. H. (2006). Comparison of effector-specific signals in frontal and parietal cortices. *Journal of Neurophysiology, 96*(3), 1393–1400. doi: 10.1152/jn.01368.2005

Leclercq, M., & Sturm, W. (2002). Rehabilitation of attention disorders: a literature review. Applied Neuropsychology of Attention. *Theory, Diagnosis and Rehabilitation*, 341-264.

Lee, D. (1999). Effects of exogenous and endogenous attention on visually guided hand movements. *Cognitive Brain Research, 8*(2), 143-156. doi: 10.1016/s0926-6410(99)00014-2

Lee, D., Poizner, H., Corcos, D. M., & Henriques, D. Y. (2014). Unconstrained reaching modulates eye-hand coupling. *Experimental Brain Science, 232*(1), 211–223. doi: 10.1007/s00221-013-3732-9

Levy, I., Schluppeck, D., Heeger D. J., & Glimcher, P. W. (2007). Specificity of human cortical areas for reaches and saccades. *Journal of Neuroscience, 27*(17), 4687–4696. doi: 10.1523/JNEUROSCI.0459-07.2007

Li, A. S., Zhang, G. L., Miao, C. G., Wang, S., Zhang, M., & Zhang, Y. (2017). The Time Course of Inhibition of Return: Evidence from Steady-State Visual Evoked Potentials. *Frontiers in psychology, 8*, 1562.

Liu, W., Whitall, J., & Kepple, T. M. (2013). Multi-joint coordination of functional arm reaching: induced position analysis. *Journal of applied biomechanics, 29*(2), 235-240. doi: 10.1123/jab.29.2.235

Liu, Y., Yttri, E. A., & Snyder, L. H. (2010). Intention and attention: different functional roles for LIPd and LIPv. *Nature Neuroscience, 13*(4), 495–500. doi: 10.1038/nn.2496

Loetscher, T., & Lincoln, N. B. (2013). Cognitive rehabilitation for attention deficits following stroke. Cochrane *Database of Systematic Reviews, 2013*(5), 1-58. doi: 10.1002/14651858.CD002842.pub2

Lubbe, R. H. van der, Vogel, R. O., & Postma, A. (2005). Different effects of exogenous cues in a visual detection and discrimination task: delayed attention withdrawal and/or speeded motor inhibition? *Journal of Cognitive Neuroscience, 17*(12), 1829–1840. doi: 10.1162/089892905775008634

Luciw, M. D., Jarocka, E., & Edin, B. B. (2014). Multi-channel EEG recordings during 3,936 grasp and lift trials with varying weight and friction. *Scientific data, 1*:140047, 1–11. doi: 10.1038/sdata.2014.47

Luck, S. J., & Vogel, E. K. (1997). The capacity of visual working memory for features and conjunctions. *Nature, 390*(6657), 279.

Lünenburger, L., Kleiser, R., Stuphorn, V., Miller, L. E., & Hoffmann, K. P. (2001). A possible role of the superior colliculus in eye-hand coordination. *Progress in Brain Research, 134*, 109–125. doi: 10.1016/S0079-6123(01)34009-8

Lünenburger, L., Kutz, D. F., & Hoffmann, K. P. (2000). Influence of arm movements on saccades in humans. *European Journal of Neuroscience, 12*(11), 4107–4116. doi: 10.1046/j.1460-9568.2000.00298.x

Luppino, G., & Rizzolatti, G. (2000). The organization of the frontal motor cortex. *Physiology, 15*(5), 219-224.

Macaluso, E., & Doricchi, F. (2013). Attention and predictions: control of spatial attention beyond the endogenous-exogenous dichotomy. *Frontiers in human neuroscience, 7*, 685.

MacInnes, W. J., Krüger, H. M., & Hunt, A. R. (2015). Just passing through? Inhibition of return in saccadic sequences. *The Quarterly Journal of Experimental Psychology, 68*(2), 402-416.

Malienko, A., Harrar, V., & Khan, A. Z. (2018). Contrasting effects of exogenous cueing on saccades and reaches. *Journal of Vision*, 18(9), 1-16. doi: 10.1167/18.9.4

Marconi, B., Genovesio, A., Battaglia-Mayer, A., Ferraina, S., Squatrito, S., Molinari, M., Lacquaniti, F., & Caminiti, R. (2001). Eye–hand coordination during reaching. I. Anatomical relationships between parietal and frontal cortex. *Cerebral Cortex, 11*(6), 513-527.

Martinez-Conde, S., Macknik, S. L., Troncoso, X. G., & Hubel, D. H. (2009). Microsaccades: a neurophysiological analysis. *Trends in neurosciences, 32*(9), 463-475.

Mason, C. R., Gomez, J. E., & Ebner, T. J. (2001). Hand synergies during reach-to-grasp. *Journal of Neurophysiology, 86*(6), 2896–2910. doi: 10.1152/jn.2001.86.6.2896

May, P. J. (2006). The mammalian superior colliculus: laminar structure and connections. *Progress in brain research, 151*, 321-378.

Mayer, A. R., Dorflinger, J. M., Rao, S. M., & Seidenberg, M. (2004). Neural networks underlying endogenous and exogenous visual–spatial orienting. *Neuroimage, 23*(2), 534-541.

Maylor, E. A. & Hockey, R. (1985). Inhibitory component of externally controlled covert orienting in visual space. *Journal of Experimental Psychology: Human Perception and Performance, 11*(6), 777–787. doi: 10.1037/0096-1523.11.6.777

Maylor, E. A., & Hockey, R. (1987). Effects of repetition on the facilitatory and inhibitory components of orienting in visual space. *Neuropsychologia, 25*(1), 41-54. doi: 10.1016/0028-3932(87)90042-x

Mazer, B. L., Sofer, S., Korner-Bitensky, N., Gelinas, I., Hanley, J., & Wood-Dauphinee, S. (2003). Effectiveness of a visual attention retraining program on the driving performance of clients with stroke. *Archives of physical medicine and rehabilitation, 84*(4), 541-550.

McPeek, R. M., & Keller, E. L. (2001). Short-term priming, concurrent processing, and saccade curvature during a target selection task in the monkey. *Vision Research*, 41(6), 785-800.

McPeek, R. M., & Keller, E. L. (2002). Superior colliculus activity related to concurrent processing of saccade goals in a visual search task. *Journal of Neurophysiology, 87*(4), 1805–1815. doi: 10.1152/jn.00501.2001

McPeek, R. M., Han, J. H., & Keller, E. L. (2003). Competition between saccade goals in the superior colliculus produces saccade curvature. *Journal of Neurophysiology, 89*(5), 2577–2590. doi: 10.1152/jn.00657.2002

McSorley, E., Haggard, P., & Walker, R. (2004). Distractor modulation of saccade trajectories: spatial separation and symmetry effects. *Experimental Brain Research, 155*(3), 320-333.

McSorley, E., Haggard, P., & Walker, R. (2005). Spatial and temporal aspects of oculomotor inhibition as revealed by saccade trajectories. *Vision Research, 45*(19), 2492–2499. doi: 10.1016/j.visres.2005.04.012

McSorley, E., Haggard, P., & Walker, R. (2006). Time course of oculomotor inhibition revealed by saccade trajectory modulation. *Journal of Neurophysiology, 96*(3), 1420–1424. doi: 10.1152/jn.00315.2006

Medendorp, W. P., Goltz, H. C., Crawford, J. D., & Vilis, T. (2005). Integration of target and effector information in human posterior parietal cortex for the planning of action. *Journal of Neurophysiology, 93*(2), 954-962. doi: 10.1152/jn.00725.2004

Medendorp, W. P., Goltz, H. C., Vilis, T., & Crawford, J. D. (2003). Gaze-centered updating of visual space in human parietal cortex. *Journal of neuroscience, 23*(15), 6209-6214.

Melamed, L. E., Beckett, P. A., & Halay, M. (1979). Individual differences in the visual component of prism adaptation. *Perception, 8*(6), 699-706. doi: 10.1068/p080699

Messier, J. & Kalaska, J. F. (1999). Comparison of variability of initial kinematics and endpoints of reaching movements. *Experimental Brain Research, 125*(2), 139–152.

Michel, C., Pisella, L., Prablanc, C., Rode, G., & Rossetti, Y. (2007). Enhancing visuomotor adaptation by reducing error signals: single-step (aware) versus multiple-step (unaware) exposure to wedge prisms. *Journal of Cognitive Neuroscience, 19*(2), 341-350.

Mooshagian, E., & Snyder, L. H. (2018). Spatial eye–hand coordination during bimanual reaching is not systematically coded in either LIP or PRR. *Proceedings of the National Academy of Sciences, 115*(16), E3817–E3826. doi: 10.1073/pnas.1718267115

Munoz, D. P., & Wurtz, R. H. (1993). Fixation cells in monkey superior colliculus. I. Characteristics of cell discharge. *Journal of neurophysiology, 70*(2), 559-575.

Munoz, D. P., & Wurtz, R. H. (1995). Saccade-related activity in monkey superior colliculus. I. Characteristics of burst and buildup cells. *Journal of neurophysiology, 73*(6), 2313-2333.

Nakayama, K., & Mackeben, M. (1989). Sustained and transient components of focal visual attention. *Vision Research, 29*(11), 1631-1647.

Neggers, S. F. W. & Bekkering, H. (1999). Integration of visual and somatosensory target information in goal-directed eye and arm movements. *Experimental Brain Research, 125*(1), 97–107. doi: 10.1007/s002210050

Neggers, S. F. W. & Bekkering, H. (2002). Coordinated control of eye and hand movements in dynamic reaching. *Human Movement Science, 21*(3), 37–64. doi: 10.1016/S0167-9457(02)00120-3

Neggers, S. F., & Bekkering, H. (2000). Ocular gaze is anchored to the target of an ongoing pointing movement. *Journal of Neurophysiology, 83*(2), 639-651.

Niechwiej-Szwedo, E., McIlroy, W. E., Green, R., & Verrier, M. C. (2005). The effect of directional compatibility on the response latencies of ocular and manual movements. *Experimental Brain Research, 162*(2), 220–229. doi: 10.1007/s00221-004-2146-0

Nissens, T. & Fiehler, K. (2017). Saccades and reaches curve away from the other effector's target in simultaneous eye and hand movements. *Journal of Neurophysiology, 119*(1), 118-123. doi:10.1152/jn.00618.2017

Oristaglio, J., Schneider, D. M., Balan, P. F., & Gottlieb, J. (2006). Integration of visuospatial and effector information during symbolically cued limb movements in monkey lateral intraparietal area. *Journal of Neuroscience, 26*(32), 8310–8319. doi: 10.1523/JNEUROSCI.1779-06.2006

Pastukhov, A., Vonau, V., Stonkute, S., & Braun, J. (2013). Spatial and temporal attention revealed by microsaccades. *Vision Research*, 85, 45-57.

Peelen, M. V., Heslenfeld, D. J., & Theeuwes, J. (2004). Endogenous and exogenous attention shifts are mediated by the same large-scale neural network. *Neuroimage, 22*(2), 822-830.

Pelz, J., Hayhoe, M., & Loeber, R. (2001). The coordination of eye, head, and hand movements in a natural task. *Experimental Brain Research, 139*(3), 266-277. doi: 10.1007/s002210100745

Perenin, M. T., & Vighetto, A. (1988). Optic ataxia: A specific disruption in visuomotor mechanisms: I. Different aspects of the deficit in reaching for objects. *Brain, 111*(3), 643-674.

Perry, C. J., Sergio, L. E., Crawford, J. D., & Fallah, M. (2015). Hand placement near the visual stimulus improves orientation selectivity in V2 neurons. *Journal of neurophysiology, 113*(7), 2859-2870.

Petrides, M., Alivisatos, B., Evans, A. C., & Meyer, E. (1993). Dissociation of human mid-dorsolateral from posterior dorsolateral frontal cortex in memory processing. *Proceedings of the National Academy of sciences, 90*(3), 873-877.

Petzschner, F. H., & Krüger, M. (2012). How to Reach: Movement Planning in the Posterior Parietal Cortex. *Journal of Neuroscience, 32*(14), 4703-4704. doi: 10.1523/jneurosci.0566-12.2012

Pinto, Y., van der Leij, A. R., Sligte, I. G., Lamme, V. A., & Scholte, H. S. (2013). Bottom-up and top-down attention are independent. *Journal of Vision, 13*(3), 16-16.

Pisella, L., Rode, G., Farne, A., Tilikete, C., & Rossetti, Y. (2006). Prism adaptation in the rehabilitation of patients with visuo-spatial cognitive disorders. *Current Opinion in Neurology, 19*(6), 534-542. doi: 10.1097/wco.0b013e328010924b

Pisella, L., Sergio, L., Blangero, A., Torchin, H., Vighetto, A., & Rossetti, Y. (2009). Optic ataxia and the function of the dorsal stream: contributions to perception and action. *Neuropsychologia, 47*(14), 3033-3044.

Posner, M. I. & Cohen, Y. (1984). Components of Visual Orienting. In H. Bouma, & D. G. Bowhuis (Eds.), *Attention and Performance X: Control of language processes* (p. 531–556). Hillsdale, NJ: Erlbaum.

Posner, M. I. (1980). Orienting of attention. *Quarterly journal of experimental psychology, 32*(1), 3-25.

Posner, M. I., & Cohen, Y. (1984). Components of visual orienting. Attention and performance X: *Control of language processes, 32*, 531-556.

Posner, M. I., & Petersen, S. E. (1990). The attention system of the human brain. *Annual review of neuroscience, 13*(1), 25-42.

Posner, M. I., Snyder, C. R., & Davidson, B. J. (1980). Attention and the detection of signals. *Journal of experimental psychology: General, 109*(2), 160.

Prablanc, C., Echallier, J. F., Komilis, E., & Jeannerod, M. (1979). Optimal response of eye and hand motor systems in pointing at a visual target. I. Spatio-temporal characteristics of eye and hand movements and their relationships when varying the amount of visual information. *Biological Cybernetics*, 35, 115–124. doi: 10.1007/BF00337436

Ptak, R. (2012). The frontoparietal attention network of the human brain: action, saliency, and a priority map of the environment. *The Neuroscientist, 18*(5), 502-515.

Rees, G. (2007). Neural correlates of the contents of visual awareness in humans. *Philosophical Transactions of the Royal Society of London B: Biological Sciences, 362*(1481), 877-886.

Richard, N. M., O'Connor, C., Dey, A., Robertson, I. H., & Levine, B. (2018). External modulation of the sustained attention network in traumatic brain injury. *Neuropsychology, 32*(5), 541-553.

Riggio, L. & Kirsner, K. (1997). The relationship between central cues and peripheral cues in covert visual orientation. *Perception & Psychophysics, 59*(6), 885-899. doi: 10.3758/BF03205506

Robertson, I. H., Ridgeway, V., Greenfield, E., & Parr, A. (1997). Motor recovery after stroke depends on intact sustained attention: a 2-year follow-up study. *Neuropsychology, 11*(2), 290.

Roby-Brami, A., Bennis, N., Mokhtari, M., & Baraduc, P. (2000). Hand orientation for grasping depends on the direction of the reaching movement. *Brain research, 869*(1-2), 121-129. doi: 10.1016/s0006-8993(00)02378-7

Rolfs, M. (2009). Microsaccades: small steps on a long way. *Vision Research*, 49(20), 2415-2441.

Sabes, P. N., & Jordan, M. I. (1997). Obstacle avoidance and a perturbation sensitivity model for motor planning. *Journal of Neuroscience, 17*(18), 7119-7128.

Sailer, U., Eggert, T., & Straube, A. (2002). Implications of distracter effects for the organization of eye movements, hand movements, and perception. *Progress in Brain Research, 140*, 341–348. doi:10.1016/S0079-6123(02)40061-1

Sailer, U., Eggert, T., Ditterich, J., & Straube, A. (2000). Spatial and temporal aspects of eye-hand coordination across different tasks. *Experimental Brain Research, 134*(2), 163–173. doi: 10.1007/s002210000457

Sailer, U., Eggert, T., Ditterich, J., & Straube, A. (2002). Global effect of a nearby distractor on targeting eye and hand movements. *Journal of Experimental Psychology: Human Perception and Performance, 28*(6), 1432–1446. doi: 10.1037/0096-1523.28.6.1432

Samuel, A. G., & Kat, D. (2003). Inhibition of return: A graphical meta-analysis of its time course and an empirical test of its temporal and spatial properties. *Psychonomic Bulletin & Review, 10*(4), 897-906.

Schall, J. D. (1991). Neuronal activity related to visually guided saccades in the frontal eye fields of rhesus monkeys: comparison with supplementary eye fields. *Journal of Neurophysiology, 66*(2), 559–579. doi: 10.1152/jn.1991.66.2.559

Scherberger, H., & Andersen, R. A. (2007). Target selection signals for arm reaching in the posterior parietal cortex. *Journal of Neuroscience, 27*(8), 2001-2012. doi: 10.1523/jneurosci.4274-06.2007

Schiller, P. H. & Tehovnik, E. J. (2005). Neural mechanisms underlying target selection with saccadic eye movements. *Progress in Brain Research, 149*, 157–171. doi: 10.1016/S0079-6123(05)49012-3

Scudder, C. A., Kaneko, C. R., & Fuchs, A. F. (2002). The brainstem burst generator for saccadic eye movements. *Experimental Brain Research, 142*(4), 439–462. doi: 10.1007/s00221-001-0912-9

Serences, J. T., Yantis, S., Culberson, A., & Awh, E. (2004). Preparatory activity in visual cortex indexes distractor suppression during covert spatial orienting. *Journal of Neurophysiology, 92*(6), 3538–3545. 10.1152/jn.00435.2004

Sheliga, B. M., Riggio, L., & Rizzolatti, G. (1994). Orienting of attention and eye movements. *Experimental Brain Research, 98*(3), 507-522.

Sheliga, B. M., Riggio, L., & Rizzolatti, G. (1995). Spatial attention and eye movements. *Experimental brain research, 105*(2), 261-275.

Shen, L., & Alexander, G. E. (1997). Preferential representation of instructed target location versus limb trajectory in dorsal premotor area. *Journal of neurophysiology, 77*(3), 1195-1212.

Shibutani, H., Sakata, H., & Hyvärinen, J. (1984). Saccade and blinking evoked by microstimulation of the posterior parietal association cortex of the monkey. *Experimental brain research, 55*(1), 1-8.

Shomstein, S., & Yantis, S. (2004). Configural and contextual prioritization in object-based attention. *Psychonomic bulletin & review, 11*(2), 247-253.

Smeets, J. B., Hayhoe, M. M., & Ballard, D. H. (1996). Goal-directed arm movements change eye-head coordination. *Experimental Brain Research, 109*(3), 434-440. doi: 10.1007/bf00229627

Smith, P. L., Wolfgang, B. J., & Sinclair, A. J. (2004). Mask-dependent attentional cuing effects in visual signal detection: The psychometric function for contrast. *Perception & Psychophysics, 66*(6), 1056-1075.

Snyder, L. H., Batista, A. P., & Andersen, R. A. (1997). Coding of intention in the posterior parietal cortex. *Nature, 386*(6621), 167.

Snyder, L. H., Calton, J. L., Dickinson, A. R., & Lawrence, B. M. (2002). Eye-hand coordination: saccades are faster when accompanied by a coordinated arm movement. *Journal of Neurophysiology, 87*(5), 2279-2286.

Soechting, J. F., Engel, K. C., & Flanders, M. (2001). The Duncker illusion and eye–hand coordination. *Journal of Neurophysiology, 85*(2), 843–854. doi: 10.1152/jn.2001.85.2.843

Sohlberg, M. M., & Mateer, C. A. (1989). Introduction to cognitive rehabilitation: *Theory and practice*. Guilford Press.

Song, J. H., & McPeek, R. M. (2009). Eye-hand coordination during target selection in a pop-out visual search. *Journal of Neurophysiology, 102*(5), 2681–2692. doi: 10.1152/jn.91352.2008

Song, J. H., & McPeek, R. M. (2014). Neural correlates of target selection for reaching movements in superior colliculus. *Journal of Neurophysiology*, 113(5), 1414-1422.

Song, J. H., & Nakayama, K. (2006). Role of focal attention on latencies and trajectories of visually guided manual pointing. *Journal of Vision*, 6(9), 11-11. doi: 10.1167/6.9.11

Song, J. H., & Nakayama, K. (2008). Target selection in visual search as revealed by movement trajectories. *Vision Research*, 48(7), 853-861. doi: 10.1016/j.visres.2007.12.015

Song, J. H., Rafal, R. D., & McPeek, R. M. (2011). Deficits in reach target selection during inactivation of the midbrain superior colliculus. *Proceedings of the National Academy of Sciences, 108*(51), E1433–E1440. doi: 10.1073/pnas.1109656108

Sparks, D. L. & Barton, E. J. (1993). Neural control of saccadic eye movements. *Current Opinion in Neurobiology, 3*(6), 966–972. doi: 10.1016/0959-4388(93)90169-Y

Sperling, G. (1960). The information available in brief visual presentations. *Psychological monographs: General and applied, 74*(11), 1.

Strache, W. (1987). Effectiveness of two modes of training to overcome deficits of concentration. *International Journal of Rehabilitation Research, 10*(4, Suppl 5), 141-145.

Sturm, W., Fimm, B., Cantagallo, A., Cremel, N., North, P., Passadori, A., Pizzamiglio, L., Rousseaux, M., Zimmerman, G., Deloche, G., & Leclercq, M. (2002). Computerized training of specific attention deficits in stroke and traumatic brain-injured patients. *Applied neuropsychology of attention: theory, diagnosis, and rehabilitation*, 365.

Sturm, W., Willmes, K., Orgass, B., & Hartje, W. (1997). Do specific attention deficits need specific training? *Neuropsychological Rehabilitation, 7*(2), 81-103.

Suzuki, M., Izawa, A., Takahashi, K., & Yamazaki, Y. (2008). The coordination of eye, head, and arm movements during rapid gaze orienting and arm pointing. *Experimental Brain Science, 184*(4), 579–585. doi: 10.1007/s00221-007-1222-7

Talgar, C. P., Pelli, D. G., & Carrasco, M. (2004). Covert attention enhances letter identification without affecting channel tuning. *Journal of Vision*, 4(1), 3-3.

Tao, G., Khan, A. Z., & Blohm, G. (2018). Corrective response times in a coordinated eye-head-arm countermanding task. *Journal of Neurophysiology*. (In Press). doi: 10.1152/jn.00460.2017

Tassinari, G., Aglioti, S., Chelazzi, L., Peru, A., & Berlucchi, G. (1994). Do peripheral non-informative cues induce early facilitation of target detection? *Vision Research*, 34(2), 179-189 doi: 10.1016/0042-6989(94)90330-1

Taylor, T. L., & Klein, R. M. (2000). Visual and motor effects in inhibition of return. *Journal of Experimental Psychology: Human Perception and Performance, 26*(5), 1639.

Theeuwes, J. & Godijn, R. (2004). Inhibition-of-return and oculomotor interference. *Vision Research, 44*(12), 1485–1492. doi: 10.1016/j.visres.2003.09.035

Theeuwes, J. (1991). Exogenous and endogenous control of attention: The effect of visual onsets and offsets. *Perception & psychophysics, 49*(1), 83-90.

Theeuwes, J. (1994). Stimulus-driven capture and attentional set: selective search for color and visual abrupt onsets. *Journal of Experimental Psychology: Human perception and performance, 20*(4), 799.

Theeuwes, J. (2004). Top-down search strategies cannot override attentional capture. *Psychonomic bulletin & review, 11*(1), 65-70.

Theeuwes, J., Kramer, A. F., Hahn, S., Irwin, D. E., & Zelinsky, G. J. (1999). Influence of attentional capture on oculomotor control. *Journal of Experimental Psychology: Human Perception and Performance, 25*(6), 1595–1608. doi: 10.1037/0096-1523.25.6.1595

Thompson, K. G., & Bichot, N. P. (2005). A visual salience map in the primate frontal eye field. *Progress in Brain Research, 147*, 249–262. doi: 10.1016/S0079-6123(04)47019-8

Thura, D., Hadj-Bouziane, F., Meunier, M., & Boussaoud, D. (2008). Hand position modulates saccadic activity in the frontal eye field. *Behavioural Brain Research, 186*(1), 148–153. doi: 10.1016/j.bbr.2007.07.035

Timmermans, A. A., Seelen, H. A., Willmann, R. D., & Kingma, H. (2009). Technology-assisted training of arm-hand skills in stroke: concepts on reacquisition of motor control and therapist guidelines for rehabilitation technology design. *Journal of neuroengineering and rehabilitation, 6*(1), 1.

Tipper, S. P., Howard, L. A., & Jackson, S. R. (1997). Selective reaching to grasp: Evidence for distractor interference effects. *Visual cognition, 4*(1), 1-38.

Tipper, S. P., Lortie, C., & Baylis, G. C. (1992). Selective reaching: evidence for action-centered attention. *Journal of Experimental Psychology: Human Perception and Performance, 18*(4), 891.

Tipper, S. P., Rafal, R., Reuter-Lorenz, P. A., Starrveldt, Y., Ro, T., Egly, R., & Weaver, B. (1997). Object-based facilitation and inhibition from visual orienting in the human split-brain. *Journal of Experimental Psychology: Human Perception and Performance, 23*(5), 1522-32. doi: 10.1037//0096-1523.23.5.1522

Todd, J. J., & Marois, R. (2004). Capacity limit of visual short-term memory in human posterior parietal cortex. *Nature, 428*(6984), 751.

Tong, F. (2004). Splitting the spotlight of visual attention. *Neuron, 42*(4), 524-526.

Treue, S. (2003). Visual attention: the where, what, how and why of saliency. *Current Opinion in Neurobiology, 13*(4), 428–432. doi: 10.1016/S0959-4388(03)00105-3

Tweed, D., Glenn, B., & Vilis, T. (1995). Eye-head coordination during large gaze shifts. *Journal of Neurophysiology, 73*(2), 766–779. doi: 10.1152/jn.1995.73.2.766

Van der Stigchel, S., & Theeuwes, J. (2005). Relation between saccade trajectories and spatial distractor locations. *Cognitive Brain Research, 25*(2), 579-582.

Van der Stigchel, S., & Theeuwes, J. (2008). Differences in distractor-induced deviation between horizontal and vertical saccade trajectories. *Neuroreport, 19*(2), 251-254.

van Donkelaar, P., Langan, J., Rodriguez, E., Drew, A., Halterman, C., Osternig, L. R., & Chou, L. S. (2005). Attentional deficits in concussion. *Brain Injury, 19*(12), 1031-1039.

van Zoest, W., Donk, M., & Theeuwes, J. (2004). The role of stimulus-driven and goal-driven control in saccadic visual selection. *Journal of Experimental Psychology: Human perception and performance, 30*(4), 746.

Vazquez, Y., Federici, L., & Pesaran, B. (2017). Multiple spatial representations interact to increase reach accuracy when coordinating a saccade with a reach. *Journal of Neurophysiology, 118*(4), 2328–2343. doi: 10.1152/jn.00408.2017

Vercher, J. L., Magenes, G., Prablanc, C., & Gauthier, G. M. (1994). Eye-head-hand coordination in pointing at visual targets: spatial and temporal analysis. *Experimental Brain Research, 99*(3), 507–523. doi: 10.1007/BF00228987

Vogel, E. K., & Machizawa, M. G. (2004). Neural activity predicts individual differences in visual working memory capacity. *Nature, 428*(6984), 748.

Wade, D. T. (2000). Personal context as a focus for rehabilitation. *Clinical Rehabilitiation, 14*, 115-118.

Walker, R., Kentridge, R. W., & Findlay, J. M. (1995). Independent contributions of the orienting of attention, fixation offset and bilateral stimulation on human saccadic latencies. *Experimental Brain Research, 103*(2), 294–310. doi: 10.1007/BF00231716

Werner, W. (1993). Neurons in the primate superior colliculus are active before and during arm movements to visual targets. *European Journal of Neuroscience, 5*(4), 335-340.

Werner, W., Dannenberg, S., & Hoffmann, K. P. (1997). Arm-movement-related neurons in the primate superior colliculus and underlying reticular formation: comparison of neuronal activity with EMGs of muscles of the shoulder, arm and trunk during reaching. *Experimental Brain Research, 115*(2), 191-205.

Werner, W., Hoffmann, K. P., & Dannenberg, S. (1997). Anatomical distribution of arm-movement-related neurons in the primate superior colliculus and underlying reticular formation in comparison with visual and saccadic cells. *Experimental Brain Research, 115*(2), 206-216.

White, C. T., Eason, R. G., & Bartlett, N. R. (1962). Latency and duration of eye movements in the horizontal plane. *Journal of the Optical Society of America, 52*(2), 210–213. doi: 10.1364/JOSA.52.000210

Wilder, J. D., Kowler, E., Schnitzer, B. S., Gersch, T. M., & Dosher, B. A. (2009). Attention during active visual tasks: Counting, pointing, or simply looking. *Vision Research, 49*(9), 1017-1031.

Woldag, H., & Hummelsheim, H. (2002). Evidence-based physiotherapeutic concepts for improving arm and hand function in stroke patients. *Journal of neurology, 249*(5), 518-528.

Wong, A. L., Goldsmith, J., & Krakauer, J. W. (2016). A motor planning stage represents the shape of upcoming movement trajectories. *Journal of neurophysiology, 116*(2), 296-305. doi: 10.1152/jn.01064.2015

Wong, A. L., Haith, A. M., & Krakauer, J. W. (2015). Motor planning. *The Neuroscientist, 21*(4), 385-398. doi: 10.1177/1073858414541484

Wulf, G. & Prinz, W. (2001). Directing attention to movement effects enhances learning: A review. *Psychonomic Bulletin & Review, 8*(4), 648–660. doi: 10.3758/BF03196201

Yantis, S., & Jonides, J. (1990). Abrupt visual onsets and selective attention: voluntary versus automatic allocation. *Journal of Experimental Psychology: Human perception and performance, 16*(1), 121.

Yttri, E. A., Liu, Y., & Snyder, L. H. (2013). Lesions of cortical area LIP affect reach onset only when the reach is accompanied by a saccade, revealing an active eye–hand coordination circuit. *Proceedings of the National Academy of Sciences, 110*(6), 2371–2376. doi: 10.1073/pnas.1220508110

Zelinsky, G. J. & Bisley, J. W. (2015). The what, where, and why of priority maps and their interactions with visual working memory. *Annals of the New York Academy of Sciences, 1339*(1), 154–164. doi: 10.1111/nyas.12606