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Rôle de la vision pour le contrôle de la dynamique du mouvement lors d'un geste de pointage manuel chez l'adulte ainsi que chez l'enfant

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Cette thèse intitulée :

Rôle de la vision pour le contrôle de la dynamique du mouvement lors d'un geste de pointage manuel chez l'adulte ainsi que chez l'enfant

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Résumé

Antérieurement, la contribution relative des informations visuelles et proprioceptives pour le contrôle de la cinématique et de la dynamique était évaluée de façon indépendante. Il était généralement accepté que l'information visuelle représentait la modalité sensorielle dominante pour la planification et le contrôle en ligne de la cinématique tandis que les informations proprioceptives contribuaient de façon plus importante aux mécanismes soutenant la dynamique du mouvement. Cependant, il demeure incertain comment le système nerveux central intègre les informations visuelles pour le contrôle de la dynamique du mouvement.

Une première hypothèse propose un traitement indépendant des différentes informations sensorielles lors du geste de pointage manuel. Une seconde hypothèse propose une interférence entre les processus basés sur le traitement de la vision et ceux soutenant la dynamique du mouvement. En effet, l'hypothèse de la spécificité de la pratique propose que les informations visuelles soient traitées au détriment des autres informations sensorielles pour le contrôle en ligne du mouvement et par le fait même, pour le contrôle en ligne de la dynamique. Nous avons voulu déterminer comment la vision et la proprioception étaient utilisées pour le contrôle en temps réel du mouvement.

Les résultats nous ont permis

- de déterminer que le traitement de la vision ne s'effectue pas au détriment du traitement de la proprioception. De façon plus importante, nous avons mis à jour un mécanisme de modulation de la partie initiale du mouvement sur la base des informations visuelles

- d'établir que les rôles complémentaires de la vision et de la proprioception ainsi que le poids des modalités sensorielles sont intégrés dans la représentation du mouvement tôt dans l'enfance. De plus, nous avons démontré que l'apprentissage du modèle interne dynamique, dans un contexte de développement chez l'enfant, ne s'effectuait pas de façon uniforme dans l'espace de travail.

- de mettre en évidence que la modulation en ligne du mouvement sur la base de la vision n'interfère pas avec l'apprentissage d'une nouvelle représentation interne de la dynamique. Plutôt, le développement d'un nouveau modèle interne dynamique interfère avec le rôle usuel de la vision pour moduler la partie initiale du mouvement.

En conclusion, l'ensemble des résultats de cette thèse soutient que le contrôle de la dynamique repose sur le traitement des informations proprioceptives plutôt que visuelles. Cependant, l'information visuelle maintien un rôle dominant pour la modulation en ligne tôt dans l'exécution du mouvement, lorsque le mouvement n'était pas perturbé, ainsi que pour assurer une précision spatiale optimale. Cependant, cette dominance n'était pas immuable. Finalement, le développement du modèle interne dynamique chez l'enfant suivrait une distribution particulière; de la ligne médiane vers un espace de travail excentré.

Mots clés : Information visuelle, information proprioceptive, modèle interne, dynamique, cinématique, modulation en ligne, correction en ligne, contrôle, apprentissage, enfants, pointage vidéo

Abstract

In previous research, the contribution of each source of sensory information for kinematic and dynamic processes has been studied independently. It is generally accepted that the visual afferent plays a dominant role for planning and control of kinematics, whereas the proprioceptive afferent is mostly linked to mechanisms underlying movement dynamics. However, it remains unclear how the central nervous system (CNS) integrates visual information in order to control said movement dynamics.

A first hypothesis suggests that the two different sources of sensory information, vision and proprioception, are processed independently to sustain kinematic and dynamic control, respectively. A second hypothesis puts forward that mechanisms relying on vision interact with those that control movement dynamics. Indeed, the *Specificity of practice* hypothesis stipulates that visual information is processed at the expense of others sources of information for online control, possibly including online dynamic control. The goal of this thesis is to describe the role of visual and proprioceptive information in dynamic and kinematic online movement control.

Our results show that:

-Visual information is not processed at the expense of proprioceptive information. Most importantly, we have described a mechanism based on visual information which modulates the trajectory in the initial part of movement.

-The complementary roles of visual and proprioceptive information, as well as their relative importance, are integrated in the neural representation of movement early on during childhood. We have also demonstrated that the development of an internal model of limb dynamic in children does not develop uniformly through the workspace.

-Online modulation based on vision does not interfere with the development of a new internal dynamic model. Instead, its development interferes with the role of visual information which usually allows for modulations in the first portion of the trajectory.

To summaries, our results support that the control of movement dynamics rely mostly on the processing of proprioceptive rather than visual information. On the other hand, we have demonstrated that visual information maintains its role for online modulation of movement (1) in the early part of movement trajectory (2) when dynamic is not perturbed (3) to sustain spatial accuracy. As we have established earlier, visual information's dominance for kinematic control is not absolute. Developing a new internal model of limb dynamic interferes with early visual control. Finally, the development of an internal model of limb dynamic in children is not uniformly distributed across the workspace; it begins close to one's midline and continues through eccentric workspace.

Keys words: Visual information, proprioceptive information, internal model, dynamic, kinematics, online modulation, online correction, control, learning, children, video-aiming

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Liste des sigles et abréviations

Abréviations internationales :

al.: collaborateurs
cm: centimètre
Hz: hertz
kg: kilogramme
mm: millimètre
mm/s : millimètre par seconde (valeur de vitesse)
mm/s^2 : millimètre par seconde carrée (valeur d'accélération/ décélération)
ms: milliseconde

Abréviations spécifiques au domaine de recherche et à la thèse :

Acc: acceleration
Acq: acquisition
CCW : counter clockwise
CEV: coefficient of extent variability
CDN: canadian
CNS: central nervous system
CW: clockwise
Dec: deceleration
End: movement endpoint
Fig: figure
KR : knowledge of result
NV : normal vision
TO: target-only
Vel: velocity

Sigles:

(°): degré
%: pourcentage

À mes parents
qui m'ont permis de réussir ce que j'entreprenais

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Chapitre I

Introduction générale à la thèse

Lors d'un geste de pointage manuel, le système nerveux central utilise diverses informations sensorielles pour planifier et contrôler les différentes composantes du mouvement. Spécifiquement, il est généralement accepté que le traitement des informations visuelles, proprioceptives, vestibulaires et auditives est à la base du contrôle sensorimoteur. Cependant, la contribution relative des différentes informations sensorielles n'est pas uniforme, elle varie en fonction des aspects cinématiques et dynamiques du mouvement. Plus particulièrement, nous nous intéresserons aux contributions relatives des informations visuelles et proprioceptives.

La cinématique du mouvement fait référence au déplacement (déplacement articulaire, de la main, du curseur, etc....). Avant l'amorce du mouvement, un modèle interne cinématique définit un vecteur de référence, caractérisant la direction du mouvement ainsi que le facteur de gradation entre la commande motrice et l'étendue du mouvement. En cours d'exécution, si la trajectoire produite dévie de la trajectoire désirée, alors le mouvement sera corrigé. Plusieurs auteurs ont démontré que l'élaboration du vecteur de référence (Sober et Sabes 2003) ainsi que la modulation en ligne de la trajectoire (Saunders et Knill 2003, 2004, 2005; Sarlegna, Blouin, Bresciani, Bourdin, Vercher, Gauthier 2003; Sarlegna, Blouin, Vercher, Bresciani, Bourdin, Gauthier 2004) s'effectuaient essentiellement sur la base des informations visuelles.

Les travaux issus de notre laboratoire corroborent cette dernière proposition. Plus particulièrement, les travaux de Proteau et collègues ont démontré que l'information visuelle représentait la source d'afférence optimale pour assurer la précision spatiale du geste (Proteau 1992, 2005; Soucy et Proteau 2001; Tinjust et Proteau, 2009; Tremblay et Proteau 1998). En effet, ces auteurs ont observé que la présence des informations visuelles permettait une meilleure précision spatiale que lorsque ces dernières n'étaient pas disponibles, et ce même après beaucoup de pratique sans les afférences visuelles. Également, le retrait de la vision lors d'un test de transfert résultait en une importante diminution de la performance. Il semble que les individus deviennent dépendants des informations visuelles avec la pratique, vraisemblablement parce que cette source d'information est dominante pour le contrôle de la cinématique. Proteau et collègues proposaient même que les informations visuelles étaient traitées à l'exclusion des autres sources d'informations sensorielles et plus précisément, à l'exclusion des informations proprioceptives, pour assurer le contrôle cinématique du mouvement et, ultimement la précision du geste.

La dynamique du mouvement fait référence aux forces appliquées (ou réactives) aux différentes parties du bras d'un individu. Le modèle interne dynamique détermine la grandeur ainsi que l'organisation temporelle des forces produites. En cours d'exécution, le modèle interne dynamique est sollicité pour apporter d'éventuelles corrections, par exemple, pour modifier la force appliquée au bras, à l'avant-bras ou à la main, pour contrecarrer une résistance non-anticipée au déplacement de cette dernière. De récentes études ont démontré un rôle prédominant des informations proprioceptives pour le développement d'un modèle interne dynamique (Ghez et Sainburg 1995; Ghilardi, Gordon et Ghez 1995; Gordon, Ghilardi, Cooper et Ghez 1994; Sainburg, Ghilardi, Poizner et Ghez 1995; Sainburg, Ghez et Kalakanis 1999; Wang et Sainburg 2004). De plus, Krakauer et collègues (1999) ont établi que le développement d'un nouveau modèle interne dynamique n'était pas facilité par la disponibilité des afférences visuelles. Ces auteurs proposaient que cet apprentissage ne s'effectue que sur la base des informations proprioceptives.

En résumé, plusieurs études ont mis en évidence une contribution plus importante de la vision pour le contrôle de la cinématique du mouvement et une contribution plus importante de la proprioception pour le contrôle de la dynamique du mouvement. Cependant, la contribution relative des informations sensorielles pour le contrôle de la cinématique et de la dynamique était évaluée à l'intérieur de protocoles expérimentaux indépendants. Dans la présente thèse, nous avons voulu déterminer la contribution des informations visuelles en considérant simultanément les aspects cinématiques et dynamiques du mouvement.

Pour répondre aux différentes considérations fondamentales exposées dans cette thèse, nous avons étudié le geste de pointage vidéo chez le jeune adulte ainsi que chez l'enfant. Spécifiquement, les participants devaient déplacer un manipulandum à partir d'une base de départ fixe vers différentes cibles. Ces dernières étaient localisées de part et d'autre de l'axe sagittal médian (entre -50° et 50°) et situées à 150 mm (article 1 et 2) ou 320 mm (article 3) de la base de départ. Cent huit participants adultes (âgés entre 20 et 25 ans) et trente-six enfants (âgés entre 6 et 12 ans) ont participé volontairement aux études présentées dans cette thèse. Quatre stratégies expérimentales ont été utilisées pour atteindre nos objectifs: l'utilisation des différences inertielles en fonction de la direction du mouvement de pointage (anisotropie), le changement de configuration du membre (article 1), l'utilisation d'un mouvement d'aller-retour dans le but d'étudier le contrôle des forces intersegmentaires chez l'enfant (article 2) et l'altération des interactions dynamiques entre les segments par l'ajout d'une masse excentrée (article 3). Pour évaluer le rôle de la vision, une condition de vision normale était comparée à une condition de cible seulement dans les différentes études.

Objectifs et hypothèse spécifiques

Sur la base des considérations exposées plus haut et en nous appuyant sur l'ensemble des travaux disponibles, nous avons étudié la contribution de l'information visuelle dans différents contextes dynamiques (normal, perturbé et en développement). En premier lieu, nous avons étudié le contrôle visuel dans un contexte où les modèles internes cinématiques et dynamiques étaient stables et bien établis. Le premier processus à l'étude était celui du contrôle en ligne responsable de l'élimination de l'anisotropie retrouvée entre des mouvements réalisés à gauche ou à droite de l'axe sagittal médian. Le second processus à l'étude correspondait à la mise à jour du modèle interne dynamique en fonction de la configuration initiale du bras. Considérant que l'information visuelle représente la source d'information sensorielle dominante pour la modulation en ligne du mouvement, nous avons posé comme hypothèse que cette dernière contribuerait de façon majeure à l'élimination des effets de l'anisotropie (contrôle de la dynamique). Dans la même veine, nous proposions que la forte dépendance aux informations visuelles interfère avec la mise à jour du modèle interne dynamique. L'un des principaux résultats démontrait que l'information visuelle n'était pas traitée au détriment des informations proprioceptives. Plutôt, nous avons mis en évidence que le traitement des informations visuelles et proprioceptives soutenait deux mécanismes de contrôle indépendants, l'un cinématique et l'autre dynamique, pour assurer la précision spatiale en étendue. Cette observation a mené à notre second objectif qui était de déterminer si ce traitement simultané des informations sensorielles en fonction de la composante du mouvement était établi pendant l'enfance.

Certaines évidences (Deutsch et Newell 2001; Goble et al. 2005) suggéraient que l'enfant serait davantage disposé à utiliser les informations visuelles que l'adulte pour contrôler la dynamique du mouvement. L'un des objectifs était de tester cette hypothèse. Nos travaux se distinguaient des travaux antérieurs notamment parce que nous avons étudié le contrôle des forces transmises lorsque ces dernières étaient générées par la commande motrice plutôt que par l'environnement. Ainsi, nous avons utilisé une tâche d'aller-retour plutôt qu'une tâche de pointage contre une résistance variable (i.e., champ de force). Nos résultats indiquent que les enfants éprouvaient de la difficulté à organiser l'aspect temporel de leur commande motrice afin de contrôler les forces intersegmentaires. Cependant, la disponibilité des informations visuelles permettait de moduler de façon importante la trajectoire du mouvement de retour. Ces résultats étaient observés chez l'enfant ainsi que chez l'adulte. L'ensemble des résultats de nos deux premières expériences a mis en évidence un rôle complémentaire des informations visuelles et proprioceptives. Cependant, tel est-il le cas lorsque l'on doit apprendre un nouveau modèle interne dynamique?

Dans un premier temps, nous avons évalué l'apport des afférences visuelles à la précision du geste dans un contexte où la dynamique du mouvement était perturbée et pour lequel l'apprentissage d'un nouveau modèle interne dynamique était requis. Nous avons posé l'hypothèse que l'importance des afférences visuelles serait maintenue pour assurer une précision spatiale optimale lors de l'apprentissage d'un nouveau modèle interne dynamique. Dans un second temps, nous avons voulu déterminer s'il existait une interaction entre les processus de modulation en ligne du mouvement sur la base de la vision et l'apprentissage d'un nouveau modèle interne dynamique sur la base de la proprioception. À notre connaissance, cette question n'avait jamais été considérée. Les résultats de cette étude confirment le rôle prépondérant des afférences proprioceptives pour l'apprentissage d'un nouveau modèle interne dynamique. De fait, pour la première fois, nous observions que ce rôle est tellement important qu'il interfère avec le rôle important des afférences visuelles pour la planification et le contrôle en ligne de la portion initiale du mouvement.

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Chapitre II

Revue de la littérature

Le contrôle sensorimoteur fait référence à l'utilisation des informations sensorielles pour l'exécution du mouvement. Plus particulièrement, le traitement des afférences visuelles et proprioceptives a fait l'objet de plusieurs études, lesquelles ont exposé la contribution respective de ces deux sources d'afférence lors de l'exécution du mouvement.

1 LES MODÈLES POUR L'EXÉCUTION DU MOUVEMENT

Au cours du vingtième siècle, différents modèles ont été proposés pour expliquer comment l'être humain guidait ses réponses motrices. Les différentes considérations théoriques sur le rôle des informations sensorielles pour le contrôle du mouvement seront présentées dans cette section.

1.1 Les modèles à boucle fermée

La principale caractéristique des modèles à boucle fermée est que la rétroaction sensorielle est utilisée et comparée à une référence en cours de mouvement pour réduire l'erreur. Dans la théorie en boucle fermée d'Adams (1971), deux états de mémoire sont responsables de la production d'un geste de positionnement. La trace mnésique représente un modeste programme moteur et est en charge de l'amorce du geste. De plus, avant l'amorce du mouvement, la trace mnésique choisit la trace perceptuelle appropriée au geste à produire. Ce second état de mémoire est responsable du guidage du membre lors de l'exécution du mouvement. La trace perceptuelle est formée à partir des conséquences sensorielles passées et représente la référence de correction contre laquelle la rétroaction sensorielle est comparée. En cours d'exécution, si une différence advenait entre la rétroaction sensorielle et les conséquences sensorielles attendues (i.e., la trace perceptuelle), alors, le mouvement serait corrigé et poursuivi jusqu'à ce que le membre atteigne la localisation correcte. Bien que la théorie d'Adams sur le contrôle sensorimoteur en ligne soit plausible pour des mouvements lents, étant donné les délais requis pour effectuer cette boucle de rétroaction, il est peu probable que ce processus de détection et de correction des erreurs soit responsable du contrôle moteur des mouvements rapides.

1.2. Les modèles à boucle ouverte

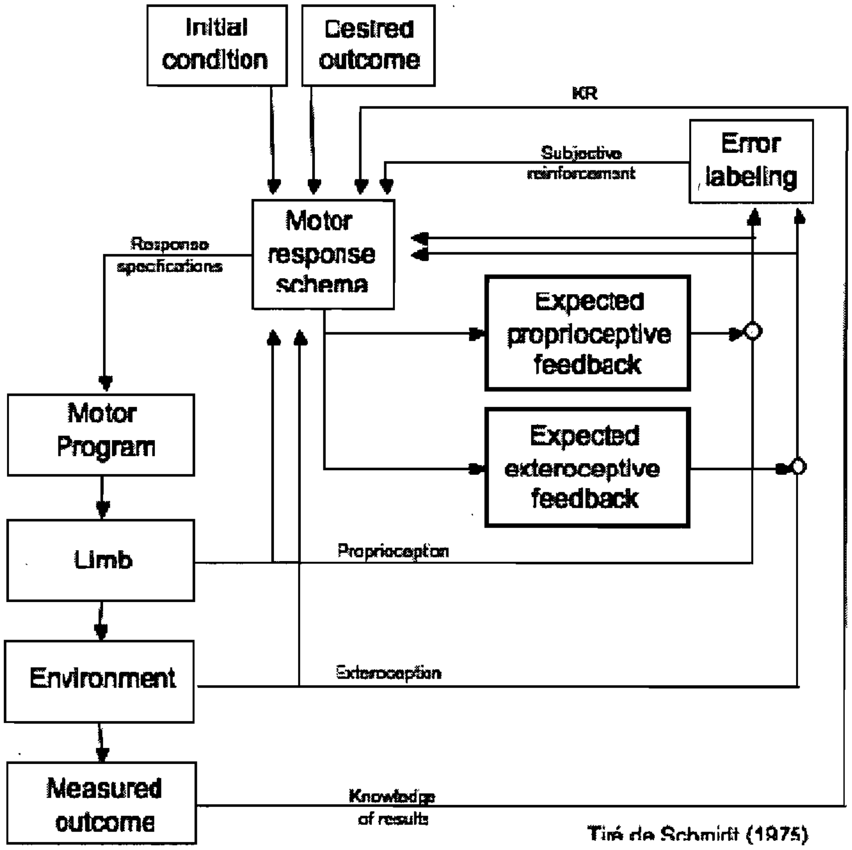
Une vue plus centraliste du contrôle moteur proposait que le mécanisme de rétroaction sensorielle ait une contribution limitée, voire inexistante, pour le contrôle en ligne du mouvement, et ce, principalement à cause des délais de transport et de traitement des informations sensorielles (Houk et Rymer 1981; Keele et Posner 1968 ; Rack 1981). Plutôt, le geste à produire serait entièrement préparé avant son amorce ; il serait réalisé sans que les informations sensorielles ne soient utilisées en cours d'exécution. La structure responsable de l'organisation du mouvement serait le programme moteur (Keele 1968). Pour réaliser un geste, les fonctions exécutives supérieures n'auraient qu'à choisir le programme moteur approprié. Les études réalisées chez des patients souffrant d'une neuropathie sensorielle conforte cette vue centraliste du contrôle du mouvement. En effet, bien que ces patients ne reçoivent plus d'information sensorielle (proprioceptive) provenant de leurs membres, ces derniers demeurent en mesure de produire des mouvements quoique pas très précis (Gordon, Ghilardi, et Ghez. 1995 ; Lashley 1917 ;

Sainburg, Ghilardi, Poizner et Ghez 1995). Cependant, l'argument central de cette théorie, selon lequel le délai des boucles de rétroaction ne permettrait pas l'utilisation des informations sensorielles en ligne pour des mouvements très rapides, ne semble pas représenter la réalité. En effet, les études sur la saccade oculaire ont démontré que les mouvements balistiques pouvaient être influencés en ligne par l'information sensorielle (Bizzi, Kalil et Tagliasco1971 ; Morasso, Bizzi et Dichgans 1973). En vue de corriger les faiblesses des différents modèles en boucle fermée ou en boucle ouverte, c'est en 1975 que Schmidt proposa un modèle hybride du contrôle du mouvement humain.

1.3. Les modèles hybrides

Les modèles hybrides proposent une planification centrale du mouvement ainsi qu'un traitement des informations sensorielles pour la correction en ligne du mouvement ou pour l'analyse de la performance (Abbs, Gracco et Cole 1984; Schmidt 1975). Selon la théorie de Schmidt (1975), le schéma de rappel représenterait un programme moteur généralisé qui gouvernerait les différents mouvements ayant les mêmes caractéristiques de base. Quatre sources d'information sont essentielles pour la formation du schéma de rappel soit, les conditions initiales, les spécifications de la réponse, les conséquences sensorielles et le résultat obtenu. Avec la pratique, la formation du schéma consisterait en l'élaboration de différentes règles qui régissent une classe particulière de mouvements. Ces règles seraient issues de la relation qui existe entre les quatre sources d'information présentées précédemment. Une seconde structure proposée dans la théorie de Schmidt est le schéma de reconnaissance. Tel que suggéré dans la théorie en boucle fermée d'Adams (1971), le schéma de reconnaissance génère les conséquences sensorielles attendues contre lesquelles, si le temps le permet, la rétroaction sensorielle sera comparée en cours de mouvement. Dans le cas où le temps de mouvement serait inférieur à 200 ms (temps minimum évalué pour effectuer une boucle de rétroaction au moment où cette théorie a été présentée), les informations sensorielles ne permettraient pas de corriger une erreur en cours de mouvement. Il n'en demeure pas moins, toutefois, qu'elles seraient traitées. Selon cette théorie, la rétroaction sensorielle serait utilisée suite à la réalisation du mouvement pour l'analyse de la performance. Cette information permettrait de modifier ou de consolider le programme moteur généralisé en fonction de la performance. Cette information permettrait aussi de déterminer si les commandes motrices utilisées étaient les bonnes pour atteindre l'objectif.

Une première classe de conséquences sensorielles est la rétroaction proprioceptive attendue tandis qu'une seconde classe est la rétroaction extéroceptive attendue (telle que la rétroaction visuelle). Tel qu'illustré à la Figure 1, les références sensorielles sont indépendantes et sont représentées dans deux systèmes de référence sensorimotrice distincts, l'un proprioceptif et l'autre visuel. Une autre considération importante est que ces systèmes de référence muteraient en fonction de la pratique. Cette théorie prédit qu'en début de pratique les informations proprioceptives et visuelles seraient importantes pour la détection et la correction des erreurs tandis que seules les informations proprioceptives seront importantes tard dans la pratique. Proposition jadis partagée par Fleishman et Rich (1963) et Adams, Gopher et Lintern (1977). Plus particulièrement, Adams, Gopher et Lintern (1977) proposaient que la contribution relative de la proprioception pour le contrôle du mouvement augmente avec la pratique. Dans un même ordre d'idée, mais ayant une position sensiblement distincte, MacNeilage et MacNeilage (1973) ont proposé une diminution du rôle des afférences sensorielles avec la pratique. En fait, dû aux délais associés au traitement des afférences sensorielles, ces auteurs proposaient que les individus passaient d'un mode de contrôle en boucle fermée vers un mode de contrôle en boucle ouverte. Ces prédictions ont suscité beaucoup d'intérêt et ont été soumises à l'épreuve expérimentale.



Tiré de Schmidt (1975)

Figure 1. Le schéma moteur (Schmidt 1975). En relation avec le geste à produire, le schéma engendre la spécification de la réponse (un programme moteur spécifique) ainsi que les conséquences sensorielles attendues. Les conséquences sensorielles attendues sont représentées dans deux systèmes de références indépendants : proprioceptif et extéroceptif.

2 INFORMATION SENSORIELLE ET CONTRÔLE DE LA CINÉMATIQUE

La cinématique du mouvement fait référence au déplacement (déplacement articulaire, déplacement de la main ou d'un curseur, etc.) lors de l'exécution du geste. Les différentes études présentées dans la prochaine section ont utilisé des tâches de pointage manuel pour déterminer le rôle des informations sensorielles pour le contrôle de la cinématique et par extension, pour la précision spatiale du geste.

2.1 La vision est intégrée dans la représentation sensorimotrice avec la pratique

Maintes études ont démontré que la vision de la main en cours d'exécution permettait une meilleure précision spatiale que lorsque la vision de la cible seulement était disponible (Carlton 1981 ; Chua et Elliott 1993 ; Hay et Beaubaton 1985,1986 ; Khan et Franks 2003 ; Proteau, Marteniuk, Girouard et Dugas 1987 ; voir Proteau 1992, pour une revue ; Proteau 2005). Toutefois, c'est en 1987 que Proteau, Marteniuk, Girouard et Dugas ont étudié l'indépendance des systèmes de référence sensorielle (tel qu'énoncé par Schmidt 1975) ainsi que l'impact de la pratique sur l'utilisation des informations sensorielles.

Les participants devaient effectuer une tâche de pointage manuel vers une cible localisée à 90 cm de la base de départ. Un premier groupe pratiquait la tâche pour 200 essais tandis qu'un second groupe pratiquait la tâche pour 2,000 essais. À l'intérieur des deux niveaux de pratique, les participants étaient regroupés selon deux conditions visuelles. En condition de vision complète, les informations visuelles relatives au déplacement au bras ainsi qu'à la cible étaient disponibles lors de l'exécution du mouvement (LT). En condition de cible seulement (T), le déplacement du bras n'était pas visible, seule la cible l'était. La connaissance du résultat était donnée après chacun des essais. Suite à la pratique, tous les participants effectuaient un test de transfert en condition de cible seulement sans connaissance du résultat. Afin d'évaluer la précision spatiale, les auteurs ont analysé l'erreur quadratique moyenne sur la composante en abscisse (X) et en ordonnée (Y) du mouvement. Selon les auteurs, si les informations visuelles et proprioceptives sont évaluées à l'intérieur de systèmes de référence indépendants, alors le retrait de l'information visuelle relative au déplacement bras (pour le groupe vision complète) ne devrait pas avoir d'impact sur la précision spatiale suite à une pratique extensive. Tel serait le cas, puisque tard dans la pratique seule la proprioception (Fleishman & Rich, 1963) ou un modèle de contrôle en boucle ouverte (MacNeilage & MacNeilage, 1973 ; Schmidt, 1975) assurerait le contrôle du mouvement.

Durant la phase de pratique, les groupes en vision complète (LT-200 et LT-2000) démontraient une meilleure précision spatiale que les groupes cible seulement (T-200 et T-2000). Il semble donc que les informations visuelles soient nécessaires pour assurer une précision spatiale optimale, et ce, même tard dans la pratique. De plus, on observe que le groupe cible seulement améliorait sa performance au cours des 2,000 essais de pratique. La performance lors de la phase de transfert indiquait que les groupes vision complète et cibles seulement étaient moins précis suite à une pratique modérée, de 67% à 100%, respectivement. Cependant, suite à la pratique prolongée, seul le groupe en vision complète démontrait une détérioration de la précision spatiale. Cette détérioration était de l'ordre de 400% par rapport à la performance notée en pratique. Ce résultat a été interprété comme indiquant que la pratique permet au système nerveux central de développer une représentation multi sensorielle intégrée des conséquences sensorielles attendues. Le retrait d'une source d'information sensorielle (dans ce cas la vision) entraînerait donc une diminution de la performance, puisque l'individu n'aurait accès qu'à une rétroaction sensorielle incomplète de son mouvement. Ces résultats vont à l'encontre des prédictions antérieures qui proposaient que les systèmes de référence sensorielle étaient indépendants et selon lesquelles la contribution relative de la vision pour assurer la précision du geste diminuait en fonction de la pratique.

La faible détérioration de la précision spatiale observée en transfert pour le groupe cible seulement résulterait de la formation d'une représentation sensorimotrice basée uniquement sur les informations proprioceptives. Le seul retrait de la connaissance du résultat dans la phase de transfert ne modifierait pas cette représentation sensorimotrice. Proteau, Marteniuk, Girouard et Dugas (1987) ont alors proposé que la formation d'une représentation sensorimotrice était spécifique aux informations sensorielles disponibles lors de la pratique.

2.2 Évidences supportant l'hypothèse de la spécificité de la pratique

Dans la foulée de l'étude réalisée par Proteau, Marteniuk, Girouard et Dugas (1987) plusieurs auteurs ont reproduit les effets de la spécificité de la pratique. Ainsi, le retrait d'une source d'information sensorielle (i.e., information visuelle) suite à la pratique résultait en une diminution de la performance (Elliott et Lee 1995; Khan, Elliott, Coull, Chua et Lyons 2002; Khan, Franks et Goodman 1998, Proteau et Cournoyer 1990, Proteau et Isabelle 2002, Proteau 2005, Tremblay et Proteau 1998). L'ensemble de ces résultats suggère que les informations visuelles soient la source d'information dominante pour le contrôle de la cinématique.

Dans cette veine, Proteau, Marteniuk et Lévesque (1992) ont démontré que l'ajout des informations visuelles en transfert suite à une pratique prolongée en condition de cible seulement entraînait une diminution de la performance (voir aussi Elliott et Jaeger 1988, pour des résultats similaires). D'une part, cette observation met en évidence que la représentation sensorimotrice développée en cours de pratique est spécifique aux sources d'information sensorielle disponibles lors cette pratique. En effet, il semble que les informations visuelles n'ont pu être utilisées efficacement en transfert, car la représentation sensorimotrice développée au cours de la pratique concernait uniquement la rétroaction proprioceptive. D'autre part, la diminution de performance associée à l'ajout de la vision démontrait que cette source d'information était dominante. Comme la représentation sensorielle développée pendant la pratique n'était basée que sur la rétroaction proprioceptive, les participants auraient dû n'utiliser que cette source d'afférence pour maintenir leur performance. Toutefois, le fait que ces derniers utilisaient tout de même les informations visuelles suggère que le traitement de la vision domine le traitement de la proprioception. De surcroît, ceci dénote la possibilité que la vision soit traitée au détriment des informations proprioceptives.

Les dernières observations concernant le rôle de la vision pour le contrôle du mouvement ont incité Proteau et ses collègues (Proteau 2005; Soucy et Proteau 2001; Tremblay et Proteau 1998) à proposer que les individus deviennent dépendants de la vision pour assurer la précision du geste et que cette dernière soit traitée au détriment des autres sources d'information sensorielles pour assurer cette précision.

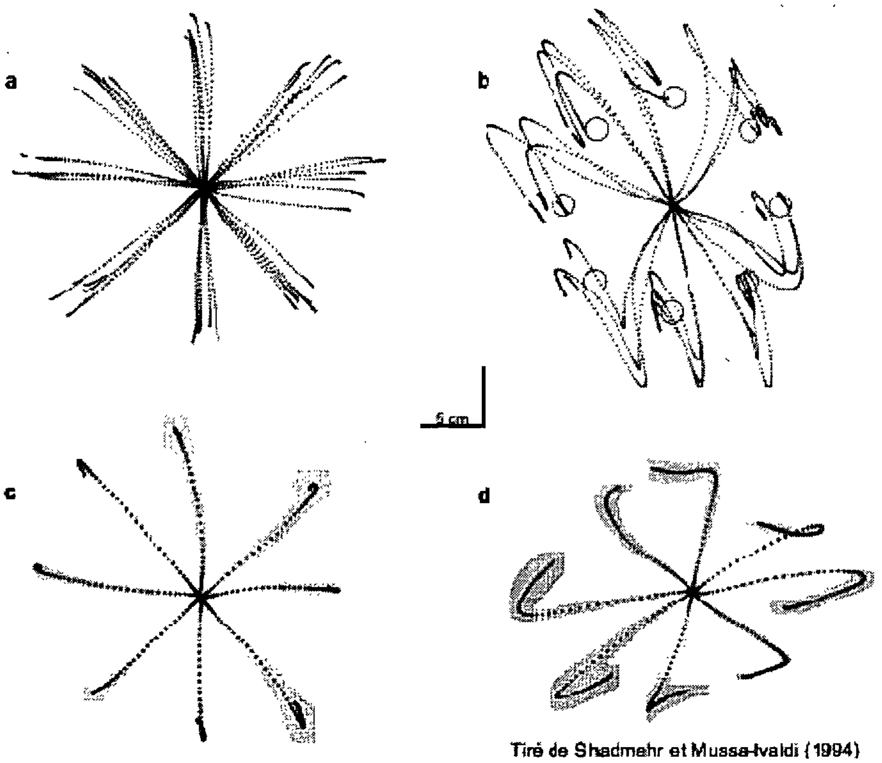
3 TYPE D'INFORMATION UTILISÉE POUR LE CONTRÔLE DE LA DYNAMIQUE DU MOUVEMENT

Nous avons démontré dans la section précédente un rôle presque exclusif des informations visuelles pour le contrôle de la cinématique, lorsque disponibles. En ce qui concerne la dynamique du mouvement, plusieurs études tendent à démontrer un rôle plus important des informations proprioceptives. La dynamique du mouvement fait référence aux forces appliquées au membre lors de la production d'un geste. Dans les différentes études présentées dans la prochaine section, les auteurs ont utilisé des tâches de pointage vidéo pour étudier le rôle des informations proprioceptives pour le contrôle de la dynamique du mouvement.

3.1 Le contrôle de la dynamique est basé sur le développement / la mise à jour d'un modèle interne dynamique

Shadmehr et Mussa-Ivaldi (1994) ont étudié comment le système nerveux central contrôle les mouvements dans différentes conditions dynamiques ainsi que le processus à la base de l'apprentissage d'une nouvelle dynamique. Les participants devaient déplacer un «*robot manipulandum*» pour réaliser des mouvements de pointage en direction de cibles (réparties sur 360 degrés) disposées sur un cercle. L'utilisation du robot avait pour fonction de produire un nouvel environnement dynamique. Ce robot produisait un champ de force qui assistait ou qui s'opposait au déplacement du bras lors de l'exécution d'un mouvement de pointage. Au cours des 1000 essais effectués, les participants étaient exposés au champ de force de façon continuelle à l'exception de 96 essais pour lesquels le champ de force était inopinément retiré (champ nul) à l'insu des participants. Pour 808 essais, le déplacement du manipulandum (représenté par un curseur) ainsi que la localisation de la cible à atteindre étaient présentés sur un écran d'ordinateur. Pour les 192 essais restant ainsi que pour les 96 essais en condition de champ nul seule la cible était visible. Les résultats sont illustrés à la Figure 2.

Lors des premiers essais réalisés en présence du champ de force, le mouvement de pointage déviait significativement de la trajectoire rectiligne normalement observée lors d'une tâche de pointage manuel. Également, la fin de la trajectoire était caractérisée par une grande correction en direction de la cible. Au fil des essais, la convergence des mouvements vers une trajectoire rectiligne et sans correction indiquait que les participants s'étaient adaptés au nouvel environnement dynamique. Pour déterminer le processus à la base de cette adaptation, les auteurs ont analysé les mouvements pour lesquels le champ de force était inopinément retiré. Les effets consécutifs observés suite au retrait du champ de force indiquaient une déviation de la trajectoire dans la direction opposée au champ de force ainsi qu'en correction en fin de mouvement. Comme l'adaptation à l'ajout ou au retrait du champ de force était observée tôt après l'amorce du mouvement (au sommet de vitesse), ceci suggère que le système nerveux central a développé un nouveau modèle interne de la dynamique du mouvement. Ce modèle prédisait les forces à générer pour contrecarrer le champ de force imposé. L'observation d'effets consécutifs conforte cette hypothèse. En effet, lorsque le champ de force était retiré à l'insu du participant, ce dernier amorçait son mouvement sur la base du nouveau modèle interne dynamique développé au cours de la pratique, lequel générait une commande motrice qui n'était plus appropriée en condition de champ nul. Le contrôle de la dynamique dépend donc d'un processus anticipatoire.



Tiré de Shadmehr et Mussa-Ivaldi (1994)

Figure 2. *a)* Trajectoires normales (rectilignes) avant l'exposition au champ de force *b)* déviation des trajectoires et fins de mouvement caractérisées par un crochet lorsque initialement exposé au champ de force *c)* réapparition d'une trajectoire rectiligne avec la pratique d) effets consécutifs en sens opposé lors du retrait du champ de force.

3.2. Le contrôle de la dynamique dépend du traitement de la proprioception

Plusieurs études ont démontré que le contrôle de la dynamique du mouvement s'effectuait à partir d'un modèle interne, dit « dynamique » (Gandolfo, Mussa-Ivaldi et Bizzi 1996; Lackner and Dizio 1994; Shadmehr et Mussa-Ivaldi 1994; Wang and Sainburg 2004). Le construit de « modèle interne » est étroitement apparenté au schéma moteur antérieurement proposé par Schmidt (1975). Dans les prochaines pages, nous nous intéresserons au type d'information sensorielle utilisé par le système nerveux central pour développer ou mettre à jour un modèle interne dynamique.

Une contribution importante quant au type d'information sensorielle utilisé pour le contrôle de la dynamique provient des études effectuées chez les patients souffrant d'une neuropathie sensorielle. De façon générale, les patients déafférentés démontrent une dégradation de la performance particulièrement sévère lorsqu'ils effectuent des mouvements pluri-articulaires. Gordon, Ghilardi et Ghez (1995) ont démontré que les patients privés de proprioception produisaient de grandes erreurs *«direction-dépendante»* sur l'étendue du mouvement : un mouvement trop long ou trop court lorsque dirigé vers la droite ou vers la gauche, respectivement. La cause de ces erreurs en étendue chez les patients déafférentés serait déliée à l'inhabileté de ces derniers à compenser pour les différences inertielles du membre en fonction de la direction du mouvement de pointage. Particulièrement, un mouvement dirigé dans une direction de moindre inertie (vers la droite) résultait en un sommet d'accélération plus élevé comparativement à un mouvement dirigé dans une direction de plus grande inertie (vers la gauche). Afin d'éviter que cette anisotropie ne provoque de trop grandes erreurs en étendue, il a été observé que les participants pourvus de proprioception modulaient le temps de mouvement. Un temps de mouvement plus court ou plus long était produit afin de compenser pour une accélération plus élevée ou moins élevée, respectivement. Chez les patients déafférentés, cette modulation du temps de mouvement était limitée et la trajectoire résultante était dominée par les effets de l'anisotropie lorsque la vision n'était pas disponible. Cette observation suggère que le mécanisme d'élimination de l'anisotropie, normalement observé chez les participants sains, dépend du traitement des informations proprioceptives (Gordon, Ghilardi, Cooper et Ghez 1994).

De façon plus importante, la dégradation de la performance de mouvements pluri-articulaires résulterait de l'inaptitude de ces patients à anticiper et coordonner les forces transmises entre les articulations. Dans un protocole évaluant le contrôle des forces transmises chez des patients privés de proprioception, Sainburg, Ghilardi, Poizner et Ghez (1995) demandaient aux participants d'effectuer des mouvements d'aller-retour dans différentes directions. Afin d'exécuter le renversement avec précision, les participants devaient tenir compte des forces transmises, notamment entre le bras et l'avant-bras, et ajuster leur commande motrice en fonction des différentes directions dans lesquelles ces mouvements étaient réalisés. Les auteurs ont observé une grande dérive de la main au moment du renversement chez les patients déafférentés. Cette dérive augmentait lorsque la contribution de l'épaule pour le déplacement du bras augmentait et, ainsi, transmettait de plus grandes forces au niveau du coude. Selon ces auteurs, cette observation indiquait que les patients déafférentés éprouvaient de la difficulté à adapter l'action musculaire spécifique à chaque articulation aux variations directionnelles des forces intersegmentaires. Sainburg Ghilardi, Poizner et Ghez (1995) conclurent que l'absence de proprioception causait un déficit dans le contrôle des forces intersegmentaires, notamment au niveau de son organisation temporelle. De plus, ces auteurs proposaient qu'un mécanisme en proaction, basé sur un modèle interne dynamique, était responsable du contrôle des forces intersegmentaires. Il semble donc qu'un modèle interne dynamique nécessite la présence des informations proprioceptives pour anticiper et contrôler les différents facteurs dynamiques du mouvement. Dans la même veine et utilisant une tâche similaire d'aller-retour (chez deux patients déafférentés et chez des participants sains), Sainburg, Poizner et Ghez (1993) ont démonté que la vision du membre favorisait une trajectoire plus linéaire ainsi qu'une meilleure synchronisation de l'action articulaire lors du renversement chez les patients déafférentés. Cependant, la performance des patients déafférentés demeurait moindre que celle des participants sains. Les auteurs proposent que l'information provenant des propriocepteurs est critique et nécessaire pour le contrôle des forces intersegmentaires. En addition, la vision du membre n'avait aucun impact sur la performance des participants sains, soit sur la gestion de la dynamique du mouvement, ce qui supporte une contribution plus importante des informations proprioceptives que visuelles pour le contrôle de la dynamique (voir Franklin et al. 2007 pour des résultats similaires).

Plusieurs autres études chez des participants sains ont confirmé cette dernière proposition (Ghilardi, Gordon et Ghez 1995; Sainburg, Ghez et Kalakanis 1999; Wang et Sainburg 2004). Ces études ont permis d'établir que l'adaptation dynamique à un nouveau contexte (par exemple, addition d'un champ de force) s'effectuait par le développement d'un nouveau modèle interne dynamique qui, grâce aux informations proprioceptives, pourrait être adapté à différents espaces de travail (Malfait, Shiller et Ostry 2002; Sainburg, Ghez et Kalakanis 1999; Shadmehr et Moussavi 2000; Shadmehr et Mussa-Ivaldi 1994).

Bien que plusieurs études aient mis en évidence un rôle important des informations proprioceptives pour le contrôle de la dynamique, ceci n'exclut pas que les informations visuelles puissent contribuer au contrôle de la dynamique. Ghez, Gordon et Ghilardi (1995) ont démontré que le feedback visuel à l'essai “n” permettait aux patients déafférentés de réduire leurs erreurs (l'anisotropie, l'erreur en étendue et directionnelle, la courbure de la trajectoire) à l'essais “n+1”, lequel était exécuté en l'absence de feedback visuel. Ces auteurs ont proposé que les informations visuelles procurent de l'information quant aux propriétés dynamiques du membre et, ainsi, qu'elle serait utile pour la mise à jour d'un modèle interne dynamique. Toutefois, cet effet s'atténuait à l'intérieur de quelques minutes. Il apparaît donc que l'information visuelle puisse être substituée à la proprioception pour augmenter la performance de l'individu à court terme (angle de renversement aiguë, superposition des mouvements d'aller et de retour), mais ne contribue pas de façon importante au développement d'un nouveau modèle interne dynamique. Néanmoins, Mattar et Gribble (2005) ont démontré qu'un nouveau modèle interne mécanique pouvait être appris sur la base de l'observation, et par le fait même, sur la base seule des informations visuelles. Spécifiquement, les participants ayant observé l'apprentissage d'une tierce personne à exécuter un mouvement de pointage dans un nouvel environnement mécanique (induit par un *«robot manipulamdum»*) démontraient une meilleure performance - lorsque ultérieurement ces derniers exécutaient le mouvement de pointage dans le même environnement mécanique - que des participants n'ayant pas observé l'apprentissage du nouvel environnement mécanique. Les auteurs proposent que l'observation permet d'extraire certaines informations utiles au développement d'une nouvelle représentation interne de l'environnement mécanique. La proprioception n'étant pas sollicitée lors de l'observation, il semble que la vision seule puisse contribuer aux mécanismes sous-tendant la dynamique du mouvement.

En résumé, les différentes études proposent un rôle indéniable de la proprioception pour le contrôle de la dynamique. Cependant, au vue des récentes études sur la contribution des informations visuelles (voir aussi Scheidt et al. 2005; Bourdin et al. 2001, 2006), la contribution exacte des différentes informations sensorielles pour le contrôle de la dynamique reste à déterminer.

4 POIDS DES MODALITÉS SENSORIELLES

La littérature sur le contrôle de la cinématique et de la dynamique du mouvement soutient de façon générale les propositions précédentes selon lesquelles deux canaux sensoriels distincts, l'un visuel et l'autre proprioceptif, seraient utilisés pour la cinématique et la dynamique du mouvement, respectivement (Krakauer, Ghilardi et Ghez 1999; Wang and Sainburg 2004). Cependant, plutôt qu'une utilisation rigide et exclusive des informations sensorielles selon le processus à l'étude, il apparaît plutôt que le système nerveux central attribue un poids relatif aux différentes modalités sensorielles en fonction de leur précision respective et du cadre de référence sensoriel dans lequel la position de la cible et de la main sont encodées.

4.1 Modèle basé sur la variance minimale

Lorsque nous effectuons un geste, l'état du système peut être représenté par plus d'une modalité sensorielle (visuelle, proprioceptive, tactile, etc.). On considère que les différentes modalités sensorielles sont considérées dans une représentation sensorimotrice unique. L'hypothèse de l'intégration optimale prédit que la combinaison des multiples sources d'information permettrait au système nerveux central de minimiser l'incertitude quant aux signaux sensoriels (bruit neural, variabilité, limites dans la résolution temporelle et spatiale). De préférence, le système nerveux central considèrerait les différentes modalités sensorielles plutôt que de traiter une source d'afférence unique au détriment des autres; il accorderait cependant plus de poids à l'information la plus précise.

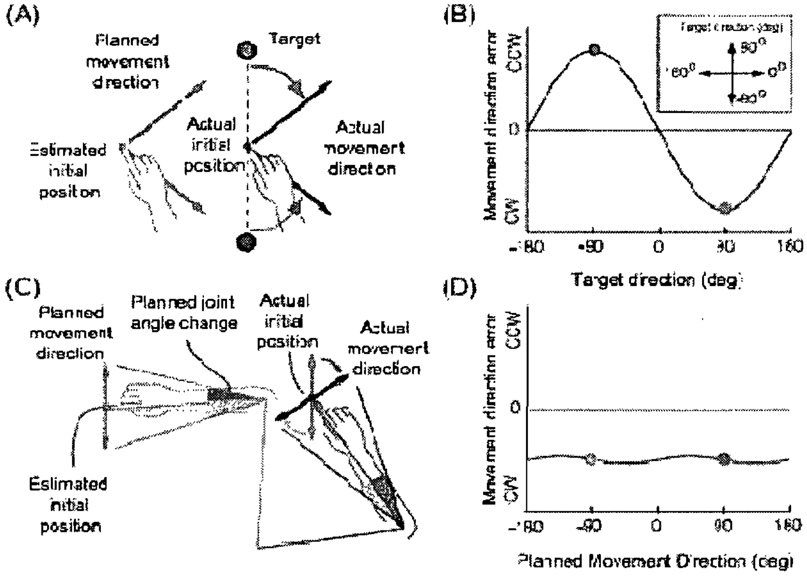
van Beers, Wolpert et Haggard (2002) ont évalué le poids des modalités sensorielles (vision et proprioception) pour le contrôle des différentes composantes de la cinématique, soit la direction et l'étendue du mouvement. Ces auteurs proposaient que le poids accordé à la vision varierait en fonction de la composante du mouvement. Tel serait le cas, parce que la précision du système visuel n'est pas uniforme; il est moins précis pour évaluer la distance que la direction (Foley et Held 1972; Foley 1976). Les auteurs ont utilisé une tâche d'adaptation dans laquelle un conflit entre les informations visuelles et proprioceptives était créé en étendue ou en direction selon la condition expérimentale.

En phase de préadaptation, les participants devaient réaliser un mouvement de pointage vers une cible présentée visuellement, proprioceptivement ou en utilisant ces deux modalités. La main utilisée pour le mouvement de pointage n'était jamais visible au cours de l'expérimentation. Durant la phase d'adaptation, la cible était représentée visuellement et proprioceptivement (si le sujet réalisait la tâche en utilisant sa main droite, son index gauche était placé directement sous la cible visuelle). Au cours des essais et à l'insu du participant, la représentation visuelle de la cible était déplacée graduellement de 5 cm en direction ou en étendue. Une divergence entre les deux représentations sensorielles de la cible était donc introduite. Pour encoder la position de la cible, l'une des modalités sensorielles devait alors s'adapter. Selon Ghahramani, Wolpert et Jordan (1997), cette adaptation prendrait place pour la modalité sensorielle non dominante dans un objectif de diminution de la variance. van Beers et al. (2002) ont proposé que l'adaptation serait visuelle pour un conflit vision-proprioception en étendue (car la vision représenterait une source d'information non dominante pour cette composante), tandis que l'adaptation serait proprioceptive pour un conflit vision-proprioception en direction. La phase de post-adaptation était identique à la phase de préadaptation. Pour évaluer l'adaptation, les auteurs ont analysé la différence entre les erreurs de pointage en pré et post-adaptation pour la cible proprioceptive (ΔP) et pour la cible visuelle (ΔV).

Les auteurs ont rapporté une adaptation plus grande de la proprioception que de la vision pour un conflit vision-proprioception en direction (67% vs. 33%, respectivement). Inversement, ils remarquaient une adaptation plus grande de la vision que de la proprioception pour un conflit vision-proprioception en étendue (72% vs. 28%, respectivement). Ces résultats suggèrent que le système nerveux central accorde plus de poids à la vision pour déterminer la direction du mouvement, tandis que plus de poids serait accordé à la proprioception pour déterminer l'étendue du mouvement (Bays et Wolpert 2007; Sainburg, Lateiner, Latash et Bagesteiro 2003; van Beers, Sitting et Denier van der Gon 1996; van Beers, Sitting et Denier van der Gon 1999).

4.2 Poids des modalités sensorielles selon les cadres de référence

Sober et Sabes (2003) ont déterminé de quelle façon la vision et la proprioception étaient combinées lors de l'estimation de la position du membre (position de la main ainsi que de la configuration du membre) lors des différentes étapes de la planification motrice. Selon ces auteurs, une première étape de planification du mouvement sert à l'élaboration du vecteur de mouvement (Georgopoulos, Kalaska, Caminiti et Massey 1982). Le vecteur de mouvement désiré serait issu de la soustraction entre la position de la cible et la position estimée de la main. Une seconde étape de la planification serait responsable de la transformation du vecteur de référence en commandes motrices. Cette transformation nécessite la connaissance de la configuration du membre avant l'amorce du mouvement. Afin d'évaluer la contribution de la vision et de la proprioception lors de ces deux étapes de planification, les auteurs ont utilisé une tâche de pointage vidéo pour laquelle l'information visuelle représentant la position de la main sur la base de départ était soit véridique ou déplacée latéralement (à gauche ou à droite) par rapport à la localisation réelle de la main. Cette perturbation était introduite à l'insu du participant. Pour la condition « avec déplacement », l'utilisation de l'information visuelle engendrerait une erreur de planification (voir Figure 3 a et c). De plus, le patron d'erreur observé différerait en fonction de l'étape de planification affectée. Une modélisation de ces erreurs est illustrée à la Figure 3 (panneaux c et d). Afin d'éviter que les participants corrigent les erreurs de planification en cours d'exécution, la représentation visuelle de la main était retirée au moment où cette dernière quittait la base de départ. Finalement, si seule l'information proprioceptive était utilisée pour représenter la position de la main ainsi que la configuration du membre, aucune erreur de planification ne serait observée. Les auteurs ont comparé les résultats expérimentaux aux modèles quantitatifs de la prédiction des erreurs pour inférer le poids relatif de la vision et de la proprioception aux deux étapes de la planification du mouvement.



Tiré de Sober et Sabes (2003)

Figure3: Erreur engendrée par l'utilisation de l'information visuelle en fonction de l'étape de planification. *a)* Erreur résultant d'un déplacement vers la gauche de l'information visuelle utilisée pour planifier le vecteur de mouvement. La direction du vecteur de référence (flèche grise) diffère de la direction que devrait prendre la main pour atteindre la cible (ligne pointillée) *b)* Erreurs directionnelles prédites dans la planification du vecteur de mouvement en fonction de la localisation des cibles. *c)* Erreur résultant d'un déplacement vers la gauche de l'information visuelle utilisée pour transformer le vecteur de mouvement en commande motrice. La direction actuelle du mouvement (flèche noire) diffère de la direction planifiée (flèche grise) *d)* Erreur de transformation en fonction de la localisation des cibles.

Les auteurs ont démontré que l'élaboration du vecteur de mouvement dépendait largement de l'information visuelle (97%) plutôt que proprioceptive (34%). Inversement, la transformation du vecteur en commande motrice dépendait essentiellement des informations proprioceptives (66%) plutôt que des informations visuelles (34%). Il semble que la planification du mouvement dépend prioritairement de différentes sources d'information en fonction de l'étape de planification considérée. Sober et Sabes (2003, 2005), proposaient que le système nerveux central accordait moins de poids à la modalité sensorielle nécessitant une transformation entre les cadres de référence dans lesquels la cible et le membre étaient représentés. Par exemple, la vision serait privilégiée si la cible et le membre sont vus avant l'amorce du mouvement. Étant donné que ce mécanisme de transformation accroît les erreurs de planification (dû au bruit qu'il occasionne), il est donc plus avantageux d'utiliser un même cadre de référence pour représenter la position de la cible et celle du membre. Dans cette étude, comme la cible et la main étaient représentées visuellement (donc ne nécessitaient pas de changement de cadre de référence), il était donc avantageux d'utiliser cette modalité sensorielle afin d'élaborer le vecteur de mouvement. Concernant la transformation du vecteur en commandes motrices, comme la configuration du membre (par exemple, la position d'un segment par rapport à l'autre) n'était pas explicitement représentée par les informations visuelles, l'estimé de la position du bras était codé dans un cadre de référence proprioceptif. Dans une certaine mesure, ces résultats supportent le modèle basé sur la variance minimale. La modalité sensorielle utilisée en fonction de l'étape de planification est celle qui engendre une variance minimale occasionnée, entre autres, par des transformations de cadre de référence.

Utilisant une tâche similaire à celle de Sober et Sabes (2003), Sainburg, Lateiner, Latash et Bagesteiro (2003) ont démontré que l'information proprioceptive était utilisée pour déterminer la commande motrice tandis que la direction du vecteur de mouvement était spécifiée sur la base des informations visuelles. Spécifiquement, l'information visuelle indiquant la position de la main était constante au cours des essais, tandis que la position réelle de la main était déplacée de sorte à raccourcir ou allonger le mouvement ou perpendiculairement à cet axe. Ces manipulations expérimentales n'ont pas affecté la direction du mouvement de pointage; cette dernière dépendait de la localisation visuelle de la main et de la cible. Cependant, et en accord avec van Beers, Wolpert et Haggard (2002), la planification de l'étendue s'effectuait en fonction de la position réelle de la main soit, sur la base des informations proprioceptives.

4.3 L'intégration sensorielle est flexible

Suite à leur étude de 2003, Sober et Sabes (2005) ont évalué l'hypothèse selon laquelle le poids des modalités sensorielles serait déterminé en fonction du cadre de référence dans lequel les positions de la cible et du membre étaient présentées. Le protocole expérimental était identique à celui utilisé par Sober et Sabes (2003) à la différence qu'une cible proprioceptive était utilisée pour certains essais. Pour ces essais, une transformation de cadre de référence n'était pas nécessaire puisque la représentation de la cible ainsi que celle du membre étaient encodées proprioceptivement. Tel que précédemment observé, l'élaboration du vecteur dépendait majoritairement de l'information visuelle lorsque la cible était présentée visuellement (88%). Cependant, si une cible proprioceptive était utilisée, le poids associé à l'information visuelle était diminué (42%). En comparant ces résultats à ceux de Sober et Sabes (2003), il apparaît que la contribution relative de la vision et de la proprioception n'est pas fixe pour la planification du mouvement. En accord avec cette proposition, Sarlegna et Sainburg (2007) ont démontré que la planification de l'étendue du mouvement s'effectuait préférentiellement sur la base des informations proprioceptives lorsque la cible était présentée proprioceptivement. Lorsque la cible était présentée visuellement, c'est sur la base des informations visuelles que l'étendue du mouvement était planifiée.

5 AFFÉRENCES VISUELLES ET CONTRÔLE DE LA DYNAMIQUE

Tel que proposé précédemment lors de la présentation de l'hypothèse de la spécificité de la pratique, les derniers résultats suggèrent qu'une source d'information sensorielle peut dominer le traitement des autres sources d'information pour le contrôle de la cinématique. Cette dominance s'explique cependant par un poids relatif plus grand accordé à une source d'afférence plutôt qu'à un traitement exclusif de celle-ci. Toutefois, nous ne connaissons pas de quelle façon le système nerveux central gère la contribution des différentes sources d'information sensorielle lorsque la cinématique et la dynamique sont simultanément considérées.

5.1 Modèle interne cinématique et dynamique

Krakauer, Ghilardi et Ghez (1999) ont voulu déterminer si les modèles internes cinématique et dynamique se développaient indépendamment l'un de l'autre. Dans cette étude, les participants réalisaient un mouvement d'aller-retour en direction de cibles (réparties sur 360 degrés) disposées sur un cercle. Dans la première condition expérimentale, la trajectoire du curseur était déviée de 30° en sens antihoraire par rapport au déplacement réel de la main du sujet. Avec la pratique, les participants apprenaient à définir un nouvel axe de référence cinématique pour assurer la précision spatiale du geste. Dans la deuxième condition expérimentale, une masse de 1.5 kg était ajoutée au manipulandum déplacée par le participant. La position de cette masse déplaçait le centre de masse de l'avant-bras. Avec la pratique, les participants apprenaient à modeler la nouvelle dynamique créée par l'ajout de la masse de sorte à produire des mouvements rectilignes. Lorsque simultanément exposés aux deux conditions expérimentales, les participants s'adaptaient aux deux transformations, cinématique et dynamique, de façon équivalente à ce qui était observé pour l'une ou l'autre de ces manipulations expérimentales. Cette observation a conduit Krakauer et al. (1999) à proposer que le développement des modèles internes cinématique et dynamique s'effectuait de façon simultanée et indépendante. De plus, comme la disponibilité de la vision n'avait pas permis d'améliorer la performance pour la condition de perturbation dynamique, les auteurs ont conclu que les afférences visuelles étaient inutiles pour l'apprentissage d'un nouveau modèle interne dynamique. Cette dernière conclusion a suscité notre intérêt parce que plusieurs auteurs avaient déjà démontré que le système nerveux central incorporait les différentes modalités sensorielles dans la représentation neurale du mouvement. Toutefois, il est important de rappeler que la condition visuelle utilisée par Krakauer et al. (1999) nécessitait aussi le développement d'un nouveau modèle interne cinématique, ce qui aurait pu diminuer le rôle des afférences visuelles pour l'apprentissage d'un nouveau modèle interne dynamique.

CONTEXTE DE LA THÈSE

Le contrôle en temps réel du mouvement permet de réduire des erreurs de planification et d'autres inhérentes au bruit neural qui afflige aussi bien les processus de planification que ceux d'exécution du mouvement. Plusieurs études utilisant un paradigme de saut de curseur ont démontré un rôle important des informations visuelles pour la correction en temps réel des erreurs de planification (Proteau et al. 2009; Saunders et Knill 2003, 2004, 2005; Sarlegna, Blouin, Bresciani, Bourdin, Vercher et Gauthier 2003; Sarlegna, Blouin, Vercher, Bresciani, Bourdin, Gauthier 2004). Spécifiquement, lors d'un paradigme de saut de curseur, la représentation visuelle de la main du participant est modifiée tôt suite à l'amorce du geste de pointage. Par exemple, pour certains essais, le curseur est subitement déplacé latéralement de plusieurs millimètres (typiquement entre 5 et 40 mm). Cette perturbation a pour fonction de simuler expérimentalement une erreur de planification. Bien que le saut de curseur ne soit pas détecté consciemment par le participant, dans toutes ces études on remarqua que les participants modifiaient rapidement la trajectoire de leur mouvement de telle sorte que le curseur atteigne l'environnement de la cible. Cette correction, qui peut atteindre 80% de l'amplitude du saut de curseur, est observée dès sa première occurrence ce qui suggère que le que la vision est traitée de façon continue pour contrôler/ moduler l'exécution du mouvement.

Un second type d'évidence attestant de l'utilisation des informations visuelles pour la modulation en ligne du mouvement provient de l'analyse des patrons de variabilité. Lors d'un mouvement de pointage vidéo, lorsque la variabilité d'une série de mouvements dirigés vers une même cible est normalisée pour la distance entre la base de départ et différents marqueurs cinématiques, on remarque une forte diminution de ces coefficients de variabilité entre la pointe d'accélération et la pointe de vélocité du mouvement, et ce, peu importe que les afférences visuelles soient disponibles ou non (Proteau 2005; Proteau et al. 2009; Tinjust et Proteau 2009; Veilleux et Proteau 2009). La première partie du mouvement est donc modulée pour réduire la variabilité inhérente aux processus de planification et d'exécution du mouvement. Dans les mêmes études, lorsque les afférences visuelles sont disponibles, on remarque une deuxième diminution de ce ces coefficients de variabilité entre la pointe de décélération et la fin de la première impulsion de mouvement. Ces diminutions de variabilité indiquent que les informations visuelles sont utilisées pour moduler la fin du mouvement chez l'adulte comme chez l'enfant (Lhuisset et Proteau 2002, 2004).

Les études de Krakauer et al. (1999) suggère que les afférences visuelles ne jouent aucun rôle pour l'apprentissage d'un nouveau modèle interne dynamique (voir aussi Franklin et al. (2007) pour des résultats similaires). Toutefois, les perturbations de la dynamique du mouvement qui ont été utilisées pour étudier le développement des modèles internes dynamiques avaient des conséquences cinématiques : le mouvement était dévié de la trajectoire anticipée. Or, nous savons que ces déviations de la trajectoire attendue peuvent être détectées très rapidement par le système visuel. De là, dans une situation où le modèle interne cinématique du mouvement est bien établi (contrairement à

Krakauer et al [1999]), est-ce que les informations visuelles domineront les informations proprioceptives pour le contrôle de la dynamique en cours d'exécution? De plus, est-ce que la modulation en ligne sur la base de la vision serait maintenue lors de l'apprentissage d'un nouveau modèle interne dynamique? Qu'en est-il en fonction du développement de l'enfance à l'âge adulte? L'objectif de la présente thèse est de répondre à ces questions.

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RESEARCH ARTICLE

Specificity of practice results from differences in movement planning strategies

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Chapitre III

Specificity of practice results from differences in movement planning strategies

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Abstract

Withdrawing visual feedback after practice of a manual aiming task results in a severe decrease in aiming accuracy. This decrease in accuracy is such that participants are often less accurate than controls who are beginning practice of the task without visual feedback. These results have been interpreted as evidence that motor learning is specific to the sources of afferent information optimizing performance, because it could be processed at the exclusion of other sources of afferent information. The goal of the present study was to test this hypothesis. To reach our goal we evaluated whether online visual feedback prevented kinesthetic information to be used for: (1) eliminating movement anisotropy resulting from difference in limb inertia when aiming in different directions and (2) creating an internal model of limb mechanics. Participants practiced a manual aiming task with or without visual feedback and with knowledge of results. After this acquisition phase, participants performed two transfer tests. The first transfer test was performed without visual feedback and/or knowledge of results. The second transfer test was similar to the first one but participants initiated their movements from a different starting base. The results showed strong specificity effects in that withdrawing visual feedback resulted in large pointing bias and variability. However, the results of the two transfer tests showed that the processing of visual feedback did not prevent the processing of kinesthetic information used to eliminate movement anisotropy or to create an internal model of limb mechanics. Rather, specificity of practice effects resulted from participants using the same motor plan in transfer as they did in acquisition even though

they had no longer access to visual feedback to modulate their movement online. These results indicate that during acquisition participants adopted different movement planning strategies depending on the source of afferent information available.

Specificity of practice results from differences in movement planning strategies

Manual aiming is likely the most often used movement of our repertoire. To be successful, manual aiming requires that a complex series of processes take place. Movement planning requires the initial location of one's hand and that of the target to be known. This information is used by the CNS to determine the appropriate movement vector and to issue a series of motor commands. Then, as the movement progresses towards the target, afferent information ensures that planning errors resulting from misperception of the hand or target localization, biomechanical factors affecting initial limb inertia, or noise in the planning and execution processes are corrected for.

Practicing manual aiming or a video-aiming movements when vision of the hand is available (hereafter called visual feedback) seems to result in one becoming "dependent" on its availability to ensure optimal aiming accuracy. Specifically, it has been repeatedly shown that withdrawing visual feedback in a transfer test resulted in a large decrease in spatial accuracy for both manual and video-aiming movements. In fact, performance often became worse than that noted early in practice for participants who did not have visual feedback available (see Proteau 1992 for a review of early work; see also Khan and Franks 2003; Proteau 2005; Soucy and Proteau 2001;Tremblay and Proteau 1998). Proteau and his colleagues interpreted this pattern of results as evidence that when one is facing a new task, the CNS quickly determines the source(s) of afferent input most likely to ensure spatial accuracy and processes it (them) for that purpose, perhaps at the exclusion of other sources of afferent information. In a manual aiming task, it was proposed that visual feedback exclusively ensured spatial accuracy if accuracy was a crucial determinant of performance. At least, this could be the case when it is known that both the effector and the target will remain visible throughout movement execution (see Hansen et al. 2006), as is usually the case. This proposition is known as the "specificity of practice hypothesis".

Nonetheless, kinesthetic feedback has also been shown to play an important role for movement planning and control. Concerning movement planning, Rossetti et al. (1995) used prisms to translate the visually perceived position of the hand prior to movement initiation. Although the aiming movements were performed without visual feedback, movement's endpoints were biased in the direction opposite to that of the prism displacement. However, this bias was only one-third of that imposed by the experimental manipulation suggesting a strong kinesthetic input for defining the hand starting position for movement planning.

Concerning movement control, Gordon et al. (1994) reported that movements initiated from the same starting position and performed without visual feedback differed in length depending on their direction. They showed that this was caused by movement planning processes not completely compensating for direction-dependent differences in inertial resistance. This resulted in movements directed 30-45° to the right of one's midline (a direction of smaller inertia) to have higher initial acceleration than movements directed 30-45° to the left of one's midline (a direction of higher inertia). However, Gordon et al. (1994) noted that these initial differences in acceleration were compensated for by a modulation of movement time, which considerably reduced the movement extent bias that should have resulted from initial acceleration. This modulation could at least partially result from the processing of kinesthetic feedback to compensate for differences in inertia for movements performed in different directions (Gordon et al. 1994; Ghilardi et al. 1995a). Although performing the task with visual feedback resulted in a similar pattern of initial acceleration as that described above, extent endpoint biases were largely reduced in comparison to the no-vision condition. The first question of interest in the present report was to determine whether the on-line correction mechanism based on the processing of kinesthetic feedback discussed above is still used when visual feedback can be used to modulate movement extent.

The direction component of video-aiming movements performed while only the target is visible (hereafter called Target-only condition) is also affected by movement's characteristics. Specifically, when initial hand location is close to one's midline, Ghilardi et al. (1995b) observed no strong systematic direction bias for movements performed in different directions. However, when the starting base was translated approximately 40 cm to the right of the participant's midline, movements were systematically completed to the right of all targets, largely regardless of their location. This systematic bias was eliminated through practice with knowledge of results (KR). This adaptation occurred only for a specific area of the workspace, however. That is, after it had occurred, asking participants to initiate their movements from a starting base close to their midline resulted in a systematic bias to the left of the targets. This suggests that, through practice, participants learned/updated an internal model of limb mechanics, which is thought to be based on the processing of kinesthetic input[1]. This is the case because deafferented patients showed large deficit in adapting their movements to altered inertial configurations of their arm (Virji-Babul et al. 1997). The second question of interest in the present report was to determine whether practicing a video-aiming task with visual feedback prevents the processing of kinesthetic feedback such that it impairs the development of a new internal model of limb mechanics.

To reach our goals, we trained participants to perform video-aiming movements towards targets located directly in front of the starting base (0°) or 25° and 50° to its left or to its right. The starting base was located either directly in front of the participant's midline (0-cm condition) or 15 cm to its right (15-cm condition). Visual feedback was (Normal vision condition) or was not (Target-only condition) available during this acquisition phase. All trials were followed by KR to help participants reduce their endpoint error as a function of practice. Then, all participants performed a transfer test in the Target-only condition but with no-KR.

If the kinesthetic input usually used to modulate movement time to compensate for differences in initial movement inertia is not processed, due to the availability of visual feedback, in transfer the Normal vision/0-cm group should show a pattern of results mimicking that of the Target-only group early in practice. Specifically, we should observe large initial acceleration in the direction of low initial inertia and a relatively weak modulation of movement time to compensate for it.

Similarly, if the availability of visual feedback impairs the development of a new internal model of limb mechanics, participants trained in the Normal vision/15-cm condition should show a general bias to the right of the targets in transfer. No such systematic bias should be observed for the remaining three groups.

Following this first transfer test, all participants performed a second transfer in the Target-only condition and with no-KR. In this second transfer test, participants who had trained in the 0-cm condition initiated their movements from the 15-cm starting base, whereas participants who had trained in the 15-cm condition initiated their movements from the 0-cm starting base. Based on Ghilardi et al. (1995b), participants who trained in the Target-only condition should have learned a new internal model of limb mechanics leading to the prediction that, in the second transfer test, participants trained in the Target-only/0 cm should show a general bias to the right of the targets whereas participants trained in the Target-only/15 cm condition should show a general bias to the left of the targets. However, if the availability of visual feedback prevents the processing of kinesthetic input, participants who trained in the Normal vision condition should not have learned a new internal model of limb mechanics. Based on Ghilardi et al. (1995b) and under the assumption that the neutral position (i.e., 0-cm starting base) is the standard model, participants who trained in the 0-cm condition should show a systematic bias to the right of all targets when transferred to the 15-cm starting base, whereas participants who trained in the 15-cm condition should show no systematic bias when transferred to the 0-cm starting base (in reality, they should show the same pattern of biases as that observed early in practice for the Target-only/0-cm group).

Method

Participants

Forty-eight participants took part in the experiment. Their mean age was 21 years (range 20-25 years). All participants reported normal or corrected to normal vision. Participants took part in a single thirty-minute experimental session and were paid $10 CDN for their time. The Health Sciences Ethics Committee of the Université de Montréal has approved this study.

Task and apparatus

The task was to move a computer's mouse-like device from a fixed starting position located close to the body towards one of five possible targets located away from the body. The apparatus is illustrated in Fig.1. It consisted of a table, a computer screen and a two-degrees of freedom manipulandum. Participants sat in front of the table. The computer screen (Mitsubishi, Color Pro Diamond 37 inches) faced the participant.

The tabletop was covered by a piece of Plexiglas over which a starting base and the manipulandum were affixed. The starting base consisted of a thin strip of Plexiglas glued to the tabletop. It was parallel to the leading edge of the table and had two small indentations on one of its face. One of these indentations was located directly in line with the lateral center of the computer screen and the participant's midline; the second one was located 15 cm to the right (see bottom panel of Fig. 1). These indentations served as starting bases for the stylus (see below). The indentations made it easy for the participants to position the stylus at the beginning of each trial.

The manipulandum consisted of two pieces of rigid Plexiglas (43 cm) joined together at one end by an axle. One free end of the manipulandum was fitted with a second axle encased in a stationary base. The other free end of the manipulandum was fitted with a small vertical shaft (length: 3 cm, radius: 1 cm), i.e., the stylus, which could be easily gripped by the participant. From the participant's perspective, the far end of the manipulandum was located 40 cm to the left of the starting base and 70 cm in the sagittal plane. Each axle of the manipulandum was fitted with a 13-bit optical shaft encoder (U.S. Digital, model S2-2048, sampled at 500 Hz, angular accuracy of 0.0439°), which enabled us to track the displacement of the stylus on-line and to illustrate it with a 1:1 ratio on the computer screen. Moving the stylus away from the body in the sagittal plane resulted in a displacement of the cursor from the bottom to the top of the screen; moving the stylus to the left or right of the starting base resulted in a similar displacement of the cursor on the screen. The bottom of the stylus and the bottom of the optical encoder located at the junction of the two arms of the manipulandum were covered with a thin piece of Plexiglas. By lubricating the working surface at the beginning of each experimental session, displacement of the stylus was near frictionless.

Procedures

Participants were asked to try stopping the cursor (black; 3 mm in diameter) on a target having a diameter of 6 mm by performing a single straight and uncorrected movement (Gordon et al. 1994). Five targets were used; they were black and presented on a white screen. The targets were located at 150 mm from the starting base. The first target was located directly in front of the starting base (0° target), whereas the other four targets were located 25°and 50° to its left and to its right, respectively.

As in previous work on this subject (Khan et al. 1998; Proteau and Carnahan 2001; Proteau 2005), participants were asked to begin their movement as they pleased following presentation of a target but were required to complete it in a movement time ranging between 480 and 620 ms (550 ms +/- 12.7%). Movement initiation was detected when the cursor was moved by 2 mm whereas movement end occurred when the cursor was not displaced by more than 2 mm, for a period of 100 ms. The procedure used to define movement endpoint made it difficult for participants to produce a discrete correction to their movements. During the acquisition phase of the experiment (see below), when movements were completed outside this movement time bandwidth, the experimenter reminded the participant of the target movement time. A movement time bandwidth is used to eliminate the possibility of different speed-accuracy trade-offs between the different experimental conditions (Fitts 1954).

All participants took part in three experimental phases: an acquisition phase and two transfer phases. In each phase, the order of target presentation was randomized with the restriction that each target be presented eight times in each successive block of 40 trials. For the acquisition phase, participants performed 24 trials towards each one of the five possible targets. At the beginning of each trial, all participants could see the cursor they had to move resting on the starting base, as well as the target to be reached.

Participants were assigned randomly to one of four experimental groups (n = 12); they could not see their hand and arm during the duration of the experiment (see Fig. 1). For the first half of the participants, the Normal vision (NV) group, vision of the cursor was permitted for the whole duration of the movement. For the remaining participants, the Target-only (TO) group, vision of the cursor was occluded as soon as it left the starting base. For each one of these two visual feedback conditions, half of the participants initiated their movements from a starting base located directly in front of their midline and in line with the center of the computer screen (group 0-cm). For the second half of the participants, movements were initiated from a starting base located 15 cm to the right of their midline and of the center of the computer screen (group 15-cm), so that the visual and kinesthetic information about the starting base location (and that of the location of the target) remained congruent (see bottom panel of Fig. 1). Following each trial, all participants were shown on the computer screen a figure illustrating their movement's path and the target they were aiming toward. Participants were also informed of their movement time in ms, when it felt outside the target movement time bandwidth.

Following the acquisition phase, all participants took part into two transfer phases. The first transfer was performed by all in the Target-only condition and with no KR. For the second transfer, participants who had performed the first two experimental phases in the 0-cm condition initiated their movements from the 15-cm starting base and vice-versa. Participants completed 40 trials in each transfer phase; there were 8 trials directed towards each one of the five possible targets. The targets used in transfer were the same as those used in acquisition. The transfer tests were performed in the same order for all participants because we wanted to determine: first, the effect of visual feedback/KR withdrawal and second, whether changing starting base location would affect aiming performance.

Data reduction

The resultant displacement data of the stylus over time were first smoothed using a second order recursive Butterworth filter with a cutting frequency of 10 Hz. The filtered data were then numerically differentiated once using a central finite technique to obtain the velocity profile of the aiming movement, a second time to obtain the acceleration profile, and a third time to obtain a jerk profile. Movement initiation was defined as the moment at which resultant velocity of the cursor reached 10 mm/s, whereas movement was deemed to be completed when the cursor was not displaced by more than 2 mm in a time frame of 100 ms.[2] From these profiles, we determined the end of the movement primary impulse (Meyer et al. 1988). It occurred when one of the following events was detected on the kinematic profiles: (1) movement reversal (velocity going from positive to negative), (2) movement lengthening (presence of a secondary movement impulse as indexed by the acceleration profile crossing the zero value for a second time) or (3), a significant disruption in the deceleration profile as indexed by zero-crossing on the jerk profile. For a secondary movement impulse to be considered as a discrete correction its duration had to be of at least 80 ms and its extent had to be of at least 2 mm. The results of the kinematic analysis revealed that less than 5% of all trials showed a discrete correction (see Method for details). The results of the trials showing a discrete correction were withdrawn from all analyses. Therefore, hereafter movement endpoint will refer to the end of the movement's primary impulse. From the kinematic profiles, we determined when and where key kinematic landmarks occurred: peak acceleration, peak velocity, peak deceleration and movement endpoint.

To facilitate reading of this article, details concerning the dependent variables of interest, the rationale for using them, and the statistical analyses that were computed are defined at the beginning of each subsection of the results presentation. Geisser-Greenhouse correction was applied when epsilon value was less than 1. All significant main effects involving more than two means were broken down using the Tukey LSD technique. Significant interactions were broken down by computing simple main effects that were followed by post hoc comparisons (Tukey LSD) when they involved more than two means. All effects are reported at $\underline{p} < .05$ (adjusted for the number of comparisons).

Results

Figure 2 illustrates individual trials performed by one participant in each experimental group early in acquisition. All temporal data are presented in Table 1.

Movement anisotropy

In this first series of analyses, we wanted to determine whether the kinesthetic input that is normally used to reduce/eliminate movement anisotropy was still processed when practicing the experimental task in the Normal vision condition. To reach that goal, the values of peak resultant acceleration, as well as the length of the movement at movement endpoint were individually contrasted in a 2 groups (NV/0-cm vs. TO/0-cm) x 2 directions (left and right) x 3 experimental phases (first and last block of acquisition, and transfer 1) using repeated measurements on the last two factors. In addition, to determine whether our experimental manipulation had a significant impact on movement variability, we computed a coefficient of extent variability (standard deviation of the length of the vector at each kinematic landmark [peak acceleration, peak velocity, peak deceleration, and movement endpoint] divided by the mean vector's length at this landmark) and submitted them to an ANOVA contrasting 2 groups (NV/0-cm vs. TO/0-cm) x 2 directions (left and right) x 4 kinematic landmarks (peak resultant acceleration, velocity, deceleration, and movement endpoint) x 3 experimental phases (first and last block of acquisition, and transfer 1) using repeated measurements on the last three factors.

Peak resultant acceleration. As illustrated in the upper portion of Fig.3, peak acceleration was significantly larger when aiming towards targets located to the right than to the left of one's midline, F (1, 22) = 90.5. It was also significantly larger in the Normal vision than in the Target-only condition, F (1, 22) = 11.12. This pattern of results remained true across all three experimental phases.

Movement endpoint. As illustrated in the middle portion of Fig. 3, movement endpoint occurred significantly later when aiming towards the left (687 ms) than the right targets (650 ms), F (1, 22) = 77.4, whereas movement's length did not differ significantly as a function of direction, F (1, 22) = 2.16, p = 0.156, regardless of any other experimental factor (see bottom portion of Fig. 3). Nonetheless, withdrawing vision to the Normal vision group resulted in longer movements in transfer 1 than late in acquisition (168 mm vs. 149 mm), whereas no such difference was noted for the Target-only group (153 mm vs. 152 mm), F (2, 44) = 3.9.

Coefficient of extent variability. The ANOVA revealed a significant main effect of direction indicating that CEV was significantly larger when aiming to the right than to the left of one's midline (0.189 vs. 0.159), F (1, 22) = 9.26. Both early and late in acquisition (see Fig. 4), CEV was significantly larger for the Target-only than for the Normal vision group (0.193 vs. 0.143). However, in transfer, we observed a significant increase in CEV for the Normal vision group who no longer differed significantly from the Target-only group (0.188 vs. 0.183), F (2, 44) = 4.23. Finally, Fig. 4 also shows that for the Normal vision group, CEV significantly decreased between peak acceleration and peak velocity (0.321 vs. 0.135) and between peak deceleration and movement endpoint (0.117 vs. 0.027). For the Target-only group, CEV significantly decreased between peak acceleration and peak deceleration (0.461, 0.131, and 0.093, respectively) and remained stable afterwards (0.080), F (3, 66) = 12.91.

Summary. We observed clear evidence of movement anisotropy for both the Target-only and the Normal vision groups. Because of larger movement inertia, peak acceleration was smaller when aiming towards the left than the right targets. This difference in acceleration was compensated for by longer movement times when aiming to the left than to the right of one's midline, resulting in movements of similar amplitude. However, the combination of larger acceleration and shorter movement times resulted in significantly larger CEV when aiming to the right than to the left targets. Finally, we observed specificity of practice effects in that movements were significantly longer and had larger CEV in transfer than in acquisition for the Normal vision group. It should also be noted that the Normal vision group also overshot the target significantly more than the Target-only group in transfer.

Movement orientation: acquisition

First, we wanted to determine whether practicing the task in the Target-only condition resulted in specific orientation biases as a function of the starting base location, and whether practice with KR would help eliminate this bias. To reach our goal, we determined the orientation bias of each movement (in degrees) at four kinematic landmarks and submitted the mean data to an ANOVA contrasting 2 visual feedback conditions (Normal vision vs. Target-only) x 2 starting positions (0 cm vs. 15 cm) x 5 target eccentricities (-50°, -25°, 0°, 25° and 50°) x 4 kinematic landmarks (peak resultant acceleration, velocity, deceleration, and movement endpoint) x 2 experimental phases (early and late acquisition) using repeated measurements on the last four factors. The orientation variability data were submitted to a similar analysis.

Orientation bias. The results of interest are illustrated in the two leftmost panels of Fig. 5. The ANOVA revealed significant starting base x kinematic landmark, $\underline{F}$ (3, 132) = 8.34, and starting base x experimental phase interactions, $\underline{F}$ (1, 44) = 14.7. The breakdown of the former interaction revealed that movements were oriented to the left of all targets at the occurrence of peak acceleration. This bias was larger, but not significantly so, for movements originating from the 15-cm rather than the 0-cm starting base (-8.1° vs. -4.7°, respectively, $\underline{F}$ [1, 44] = 3.1). Beginning at peak velocity and lasting until movement endpoint, movements initiated from the 0-cm starting base were oriented slightly more to the left of the target than movements initiated from the 15-cm starting base: velocity (-2.08° vs. 0.008°; $\underline{F}$ [1, 44] = 11.25); deceleration (-1.06° vs. 0.015°; $\underline{F}$ [1, 44] = 5.24); endpoint (-0.84° vs. -0.184°; $\underline{F}$ [1, 44] = 2.19, $\underline{p}$ = 0.146).

The breakdown of the starting base x experimental phase interaction revealed that the generally larger bias to the left observed for movements originating from the 0-cm starting base in comparison to the 15-cm starting base was significant in the first (-2.95° vs. -1.81°; $\underline{F}$ [1, 44] = 15.84) but not in the last acquisition block (-1.42° vs. -1.36°; $\underline{F}$ [1, 44] = 2.07, $\underline{p}$ = 0.57).

Orientation variability. Orientation variability was significantly larger at peak acceleration for movements initiated from the 15-cm than from the 0-cm starting base (9.8° vs. 7.0°, respectively). Regardless of the starting position, it significantly decreased as movement progressed towards the target with no further significant differences as a function of the starting base at the remaining kinematic landmarks (means of 4.06°, 3.25°, and 2.85° at peak velocity, peak deceleration, and movement endpoint, respectively, F [3, 132] = 13.36).

Orientation variability was significantly larger for the Target-only group than for the Normal vision group at all targets. However, this difference in orientation variability was smaller for the 0° target (0.9°) than for the targets located to the right (2.1°) and the left (2.9°) of one's midline, F (4, 176) = 3.6. Although orientation variability significantly decreased from the first to the last block of acquisition for the Target-only group (6.4° to 5.1°), it remained significantly larger than that observed for the Normal vision group both early and late in practice (3.6° and 3.5°, respectively), F (1, 44) = 8.1.

Finally, as noted previously, orientation variability significantly decreased for all targets as movement unfolded. For the 0° target, orientation variability decreased from 5.8° at peak acceleration to 1.7° at movement endpoint. For the targets located to the right of one's midline, orientation variability went from 7.8° to 3.1° ,whereas it went from 10.4° to 3.2° for the targets located to the left of one's midline, F (12, 528) = 8.7.

Movement orientation: Late acquisition vs. transfer 1 and transfer 2

To determine whether withdrawing KR or visual feedback in transfer would affect the pattern of biases noted in acquisition and whether changing starting base would cause new biases, we submitted the movement orientation data to an ANOVA contrasting 2 visual feedback conditions (Normal vision vs. Target-only) x 2 starting positions (0 cm vs. 15 cm) x 5 target eccentricities (-50°, -25°, 0°, 25° and 50°) x 4 kinematic landmarks (peak resultant acceleration, velocity, deceleration, and movement endpoint) x 3 experimental phases (late acquisition, transfer 1 and transfer 2) using repeated measures on the last four factors. The orientation variability data were submitted to a similar analysis.

Orientation bias. The data of interest are illustrated in the three rightmost panels of Fig. 5. Withdrawing visual feedback and/or KR (Normal vision and Target-only groups, respectively) when going from the last block of acquisition to the first transfer test had no significant impact on movement orientation, regardless of the starting base or kinematic landmark considered. However, when going from the first to the second transfer test, that is, when changing starting base, we observed that movement orientation was biased to the right of the targets when going from the 0- to the 15-cm starting base, whereas the reverse was true when going from 15- to the 0-cm starting base. This is supported by a significant starting position x landmark x experimental phase interaction, F (6, 264) = 7.40. Although these shifts in movement orientation occurred at all kinematic landmarks they were not significant at peak acceleration.

Going from late acquisition to either transfer 1 or transfer 2 had no significant impact for the Target-only group. However, for the Normal vision group, withdrawing visual feedback in transfer 1, caused a significant bias to the left of the -50° and -25° targets and to the right of the 25° and 50° targets. This is supported by a significant visual feedback condition x experimental phase x target interaction, F (8, 352) = 5.69.

Orientation variability. Late in acquisition and after the withdrawal of visual feedback and/or KR (transfer 1), initiating one's movement from the 0-cm starting base resulted in a significantly lower orientation variability at peak acceleration than initiating one's movement from the 15-cm starting base (significant for four of the five targets). This difference in orientation was no longer significant for the three remaining kinematic landmarks. Switching starting base in transfer 2 resulted in the same basic observation. The participants who went from the 0- to the 15-cm starting base showed larger orientation variability at peak acceleration than the participants who went from the 15- to the 0-cm starting base (significant only for the 25° and 50° targets, however). No significant difference was observed for the three remaining kinematic landmarks. This is supported by a significant starting position x experimental phase x target x kinematic landmark interaction, F (24, 1056) = 2.62.

Orientation variability significantly increased when the Normal vision group went from late acquisition (3.5°) to the first (5.9°, withdrawal of visual feedback) and second transfer tests (6.2°, switch of starting base), whereas no such significant difference was noted for the Target-only group (5.1°, 5.6°, and 6.3°, respectively), F (2, 88) = 7.1.

Summary. Early in practice, movements were slightly but significantly oriented more to the left of the targets when they were initiated from the 0-cm than from the 15-cm starting base. This difference became non-significant later in practice as well as when visual feedback and/or KR had been withdrawn in transfer 1, indicating significant learning of a new internal model of limb mechanics. What had been learned in acquisition was not successfully transferred to a new starting position, however. Rather, movement became biased to the right of all targets when going from the 0- to the 15-cm starting base, whereas the reverse was true when going from the 15- to the 0-cm starting base. We also noted lower orientation variability at peak acceleration for movements initiated from the 0-cm than from the 15-cm starting base in all experimental phases. Finally, we observed a strong specificity of practice effect in that withdrawing visual afferent information in transfer resulted in large orientation bias and variability for the -50°, -25°, 25°, and 50° targets.

Discussion

It has been shown repeatedly that manual aiming movements are more accurate when visual feedback is available than when it is not (for a review, see Proteau 1992). This "superiority" of visual feedback over other sources of afferent information to ensure endpoint accuracy in a manual aiming task apparently leads one to rely so heavily on it that its withdrawal results in severe aiming errors. Moreover, these errors are often larger than those observed very early in practice in the absence of visual feedback (Khan et al. 1998; Proteau et al. 1987; Proteau and Cournoyer 1990). This last observation was interpreted as evidence that the availability of visual feedback might prevent the processing of other sources of afferent information, and especially kinesthetic information, to ensure spatial accuracy (Tremblay and Proteau 1998). Our objective in the present study was to test this hypothesis.

Specificity, anisotropy, and internal model of limb mechanics

The results of the present study showed the typical specificity of practice effects in that withdrawing visual feedback in transfer resulted in a significant overshooting of the targets, bias to the left of the left targets and to the right of the right targets, as well as in increased orientation variability. These errors were larger than those observed early in acquisition in the Target-only condition. However, this deterioration in performance was neither caused by larger anisotropy effect nor by poorer learning of a new internal model of limb mechanics when visual feedback had been withdrawn.

Movement anisotropy

As Gordon et al. (1994), we observed movement anisotropy effects at the occurrence of peak acceleration for both the Target-only and the Normal vision groups. In addition, this effect did not decrease with practice and was compensated for as movement unfolded by an increase in movement time for the direction of larger inertia. Withdrawing visual feedback in the first transfer test had no significant impact on the acceleration/time movement pattern, suggesting that visual feedback did not interfere with the processes responsible for this fine interplay between acceleration and time.

Internal model of limb mechanics

In accordance with Ghilardi et al. (1995b), the results of the present experiment revealed that early in practice movements initiated from the 0-cm starting base were oriented significantly more to the left of the targets than movements initiated from the 15-cm starting base. This effect disappeared with practice and the performance observed at the end of the acquisition phase was maintained even when visual feedback and/or KR was withdrawn in transfer 1, suggesting that participants had learned a new internal model of limb mechanics. However, changing starting base in transfer 2 resulted in biases similar to those reported by Ghilardi et al. (1995b). Participants going from the 0- to the 15-cm starting base became biased to the right of all targets, whereas going from the 15- to the 0-cm starting base resulted in a bias to the left of all targets. Ghilardi et al. (1995b) proposed that this pattern of results indicated that, through practice, participants learned/updated an internal model of limb mechanics, which is thought to be based on the processing of kinesthetic input, and that could not be exported to different areas of the workspace. The observation that the pattern of biases reported above was no different for the Normal vision group than for the Target-only group indicates that the kinesthetic input used to learn/update the internal model of limb mechanics was not disregarded because of the availability of visual feedback to ensure endpoint accuracy. If that had been the case, we should have observed different pattern of biases for these two groups in transfer 2.

We also observed that initial orientation variability (i.e., at peak acceleration) was significantly larger, both in acquisition and in transfer, for movements initiated from the 15-cm rather than the 0-cm starting base. This difference was no longer significant later in movement (beginning at peak velocity and lasting until movement endpoint). These results replicate previous findings reported by Lhuisset and Proteau (2004). The larger orientation variability observed at peak acceleration for the 15-cm starting base suggests less stable movement planning in that condition, very likely because participants had more difficulty in identifying the position of their hand than when it was located along their midline. However, the observation that the noted difference did not persist at other kinematic landmarks suggests that movement orientation was quickly updated after movement initiation. We will come back to this point.

Specificity results from an optimization strategy

In the present study, the position of the starting base as well as that of the target were visible at all time and for all experimental phases. Therefore, all participants always had access to the same static visual information for movement planning. This static visual information is translated into intrinsic coordinates for defining an appropriate set of motor commands. Our results indicate that this set of motor commands differs depending on the availability of visual feedback during movement execution (see also Hansen et al. 2006).

When visual feedback will not be available, we suggest that one tries to determine the set of motor commands that will ensure optimal spatial accuracy (given the imposed movement time bandwidth in the present study) with minimal intervention of voluntary correction processes (for a similar proposition see also, Harris & Wolpert 1998; Novak et al. 2002, 2003). This position is supported by the observation that CEV and orientation variability remained very stable in the Target-only condition between the occurrence of peak velocity and movement endpoint. This suggests that extent and orientation variability in this visual feedback condition were linearly related to movement extent and, thus, that the movement trajectory was a reliable estimate of the initial movement impulse (Proteau 2005). In addition, we observed that the acceleration and deceleration phases of the movement were of approximately the same duration (50.9% and 49.1%, respectively), which also suggests that movement endpoint was largely determined by initial movement impulse (Harris & Wolpert 1998; Novak et al. 2002, 2003).

When visual feedback will be available, we observed significantly larger peak acceleration in the Normal vision than in the Target-only condition, indicating that the motor output of the movement planning process differed for these two conditions. The larger acceleration noted for the Normal vision condition resulted in peak acceleration and peak velocity to be reached sooner and closer to the starting base when visual feedback was available (14% and 40% of movement time for peak acceleration and peak velocity, respectively; see Table 1) than when it was not (18% and 52% of movement time for peak acceleration and peak velocity, respectively). With a temporally constrained task, like that used in the present study, this strategy left more time to adjust/modulate one's movement when it closed on the target (for a similar proposition, see also Elliott and Allard 1985; Elliott and Calvert 1990; Elliott et al. 1991). We will come back to this point. In addition, this strategy resulted in the participants having to hold-on rather than to add-on to the initial movement impulse, which might be an easier thing to do.

When visual feedback was withdrawn in transfer, neither peak acceleration nor its moment or location of occurrence differed from that observed in acquisition for the Normal vision group. This observation is important because it suggests that the same set of motor commands as in acquisition had been used. It also suggests that participants had no more difficulty in determining the appropriate movement vector and movement plan in transfer than in acquisition. However, peak velocity was larger, occurred later and, thus, as illustrated in Fig. 6, was reached farther from the starting base in transfer than late in acquisition (middle and left panels, respectively). This difference in the length of the vector at peak velocity between late acquisition and transfer remained largely unchanged at peak deceleration and movement endpoint, which led to a large overshooting of the target. These observations suggest that a significant modification/adaptation of the movement primary impulse occurs between peak acceleration and peak velocity in the presence of visual feedback. Withdrawing this source of afferent information in transfer eliminated the possibility of such a modification and resulted in a significant overshooting of the target location. Therefore, specificity results partially from the participants being unable to take into account in transfer that the acceleration phase of their movement had been modified online when visual feedback was available in acquisition. In the "hypothesis" portion of Fig. 6, we subtracted the difference in the length of the movement vector noted at peak velocity between late acquisition and transfer for the peak velocity, peak deceleration and movement endpoint data of the Normal vision group. The similarity of these hypothetical results and those obtained late in acquisition for the Normal vision group is striking and supports our hypothesis.

Our results suggest that specificity results in part because participants are not able to modify their initial movement impulse between the occurrence of peak acceleration and peak velocity once visual feedback has been withdrawn. Still, we observed a large decrease in variability between the occurrence of these two kinematic landmarks both in the Normal vision and the Target-only conditions. This indicates that this decrease in variability, or put into other words, modulation of the movement's initial impulse, was not mediated by the processing of visual feedback. As suggested earlier (Bédard and Proteau 2005; Lhuisset and Proteau 2004; see also Robin et al. 2005), we see this reduction in variability as indicating that movement planning is based on approximations concerning the location of one's hand and of the target in the workspace, mechanical constraints, and especially the state of the motor system (motor pathways, motoneurons pool, motor units, etc.). Because of these approximations, the CNS has developed mechanisms to quickly update the motor commands after movement initiation. In that regard, it has been suggested that a forward model of the dynamics of the arm is generated during movement execution. This model receives a copy of the motor commands that is used to predict movement endpoint and to compare it with the target location, allowing for a quick updating of the motor command (for reviews see Desmurget and Grafton 2000; Khan et al. 2006). This updating reduces movement variability because it takes into account the actual state of the system rather than mere approximations.

Our proposition that there is a modification/adaptation of the movement primary impulse that occurs in the Normal vision condition between peak acceleration and peak velocity is supported by recent evidence obtained in cursor-jump experiments (Proteau et al. 2007, unpublished data). The general procedures used in these cursor-jump experiments are very similar to those used in the present study. However, for a small proportion of the trials, the cursor shown on the computer screen was displaced by as much as 30 mm (perpendicular to its trajectory) near the occurrence of peak acceleration. Participants were able to correct the trajectory of the cursor to counteract the effect of the cursor jump even if they did not consciously detect it and even when the cursor disappeared near the occurrence of peak velocity. Thus, vision of the cursor during this very short period (~ 60 ms) was sufficient for the participants to pick up enough information to implement a very effective correction.

The "strategy" used in the Normal vision condition was not learned in the acquisition phase of our experiments. This is so, because it was apparent right from the very first trial performed by the participants. Rather, we would suggest that it is learned during childhood and thereafter used in our daily activities because of its efficacy.

Indirect support for the proposition that this strategy is learned during childhood comes from the observation that specificity effects were significantly smaller in 6-7 years old children than in older children and in adults (Charvin and Proteau 1996; Chicoine et al. 1992).

Modulation of the later part of the movement

In the acquisition phase of the present study we observed in the Normal vision group a decrease in CEV and orientation variability between the occurrence of peak deceleration and movement endpoint. This decrease in variability was no longer visible in transfer. It suggests that a portion of the specificity effect results from participants being unable to modulate the later portion of their movements. This late modulation observed only for the Normal vision group complements other correction or modification processes that we have observed between peak acceleration and peak velocity. It appears to fine-tune the ongoing movement by further reducing the variability inherent to movement planning. In that regard, it is interesting to note that, in the acquisition phase, CEV was almost identical for the Normal vision and the Target-Only groups up to peak deceleration. This suggests that this late modulation of movement extent occurred while the cursor and the target were likely seen in central vision. This late modulation required time (see Table 1), which might explain why participants trained in the Normal vision condition, especially considering our use of a target movement time bandwidth, produced much higher acceleration than participants trained in the Target-only condition. In that regard, participants spent 27.3% of movement time between peak deceleration and movement endpoint (or 181 ms) in the Normal vision condition for a reduction of CEV of 9%, in comparison to 18.7% of movement time (or 127 ms) for no reduction in CEV in the Target-only condition.

CONCLUSION

Specificity of practice does not result from the exclusive processing of the source of afferent information more likely to ensure spatial accuracy. This is so because in the present study practice in the normal vision condition did not prevent the processing of kinesthetic afferent information to reduce inertial anisotropy or impair the learning of a new internal model of limb mechanics. The most important contribution of the present study is that we showed that the movement plan developed while visual feedback is available is still used even after that source of afferent information had been withdrawn. This results in large aiming errors for two reasons. The apparently unconscious and automatic movement updating that occurs through visual feedback early after movement initiation is no longer possible; late modulation of the ongoing movement no longer takes place.

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Table 1. Moment of occurrence (standard deviation) of each kinematic landmark late in acquisition and in transfer for the Normal vision (NV) and Target-only (TO) groups.

		Kinematic landmark			
	Starting base in acquisition	Peak acceleration	Peak velocity	Peak deceleration	Movement endpoint
		Block 3: late acquisition			
NV	0 cm	96 (14)	264 (25)	470 (66)	659 (63)
	15 cm	97 (16)	278 (32)	497 (75)	670 (63)
TO	0 cm	125 (31)	343 (39)	544 (56)	667 (55)
	15 cm	106 (29)	355 (42)	552 (61)	681 (58)
		Transfer 1			
NV	0 cm	104 (20)	307 (36)	505 (64)	644 (66)
	15 cm	111 (30)	335 (49)	539 (77)	682 (81)
TO	0 cm	131 (37)	347 (42)	557 (56)	675 (59)
	15 cm	99 (24)	356 (44)	575 (73)	697 (70)
		Transfer 2			
NV	0 cm	100 (21)	322 (41)	527 (62)	657 (62)
	15 cm	115 (31)	327 (42)	522 (68)	673 (65)
TO	0 cm	120 (21)	350 (46)	556 (63)	676 (63)
	15 cm	109 (28)	344 (43)	561 (68)	692 (65)

Footnotes

[1] Note that no such bias was observed when participants were trained to initiate their movements from different starting bases in the presence of knowledge of results (Lhuisset & Proteau, 2004).

[2] This definition of movement initiation differed from that used during data collection. In addition to the normal impact of the filtering procedure on the time scale, it will result in apparently longer movement times in comparison to the movement time bandwidth accepted during data collection.

Figure captions

Figure 1. Top panel. View of the apparatus. Bottom panel. Participants performed the task from a starting base located in line with their midline and the lateral center of the screen (left; 0-cm starting base) or from a starting base located to the right of their midline and of the center of the screen (right; 15-cm starting base). Small open circles represent targets. Note that the central target is always in line with the starting base.

Figure 2. Movement trajectories towards the five targets (left to right: -50°, -25°, 0°, 25°, 50°), as a function of the visual feedback condition (NV: normal vision; TO: target-only) and the starting base (0 cm: midline; 15 cm: 15 cm to the right of the participant's midline). Data from one participant in each experimental group who are well representing mean results early in acquisition. Note the high accuracy and low variability in the NV condition, with no evidence of movement anisotropy or orientation bias. Note endpoint anisotropy in the TO condition as well as a general shift to the right of movement trajectories for the TO/15 cm condition in comparison to the TO/0 cm condition.

Figure 3. Peak acceleration (top panel), movement time (middle panel) and movement's length as a function of the visual feedback conditions, experimental phases (Acq 1: first block of acquisition; Acq 3, last block of acquisition; Transfer 1) and movement direction (L: left; R: right). Error bars indicate standard error of the mean. Note the larger peak acceleration when aiming to targets located to the right rather than to the left of one's midline. This larger acceleration was compensated for by shorter movement times when

aiming to the targets located to the right rather than to the left of one's midline. Note also the large increase in movement extent when visual feedback was no longer available to the Normal vision group in transfer.

Figure 4. Coefficient of extent variability as a function of the visual feedback conditions, experimental phases (Acq 1: first block of acquisition; Acq 3, last block of acquisition; Transfer 1), and kinematic landmarks (A: peak acceleration, V: peak velocity, D: peak deceleration, and E: end of the movement's primary impulse/movement endpoint). Error bars indicate standard error of the mean. Note the sharp decrease in extent variability between peak acceleration and peak velocity. Note also the decrease in CEV between peak deceleration and the end of the movement primary impulse when visual feedback is available.

Figure 5. Orientation bias as a function of the starting bases, the experimental phases, and the kinematic landmarks (A: peak acceleration, V: peak velocity, D: peak deceleration, and E: end of the movement's primary impulse/movement endpoint). Error bars indicate standard error of the mean. Note that changing from the 0-cm to the 15-cm starting base between Transfer 1 and Transfer 2 resulted in significant biases to the right of all targets whereas biases to the left of all targets are observed when changing from the 15-cm to the 0-cm starting base.

Figure 6. Vector's length as a function of the visual feedback conditions, the movement orientation (L: left, R: right), and kinematic landmarks (A: peak acceleration, V: peak velocity, D: peak deceleration, and E: end of the movement's primary impulse/movement

endpoint). Going from late acquisition (Late acq) to Transfer 1 for the Normal vision group (withdrawal visual feedback) resulted in a longer movement vector at the occurrence of peak velocity. In the "hypothesis" panel this difference in the length of the vector is subtracted from the data observed in transfer at peak velocity, peak deceleration and movement endpoint for the Normal vision group. Note the similarity in results for the Normal vision group late in acquisition and in the hypothesis panel. The thin vertical lines to the right of the data observed in late acquisition and in transfer illustrate the mean within-participant variability observed at that kinematic landmark for the Normal vision (black line) and the Target-only (gray line) groups. Note the large decrease in variability for the Normal vision group in acquisition between peak deceleration and the movement endpoint.

Figure 1.

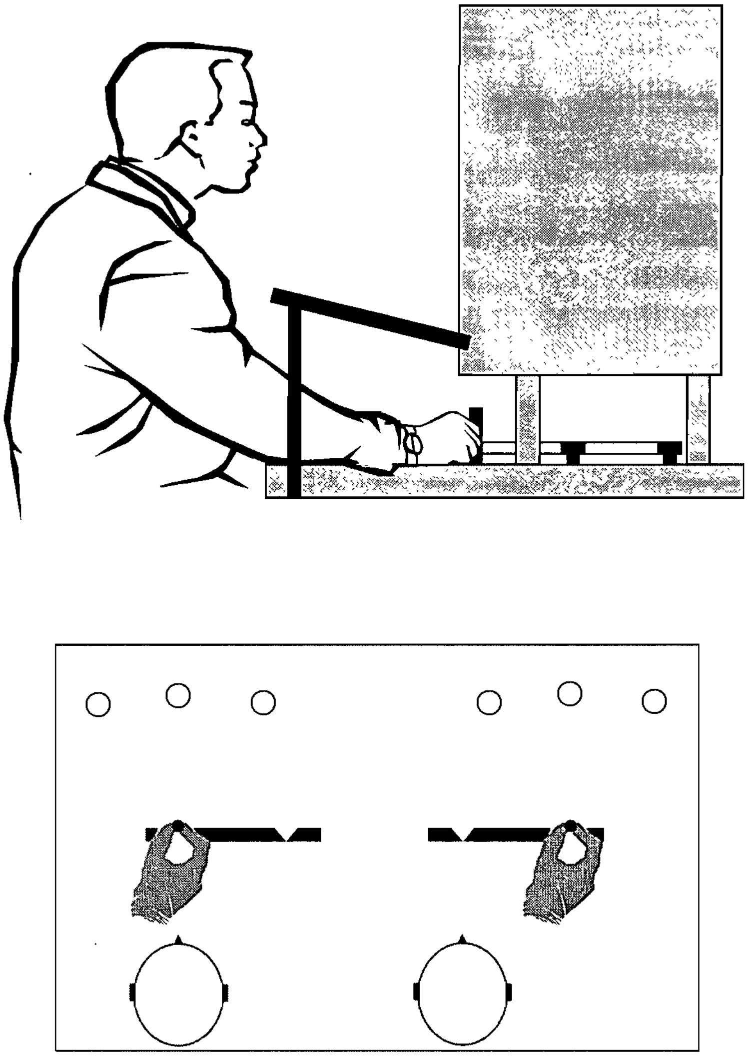


Figure 2.

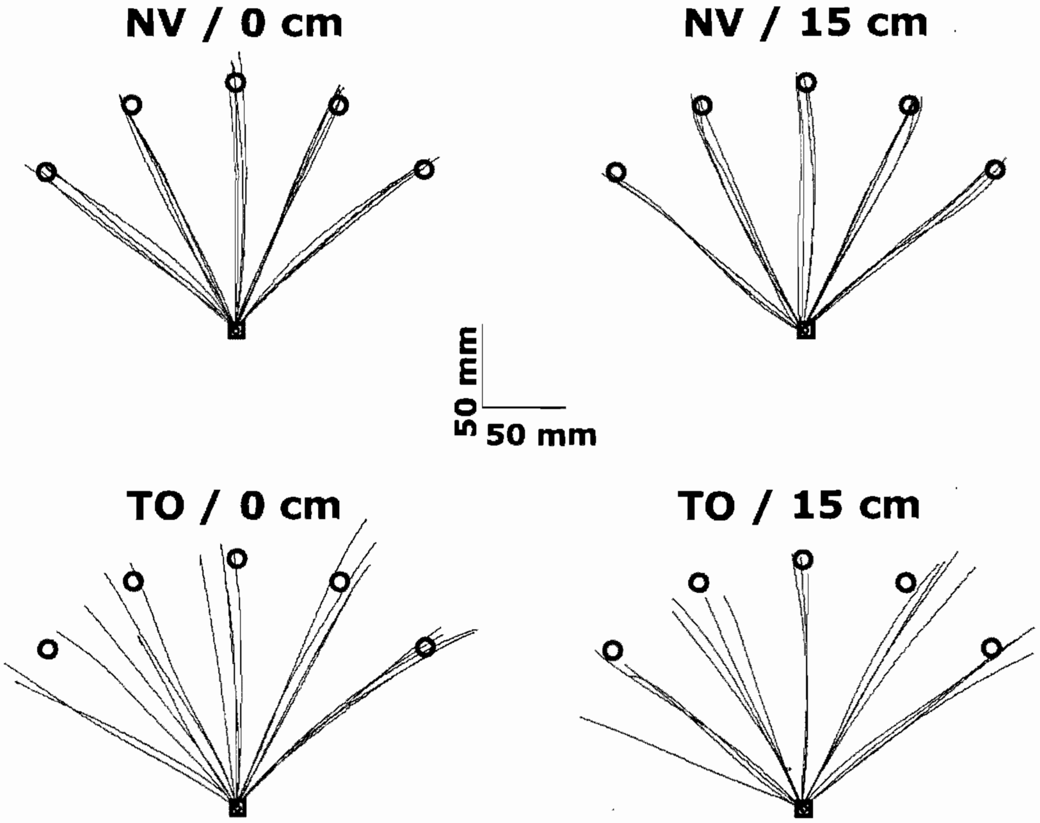


Figure 3.

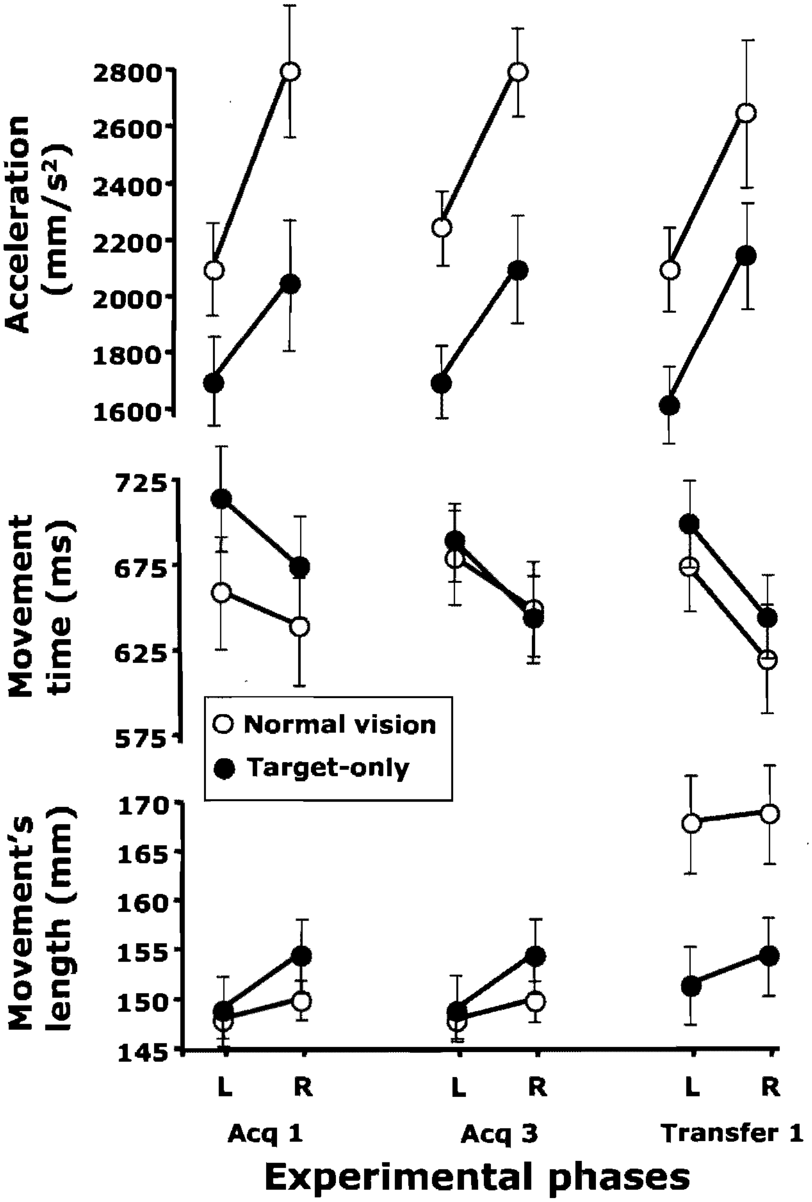

Acceleration (mm/s²)
2800
2600
2400
2200
2000
1800
1600
Movement time (ms)
725
675
625
575
○ Normal vision
● Target-only
Movement's length (mm)
170
165
160
155
150
145
L
R
L
R
L
R
Acq 1
Acq 3
Transfer 1
Experimental phases

Figure 4.

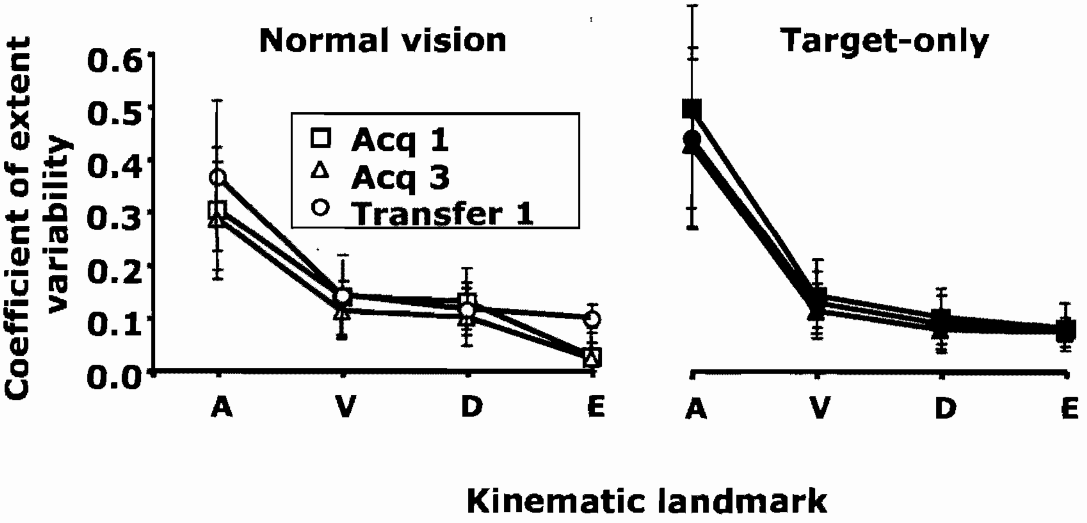

Normal vision
Target-only
Coefficient of extent variability
0.6
0.5
0.4
0.3
0.2
0.1
0.0
□ Acq 1
△ Acq 3
○ Transfer 1
A
V
D
E
A
V
D
E
Kinematic landmark

Figure 5.

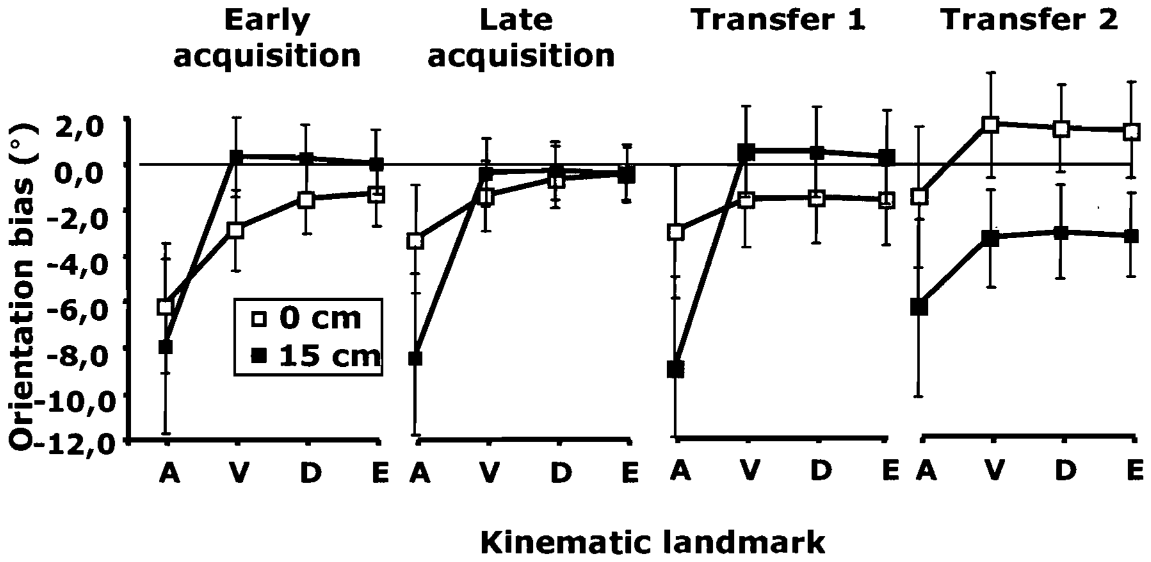
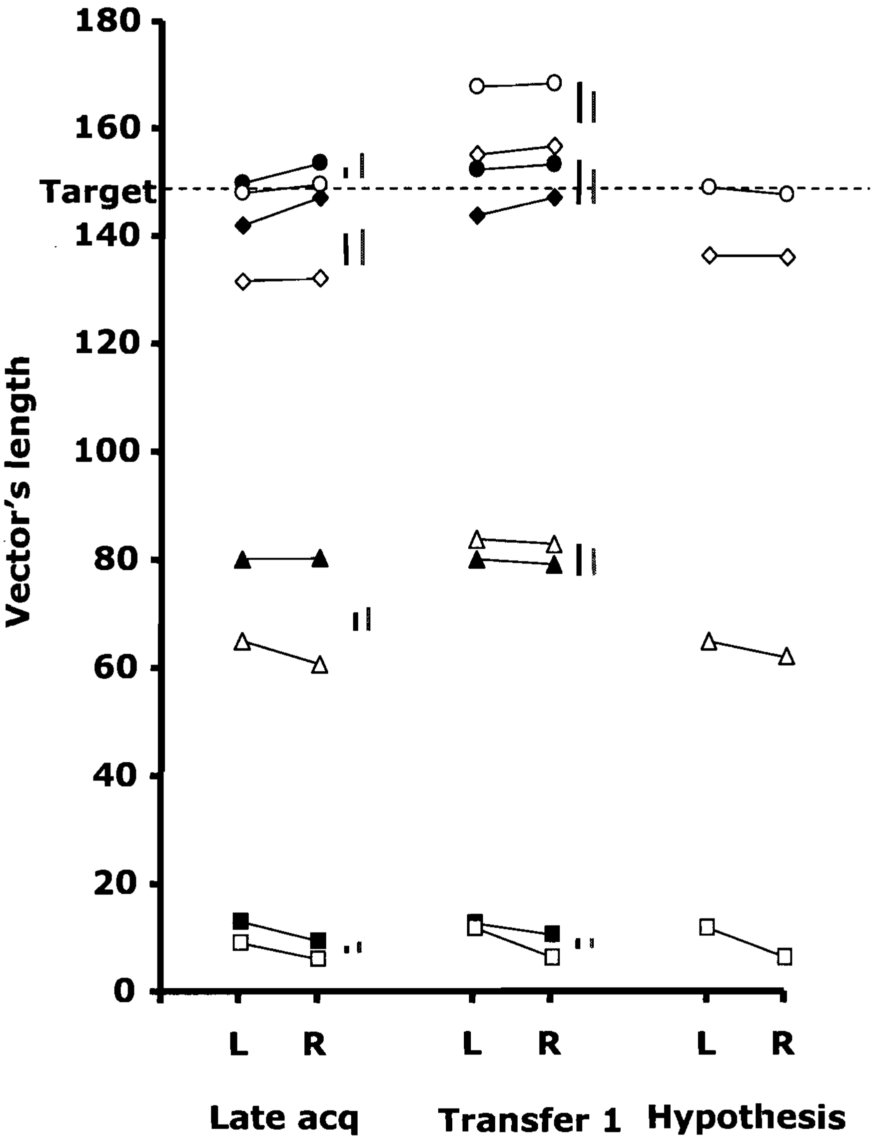

Early acquisition
Late acquisition
Transfer 1
Transfer 2
Orientation bias (°)
2,0
0,0
-2,0
-4,0
-6,0
-8,0
-10,0
-12,0
□ 0 cm
■ 15 cm
A
V
D
E
Kinematic landmark

Figure 6.


180
160
Target
140
120
100
80
60
40
20
0
Vector's length
L
R
L
R
L
R
Late acq
Transfer 1
Hypothesis

ARTICLE SCIENTIFIQUE 2

Are children able to predict the dynamic consequences of their own action?

Isabelle Mackrous· Luc Proteau

Chapitre IV

Are children able to predict the dynamic consequences of their own actions?

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Key words: movement planning, movement control, internal model, manual aiming, learning, proprioception, visual feedback, children

Abstract

Internal model of upper-limb dynamics ensures the precise joint torque control that is required for smooth and straight manual aiming movements. Our goal was to determine whether these internal models are as effective in children as in adults. To reach our goal, thirty-six children, aged between 6 and 12 years-old, and 12 young adults performed an out and back movement in a normal vision condition and in a target-only condition. The results showed that adults performed sharper movement reversal than all children for eccentric targets relative to their midline. This suggests that internal model of limb dynamics does not develop uniformly across the workspace. Visual feedback resulted in a better overlapping of the out and back portions of the movement for all age groups but significantly more so for adults than for children. This indicates more accurate online control for adults than for children.

Are children able to predict the dynamic consequences of their own actions?

From the first spontaneous aiming movement in infants to the accurate goal-directed movements of adults, the processes underlying movement dynamics and movement kinematics evolved tremendously. In reaching, movement kinematics is refined through the learning of invariant features of hand trajectory (straight line trajectory, movement peak velocity scaled to movement extent, and bell-shaped velocity profile; Fetters and Todd 1987; von Hofsten 1979, 1991; Konczak et al. 1995; Mathew and Cook 1990). Invariant kinematics features are mirrored by changes in the control of movement dynamics. For instance, Konczak et al. (1995) demonstrated that the emergence of adult-like hand kinematics in 9-month old infants resulted from a better control and a better use of the external (i.e., gravitational forces) and reactive forces (i.e., intersegmental torques) acting on the hand during movement execution.

Efficient movement dynamics result from the learning of internal models that are used to anticipate the consequences of biomechanical factors, such as intersegmental torque, and to adapt the motor commands accordingly (Jansen-Osmann et al. 2002; Konczak et al. 2003; Krakauer et al. 1999; Lackner and Dizio 1994; Sainburg et al. 1999; Sainburg 2002; Shadmehr and Mussa-Ivaldi 1994; Wang and Sainburg 2004). For example, in Konczak et al. (2003), children adapted monoarticular movements to counteract an external damping force. The observation of aftereffects when returning to a null-force condition indicated that adaptation to the damping force occurred through the development of a new internal model of limb dynamics (Lackner and Dizio 1994; Shadmehr and Mussa-Ivaldi 1994). Using a similar task, Jansen-Osmann et al. (2002)

noted persistent after-effects in children suggesting that they might result from the new internal model of limb dynamics learned through practice interfering with the retention of the pre-existing one. This led them to propose that the neural representation of the limb dynamics is unstable and imprecise in children. This might be the case when children have to adapt to external forces. However, is this still true in a more natural task like for the control of interaction torques in self-generated multi-joint movements?

As previously mentioned, an internal model of limb dynamics anticipates the consequences of different biomechanical factors acting on one's limb to apply the correct forces on each segment of the limb (Gordon et al. 1994a; Flanagan and Lolley 2001; Sainburg et al. 2003; Sober and Sabes 2003). In a reaching movement, larger acceleration at the shoulder results in greater torques at the elbow level. The adequate control of intersegmental torques requires that the internal model of limb dynamics predicts these forces, and produces a temporally adequate pattern of muscle contraction (Konczak et al. 1995; Konczak and Dichgans 1997; Sainburg et al. 1995). Our first goal was to evaluate the development of internal models of limb dynamics in children for a pluriarticular aiming movement requiring fine control of intersegmental torques.

Our second goal was to determine if and how visual feedback contributes to the control of intersegmental torques in children. In adults, it could be argued that visual feedback does not facilitate the control of intersegmental torques, because Krakauer et al. (1999) showed that learning of a new internal model of limb dynamics relied exclusively on the processing of proprioceptive input. However, this might not be the case in children for whom forward representations of hand localization is thought to be less accurate than for adults (Contreras-Vidal, 2006). This observation suggests that the control of intersegmental torques in children could be facilitated if visual feedback of the limb was permitted.

To reach our goals, children and young adults performed a single overlapping out-and-back movement from a common starting base (i.e., like slicing a loaf of bread gesture). This task was chosen because performing an overlapping out-and-back movement, produce intersegmental torques at movement reversal that has to be controlled and coordinated. All participants performed the task in both a normal vision and a target-only condition (only the target is visible during movement execution).

Based on Sainburg et al. (1995), adequate control of intersegmental torques results in a sharp reversal of the movement and a fine overlapping of the out and back movements. If the rules governing intersegmental torques are not well integrated in children, a larger reversal angle and lesser overlapping of the out and back movements should be observed in children than in adults. If vision of the cursor facilitates intersegmental torque control in children, then a smaller reversal angle and a better overlapping of the out and back trajectories should be observed in normal vision than when visual feedback is not permitted.

Finally, it has been shown that the directional variability of a series of movements aimed at the same target is large early after movement initiation (peak tangential acceleration) and then decreases as movement unfolds. For example, in Mackrous and Proteau (2007) it went from 7.0° at peak acceleration to 4.06° (peak velocity), 3.25° (peak deceleration) and 2.85° at movement endpoint. The large variability observed soon after movement initiation suggests that movement planning is based on approximations concerning the location of one's hand and of the target in the workspace, mechanical constraints, and especially the state of the motor system (motor pathways, motoneurons pool, motor units, etc.). Because of these approximations as well as variability inherent to all biological systems, the CNS has developed mechanisms to quickly update the motor commands. If, as suggested above, uncertainties about the initial state of the effector are smaller once the movement is underway, we should observe a smaller variability soon after initiation of the back portion of the movement than soon after initiation of the out portion of the movement. Our third objective was to test this hypothesis.

Method

Participants

Thirty-six children (n =12 for 6-7, 8-9 and 10-12 years old) and twelve adults (aged between 20-25 years-old) took part in this experiment. They all reported normal or corrected to normal vision. They took part in a single thirty-minute experimental session. Adults were paid $10 CDN for their time; children received a toyshop's gift card to the same amount. The Health Sciences Ethics Committee of the Université de Montréal has approved this study.

Task and apparatus

Participants performed out-and-back movements with a computer mouse-like device from a fixed starting position located close to the body toward a target located away from the body. They were instructed to perform straight and uncorrected movements (i.e., no "stop and go") and to overlap the out and back portions of their movements as accurately as possible.

The apparatus is illustrated in Figure 1a. It consisted in a table, a computer screen, a mirror, and a two-degrees of freedom manipulandum. Participants sat in front of the table. The computer screen (Mitsubishi, Color Pro Diamond 37 inches) was mounted on a ceiling-support positioned directly over the table; the computer screen was oriented parallel to the surface of the table. Its image was reflected on a mirror placed directly beneath it and also parallel to the tabletop. The distance between the computer screen and the mirror was 18.5 cm while the distance between the mirror and the tabletop was 18.5 cm permitting free displacement of the manipulandum on the tabletop. Participants could not see their hand and arm for the duration of the experiment, but the information presented on the computer screen (cursor, starting base, target) was reflected on the mirror and was visible for the participant.

The tabletop was covered by a piece of Plexiglas. The manipulandum consisted of two pieces of rigid Plexiglas (43 cm) joined together at one end by an axle. One free end of the manipulandum was fitted with a second axle encased in a stationary base affixed to the tabletop. The other free end of the manipulandum was fitted with a small vertical shaft (length: 3 cm, radius: 1 cm), i.e., the stylus, which could be easily gripped by the participant. The starting base consisted of a thin strip of Plexiglas glued to the tabletop. It was parallel to the leading edge of the table and had a small indentation on one of its face. The indentation was located directly in line with the lateral center of the computer screen and the participant's midline. Each axle of the manipulandum was fitted with a 13-bit optical shaft encoder (U.S. Digital, model S2-2048, sampled at 500 Hz, angular accuracy of 0.0439°), which enabled us to track the displacement of the stylus online and to illustrate it with a 1:1 ratio on the computer screen. Moving the stylus away from the body in the frontal and sagittal planes resulted in an identical displacement of the cursor on the computer screen. The bottom of the stylus and of the optical encoder located at the junction of the two arms of the manipulandum were covered with a thin piece of Plexiglas. By lubricating the working surface at the beginning of each experimental session, participants smoothly displaced the stylus.

Procedures

Participants used their right dominant hand (self-declared). The targets were located in line with the participant's midline (0° target) and 35° to his/her left (-35° target), both at 150 mm from the starting base. The cursor (red, 3 mm in diameter) and the targets (black, 6 mm in diameter) were presented on a white background.

Participants were asked to initiate their movement as they pleased following presentation of a target but were required to complete it in a movement time ranging between 880 ms and 1120 ms (1000 ms +/- 12%). Movement initiation was detected when the stylus was moved by 2 mm, whereas movement end occurred when the stylus was not displaced by more than 2 mm for a period of 150 ms. The procedure used to define movement endpoint encouraged participants to produce smooth single-motion movements (out and back) with an easily identifiable reversal point. When movements were completed outside the target movement time bandwidth, the experimenter reminded the participant of the target movement time. A movement time bandwidth was used to reduce the possibility of different speed-accuracy trade-offs between the age groups and experimental conditions (Fitts, 1954). Thus, differences in performance should mainly be expressed on the spatial components of the movements.

The experimental session began with familiarization trials aimed at three targets (10°, 20°, 50°, 6 trials per target) located to the right of the participant's midline and performed in a normal vision condition. At the end of this phase, all participants understood what was expected of them. Because the targets used in this phase were located in the participants' right hemifield (i.e., outside the experimental workspace) there should be no transfer of learning for the targets used in the following two experimental phases (Gandolfo et al., 1996, Sainburg et al., 1999). In the experimental phase, until movement initiation, participants could see the cursor they had to move resting on the starting base and the target to be reached. Participants first performed the task in the target-only condition for which vision of the cursor was blanked at movement onset. Then, participants performed the task in the normal vision condition for which the cursor remained visible throughout movement execution. In both the target-only and the normal vision conditions, participants performed 17 trials toward each the 0° and the -35° targets. Target presentation was randomized and no knowledge of result (KR) was provided. To maintain motivation in children, in both the target-only and the normal vision conditions, all participants performed 6 additional trials that were followed with KR (illustration of the out-and-back movement on the computer screen). For these trials, we used a target located 35° to the right of the participants' midline and at 150 mm from the starting base.

Data reduction

The tangential displacement data of the stylus over time for the out and the back portions of the movement were first smoothed using a second order recursive Butterworth filter with a cut-off frequency of 10 Hz. The filtered data were then numerically differentiated once using a central finite technique to obtain the velocity profile of the movement, a second time to obtain the acceleration profile, and a third time to obtain a jerk profile. From these profiles, we determined when and where key kinematics landmarks occurred for each portion of the movement: peak acceleration, peak velocity, peak deceleration, and movement reversal (out) or movement endpoint (back).

To facilitate reading of this article, the statistical analyses that were computed are defined at the beginning of each subsection of the results presentation. Geisser-Greenhouse correction was applied when Epsilon value was less than 1. All significant main effects involving more than two means were broken down using Dunn's technique. Significant interactions were broken down by computing simple main effects that were followed by Dunn's post hoc comparisons when they involved more than two means. All effects are reported at $\underline{p} < .05$ (adjusted for the number of comparisons).

Dependent variables

For the out portion of the movement, direction accuracy was considered as the angular difference between a reference vector (that joining the starting base and the target) and the vector defined by the starting base and the cursor at movement reversal. Movement length was considered as the vector joining the starting base and the cursor at movement reversal. To investigate the control of the intersegmental torques, two measures of performance were computed: sharpness of reversal and overlapping of the out and back portions of the movement. Sharpness of reversal was represented by the angle comprised between the out and the back portions of the movement (Fig.1b). Location of the cursor 100 ms before reversal and 100 ms after reversal were used to calculate this angle. Overlapping error was the size of the area comprised between the out and back portions of the movement (Fig.1b). To normalize for movement length, the overlapping error was divided by the vector length of the out portion of the movement. Measures of within-participant variability were also computed for these four dependent variables.

In addition, within-participant variability of movement orientation was computed at four kinematics landmarks for both the out and back portions of the movements (100 ms after movement initiation [out] or reversal [back]), peak velocity, peak deceleration and movement reversal (out) or movement endpoint (back). Movement endpoint was defined as the location of the stylus when it came within 1 mm of the Plexiglas strip encasing the starting base (see Fig. 1b). For the back movement, deviation from a new reference vector, that joining movement reversal point and the starting base, was used to compute within-participant variability.

Results

Preliminary analyses

Figure 2a illustrates out-and-back movements performed in the normal vision and the target-only conditions by a typical participant in each age group. As illustrated in Fig.2b, adults and children performed continuous movements, as revealed by the smooth bell-shaped velocity profiles observed during the out and the back portions of the movement.

Because intersegmental torque at movement reversal is influenced by target location, we determined first whether the location of movement reversal for each target was approximately the same for the different groups and experimental conditions. To this end, spatial accuracy (direction constant error [i.e., signed error], movement length) and variability data (direction and length variable errors [i.e., within-participant variability]) of the out portion of the movement were contrasted between age groups and visual feedback conditions. The data of interest were individually submitted to an ANOVA contrasting 4 age groups (6-7, 8-9 and 10-12 years-old children and adults) x 2 visual feedback conditions (target-only and normal vision condition) x 2 targets (-35° and 0°) with repeated measurements on the last two factors.

The location of movement reversal showed small orientation (< 2.5°) and vector length error (< 15 mm) for all age groups, who did not significantly differ from one another (see Lhuisset & Proteau, 2004a, b for similar observations). However, in the target-only condition, movements ended to the left of the -35° target and to the right of the 0° target (-0.87° and 0.59°, respectively), whereas no such difference was noted in the normal vision condition (-0.72° and -0.70°, respectively), F (2, 88) = 9.3. Similarly, in the target-only condition, we observed shorter movements for the -35° target than for the 0° target (153 mm vs. 163 mm, respectively), whereas no difference was noted in the normal vision condition (157 mm vs. 160 mm), F (1, 44) = 30.4. Movement length variability was significantly larger for 8-9 years-old children than for adults in the target-only condition, whereas in the normal vision condition, 6-7 years-old children were more variable than adults, F (3, 44) = 3.7. Direction variability did not differ significantly between age groups, p = 0.19.

Control of movement dynamics

To determine whether children had more difficulties than adults to control intersegmental torque at movement reversal and whether visual feedback facilitated this control, the reversal angle and the normalized overlapping error data, as well as their within-participant variability, were individually submitted to an ANOVA contrasting 4 age groups (6-7, 8-9 and 10-12 years-old children and adults) x 2 visual feedback conditions (target-only and normal vision condition) x 2 targets (-35° and 0°) with repeated measurements on the last two factors.

As illustrated in Fig.3a, adults had a sharper reversal angle than all groups of children for the -35° target. Interestingly, however, no significant age group difference was noted for the 0° target, F (3, 44) = 3.4. Visual feedback had no significant impact on this dependent variable (normal vision: 9.5°, target-only: 10.7°), F (1, 44) = 3.4, p = 0.07.

Children had significantly larger overlapping error than adults for the -35° target, whereas no significant difference between age groups was observed for the 0° target (see Fig.3b), F (3, 44) = 6.9. However, for all age groups, visual feedback permitted participants to significantly reduced their overlapping error in comparison to the target-only condition (Fig. 3b), F (1, 44) = 38.2). To better illustrate how visual feedback permitted 6-7 years-old children and adults to reduce the overlapping error, Figure 4 shows perpendicular deviation of the back portion of the movement from a straight line joining the location of movement reversal to the starting base. For the adults, we observed very little difference between the normal vision and target-only conditions up to approximately 30% of movement time. Then, deviations from the reference vector increase some in the target-only condition. This increase was larger for the -35° target than for the 0° target. This clearly indicates that visual feedback did not permit adult to better plan the back portion of their movement; however, it permitted them to correct their movement online more effectively than proprioceptive feedback alone. For children, right from movement reversal, deviation from the reference vector was slightly larger in the target-only than in the normal vision condition; it remained so until movement endpoint. This larger deviation was more pronounced for the -35° than for the 0° target. Thus, children were not as accurate as adults planning the back portion of the movement, and slightly less so in the target-only than in the normal vision condition. Concerning this last point, the difference between the normal vision and the target-only condition reached 1 mm approximately at 25% of relative movement time.

Reversal angle variability and normalized overlapping variability were significantly larger for children than adults. This was supported by a main effect of age groups, F (3, 44) = 5.3 and F (3, 44) = 9.1, respectively. Children groups did not differ significantly from one another on both these dependent variables, p > .10. In addition, reversal angle and normalized overlapping variability were significantly larger for the -35° target than for the 0° target, F (1, 44) = 60.2 and F (1, 44) = 63.4, respectively. This is illustrated in Fig.3c and d, respectively. Finally, performing the task in normal vision resulted in a significantly smaller normalized overlapping variability than in the target-only condition (Fig. 3d), F (1, 44) = 33.0.

Supplementary analyses. For the -35° target, movement reversal was not as sharp for children as for adults and larger overlapping errors were noted for children than for adults. Because movements performed along one's midline required lesser intervention from the shoulder when compared to aiming at the -35° target, the interaction torque at movement reversal was smaller for the 0° than for the -35° target (Sainburg et al., 1995). Thus, it could be that the larger errors noted for children than for adults reflect that children had more difficulty than adults dealing with larger intersegmental torque rather than difference in their internal model of limb dynamics. To test this hypothesis, we had 6 year-old children and adults performed the same task as in the main experiment but toward targets located at -35°, 0° and +35°. For the -35° target, the flexion interaction torque at movement reversal was larger than for the 0° target, whereas this flexion torque was larger for the 0° than for the +35° target (Sainburg et al., 1995). Movement reversal was significantly sharper for the 0° target than for both the -35 and the +35° targets for children (20.8°, 7°, and 21.2° for the -35°, 0°, and +35° targets, respectively) and for adults (11.5°, 6°, and 14.5°, respectively). Similarly, overlapping error was significantly smaller for the 0° target than for both the -35 and the +35° targets for children (8.5, 4.3, and 8.0 for the -35°, 0°, and +35° targets, respectively) and for adults (4.0, 3.2, and 5.0, respectively). However, for both dependent variables, these between targets differences were larger for children than for adults, and no significant difference was noted between the -35° and +35° targets (see Fig. 5). These results do not support the hypothesis that children had more difficulty than adults in dealing with larger interaction torque, which is supported by Konczak et al. (1995) who found that even the immature neuromuscular system of infant can produce task-adequate torques level.

Variability of the out-and-back movement trajectories

Orientation variability data were submitted to an ANOVA contrasting 4 age groups (6-7, 8-9 and 10-12 years-old children and adults) x 2 directions (out and back movement) x 2 visual conditions (target-only and normal vision condition) x 4 landmarks (100 ms after movement initiation, peak velocity, peak deceleration and movement reversal/endpoint) x 2 targets (-35° and 0°) with repeated measurements on the last four factors. We did not compute a similar analysis on the extent component of the task because the back portion of the movement ended on a physical stop.

Fig. 6 illustrates that, for all age groups, orientation variability was significantly smaller in the normal vision than in the target-only condition, F (1, 44) = 78.8. In addition, at the 100 ms mark, orientation variability was significantly larger for the -35°

than the 0° target. This difference decreased as movement as movement unfolded, F (3, 132) = 190.8.

Orientation variability of both the out and back portions of the movement, was significantly larger for two younger groups of children than for the adults 100 ms after movement initiation and at peak velocity, regardless of the portion (out or back) of the movement. At peak deceleration and at movement reversal/endpoint, only the youngest children remained more variable than the adults. This is supported by a significant age groups x kinematics landmarks interaction, F (9, 132) = 3.8.

The most interesting finding of this analysis revealed a significantly larger variability at the 100 ms mark for the out than for the back portion of the movement. In the target-only condition, the difference in movement variability between the out and back portions of the movement remained significant at all kinematics landmarks. In normal vision, this difference in variability between the out and back portions of the movement decreased but remained significant at peak velocity but not at peak deceleration and at movement endpoint. This is supported by a significant visual feedback x direction x landmarks, F (3, 132) = 7.8.

It is important to note that the decrease in variability noted between the out and back portions of the movement observed at 100 ms was not caused by smaller peak acceleration during the back portion of the movement. Peak acceleration values were submitted to an ANOVA contrasting 4 age groups (6-7, 8-9 and 10-12 years-old children and adults) x 2 directions (outward and back movement) x 2 visual conditions (target-only and normal vision condition) x 2 targets (-35° and 0°) with repeated measurements on the last three factors. The results revealed that peak acceleration was larger for the back portion of the movement rather than for the out portion of the movement for the 6-7 (out: 3768 mm/s^2 vs. back: 4373 mm/s^2) and 10-12 (out: 3603 mm/s^2 vs. back: 3993 mm/s^2) years-old children. No significant difference was observed for the 8-9 years-old (out: 3439 mm/s^2 vs. back: 3586 mm/s^2) and the adults (out: 3824 mm/s^2 vs. back: 3570 mm/s^2). This is supported by a significant age group x direction interaction, F (3, 44) = 3.9.

Movement time

Movement time was submitted to an ANOVA contrasting 4 age groups (6-7, 8-9 and 10-12 years-old children and adults) x 2 visual conditions (target-only and normal vision condition) x 2 targets (-35° and 0°) with repeated measurements on the last two factors. Mean movement time data are reported in Table 1.

For all children, movement time was significantly shorter in the target-only condition than in the normal vision condition for the -35° target but not for 0° target (see Table 1). We did not observe any significant movement time difference for the adults. This is supported by a significant age groups x visual condition x target interaction, F (6, 88) = 2.4.

Discussion

The fluidity of our movements when we pick up a glass of milk full to the brim and bring it up to our lips without spilling its content relies heavily on the development of internal models of limb kinematics and of limb dynamics. In the present report, we studied the development of internal models of limb dynamics in children by having participants performed overlapping out-and-back movements. For the back portion of the movement to perfectly overlap its out portion, participants had to anticipate the flexion torque produced at the elbow at movement reversal, a hallmark of internal model of limb dynamics. In addition, we wanted to determine whether visual feedback would contribute/ facilitate intersegmental torque control.

Intersegmental torque control

Adults had significantly sharper movement reversal and smaller overlapping errors than children for the -35° target but not for a target located in line with their midline. Because visual information about the starting base and target location was available at all time, our results could not be explained by age difference in perceiving the location of eccentric targets (Contreras-Vidal 2006 ; Pellizzer & Hauert 1996). This position is also supported by the observation that the accuracy and variability of the out movement was very similar across age groups. If younger participants had more difficulty than adults locating the position of their hand on the starting base and/or of the out target in the workspace, they should have been less accurate and/or more variable than adults for the out portion of the task when aiming at the -35° target, which was not the case. In addition, because sharpness of movement reversal was not significantly increased with visual feedback, the difference noted between adults and children cannot be explained by a higher accuracy of proprioceptive feedback away from one's midline for adults than for children. If that had been the case, the differences noted above between adults and children would have been larger in the target-only condition than in the normal vision condition. Finally, because the results of supplementary analyses revealed that this difference between children and adults was similar for movement reversal that created large (-35°) or small (+35°) intersegmental torque, it appears that the larger error observed for children for the eccentric targets is not related to the size of intersegmental torque.

Rather, although children did not perform the task as well as adults for the -35° target, movement reversal remained much sharper than that reported by Sainburg et al. (1995) for deafferented participants (reversal error of 53° and 143° for each one of two participants). This suggests that, as for adults, both during movement planning and movement execution, children anticipated joint interaction torque at the elbow and used proprioceptive feedback to time the activation of agonist and antagonist muscles acting at the shoulder and lower arm. However, a new important finding of the present study is that the internal model of upper-limb dynamics does not appear to develop uniformly across the workspace. It appears that these models are more precise and develop sooner in children for movements performed along or close to one's midline in comparison to angled movements. This would explain why for all age groups we observed sharper reversal and smaller overlapping error for the 0° than for the -35° targets. In addition, it would explain why these errors are larger for eccentric targets for children than for adults and why this increase in error gradually decreased as children grew older. The observation of similar overlapping errors and reversal angle for the -35° and +35° targets (Fig. 5) also support this hypothesis.

Visual feedback in intersegmental torque control

Concerning our second goal, visual feedback did not permit children or adults to have significantly sharper movement reversal than when performing the task in the target-only condition. In addition, although overlapping errors were smaller in the normal vision than in the target-only condition, we showed that this difference largely resulted from visual feedback permitting participants to correct the back movement sooner and more completely than in the target-only condition. Thus, visual feedback about the ongoing movement did not permit adults or children to better anticipate intersegmental torque to reduce overlapping errors. Rather, visual feedback permitted participants to correct errors resulting from inaccurate torque control more accurately than in the target-only condition. For adults, these results support Krakauer et al. (1999) finding that visual feedback does not facilitate intersegmental torque control. The present study extends this finding to children as young as 6-7 years-old. This observation is not surprising when the children's performance (movement reversal and overlapping errors) is at par with that of adults as it was for the 0° target. However, observing the same result for the -35° when the children's performance was not as good as that of adults provides an even stronger suppport to Krakauer' s et al. position (1999) that vision is unnecessary and does not enhance proprioceptive learning of the new internal dynamic model.

Online movement control

In goal-directed movements performed both in normal vision and in a no vision condition, Proteau and colleagues observed that, once movement variability is normalized for movement length (coefficients of variability), this normalized variability quickly decreased between peak acceleration and peak velocity (Bédard and Proteau 2005; Lhuisset and Proteau 2004; see also Robin et al. 2005). They argued that the large variability observed at peak acceleration resulted from movement planning being based on approximations concerning the initial state of the motor system (motoneurons pool, motor pathway, motor unit, biomechanical constraints, etc.) -thus the large variability-, but that dynamic information available during movement execution provided more accurate information about the state of the system, explaining the large decrease in variability at peak velocity. The results of the present study supported this proposition. Direction variability was significantly larger 100 ms after movement initiation for the out portion of the movement (movement planning was based on approximations) than 100 ms into its back portion that was likely based on the processing of dynamic information available during the out portion of the movement.

It is worth noting that children were as efficient as adults reducing initial direction variability as movement unfolded (see also Lhuisset & Proteau, 2004a). This is true both for the out and for the back portions of the movements, and indicates that even the youngest children who participated in the present study could modulate their movement online to compensate for initial error/noise in movement planning and execution processes.

Conclusion

In conclusion, the results of the present study indicated that the development of an internal model of upper limb dynamics is not constant across the workspace and appears to first developed for movements performed along one's midline. Visual feedback does not play a significant role for the development of these models in participants with intact proprioception, even when they lead to less than « optimal » performance. Finally, we found that movement updating that takes place soon after movement initiation is less variable when based on dynamic than static afferent information.

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Table 1. Movement time (standard deviation) for all age groups as a function of visual feedback and target location.

	Target-only		Normal vision	
	-35°	0°	-35°	0°
6-7 years-old	915 (47)	919 (39)	990 (61)	910 (38)
8-9 years-old	903 (31)	920 (33)	1001 (47)	970 (48)
10-12 years-old	929 (19)	902 (24)	1003 (25)	929 (33)
Adults	925 (14)	918 (20)	949 (27)	972 (33)

Figure captions

Figure 1 *a)* Experimental set up *b)* The reversal angle was calculated as the angle formed by the position of the cursor 100 ms prior to movement reversal, at movement reversal, and 100 ms after movement reversal. The area comprise between out and back portions of the movement was used to computed the overlapping error. *c)* Orientation variability of the back portion of the movement was calculated in relation to the vector joining the location of movement reversal and the starting base (100 ms: 100 ms after movement reversal; vel: peak velocity, dec: peak deceleration; end: movement endpoint occurred when the cursor was within 1 mm of the piece of Plexiglas defining the starting base).

Figure 2 *a)* Examples of out and back trajectories for all age groups. Note the sharp movement reversal and good overlapping of out-and-back trajectories for all age groups for the 0° target but only for adults for the -35° target. *b)* Out-and-back movements were performed smoothly for all age groups as revealed by smooth and bell-shaped velocity profiles.

Figure 3 *a)* Movement reversal angle *b)* Normalized overlapping error, *c)* Within-participant variability in movement reversal angle and *d)* in normalized overlapping error area for all age groups as a function of the visual feedback condition and target location. Note the larger error and variability for children than for adults when aiming at the -35° target. Note also the similar pattern of results for movements performed in normal vision and in the target-only conditions.

Figure 4 Deviation of the back movement in reference to a vector joining the location of movement reversal and the starting base (i.e., target for the back movement).

Figure 5 Typical trajectories for out-and back movements performed by 6-7 years-old children and adults when aiming at eccentric targets for which a large (-35°) or a small (+35°) interaction torque is created at movement reversal. Note the similarity of results for the two targets. Note also the sharper movement reversal and tighter overlapping of out-and-back trajectories for adults than for children.

Figure 6 Orientation variability *a)* in the target-only condition and, *b)* in the normal vision condition at key landmarks for the out and back portions of the movements for all age groups. Note the smaller variability 100 ms after movement reversal than after movement initiation. Note also the decrease in variability for all age groups as movement unfolded.

Figure 1

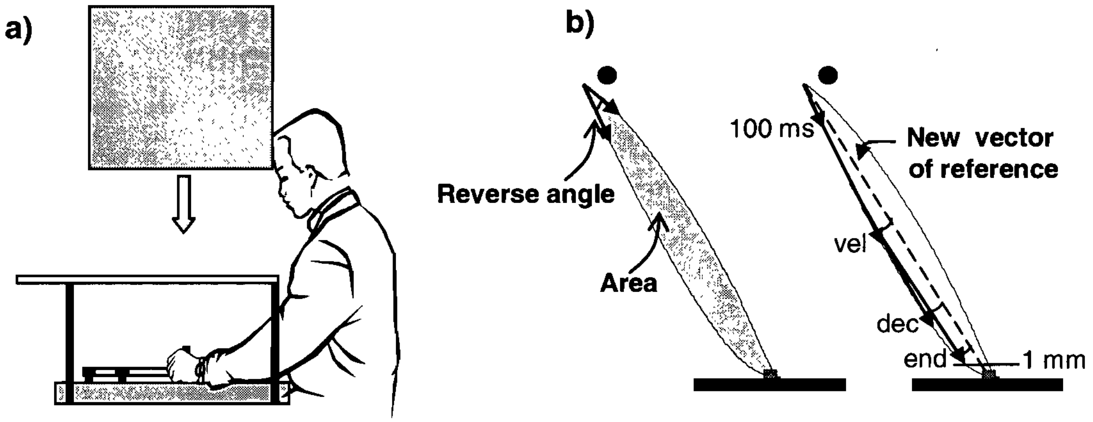

a)
b)
100 ms
New vector
of reference
Reverse angle
Area
vel
dec
end
1 mm

Figure 2

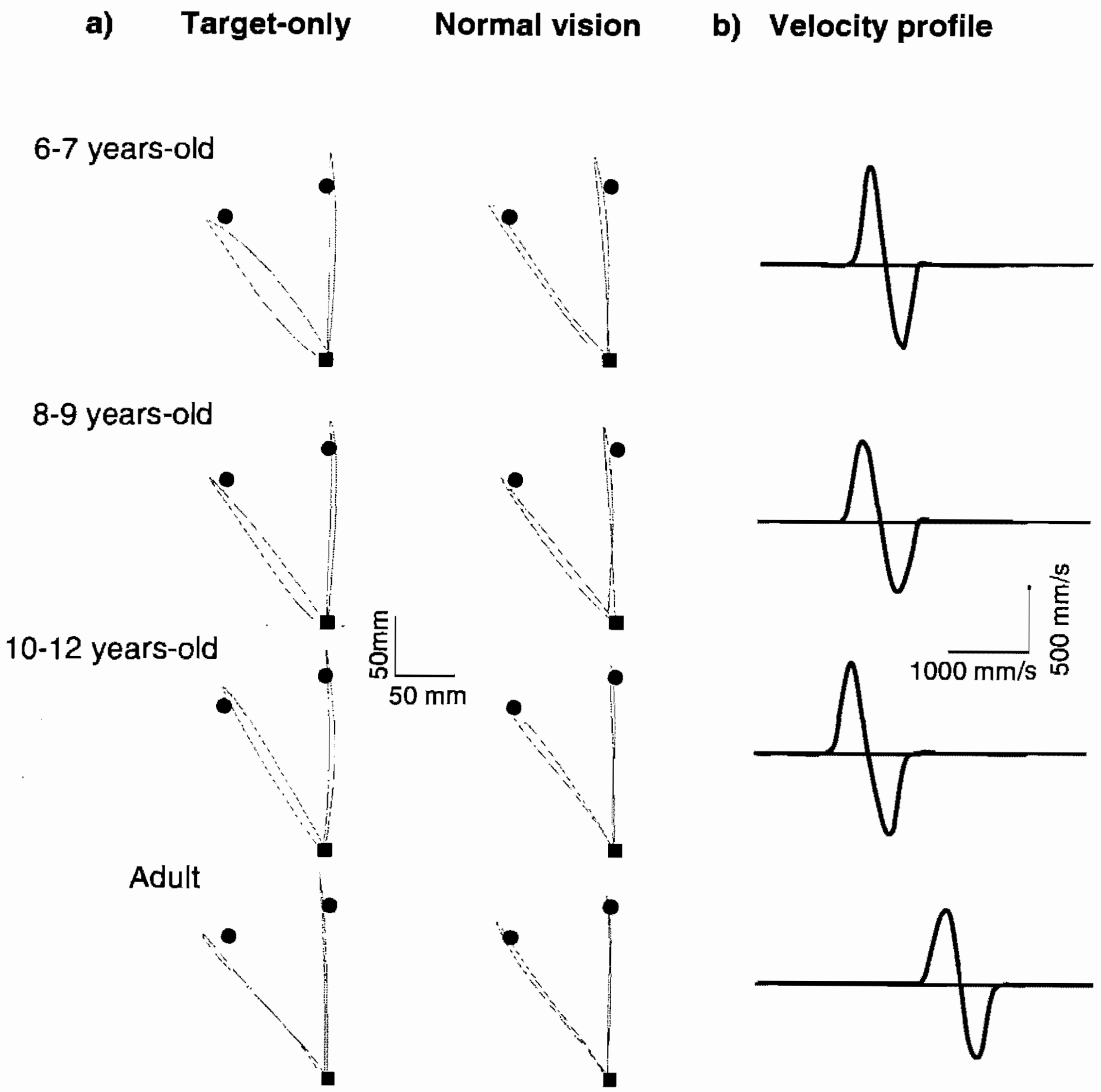

a)
Target-only
Normal vision
b)
Velocity profile
6-7 years-old
8-9 years-old
10-12 years-old
Adult
50mm
50 mm
1000 mm/s
500 mm/s

Figure 3

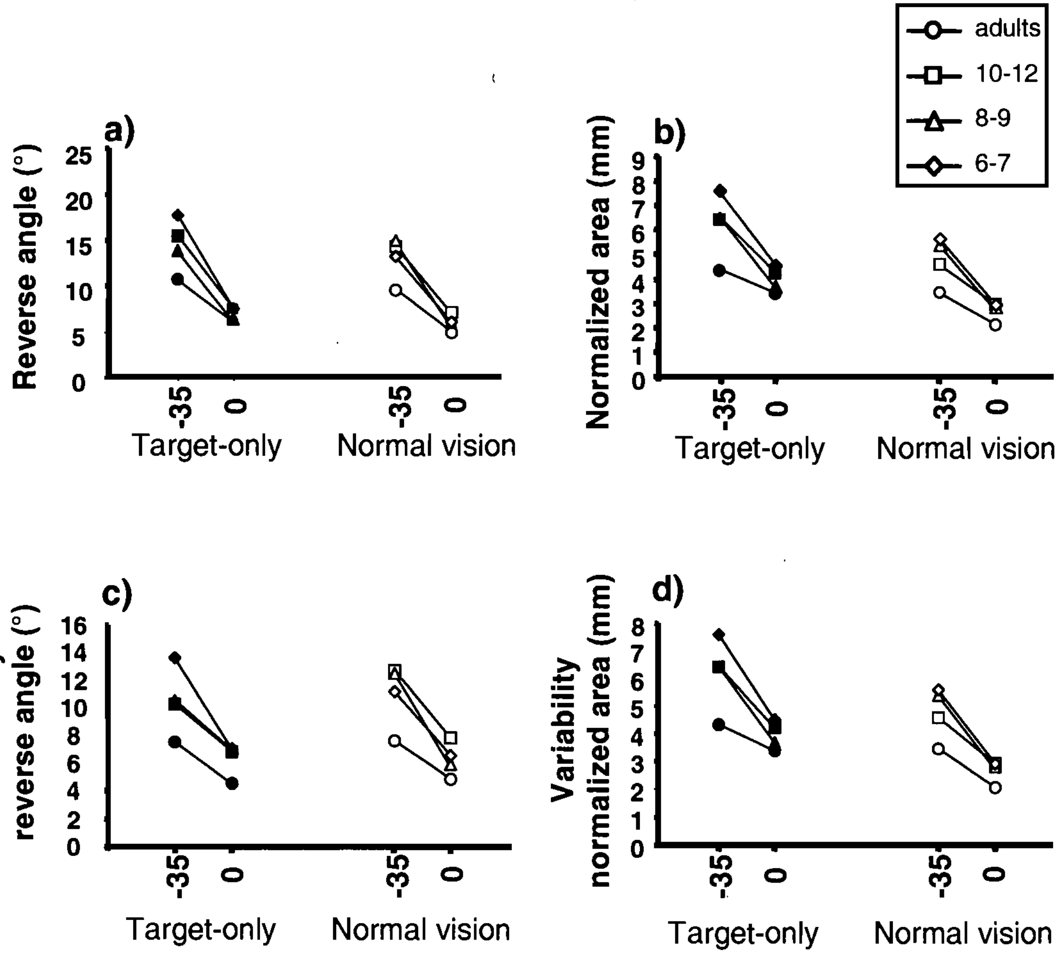

adults
10-12
8-9
6-7
a)
Reverse angle (°)
25
20
15
10
5
0
-35
0
-35
0
Target-only
Normal vision
b)
Normalized area (mm)
9
8
7
6
5
4
3
2
1
0
-35
0
-35
0
Target-only
Normal vision
c)
Variability
reverse angle (°)
16
14
12
10
8
6
4
2
0
-35
0
-35
0
Target-only
Normal vision
d)
Variability
normalized area (mm)
8
7
6
5
4
3
2
1
0
-35
0
-35
0
Target-only
Normal vision

Figure 4

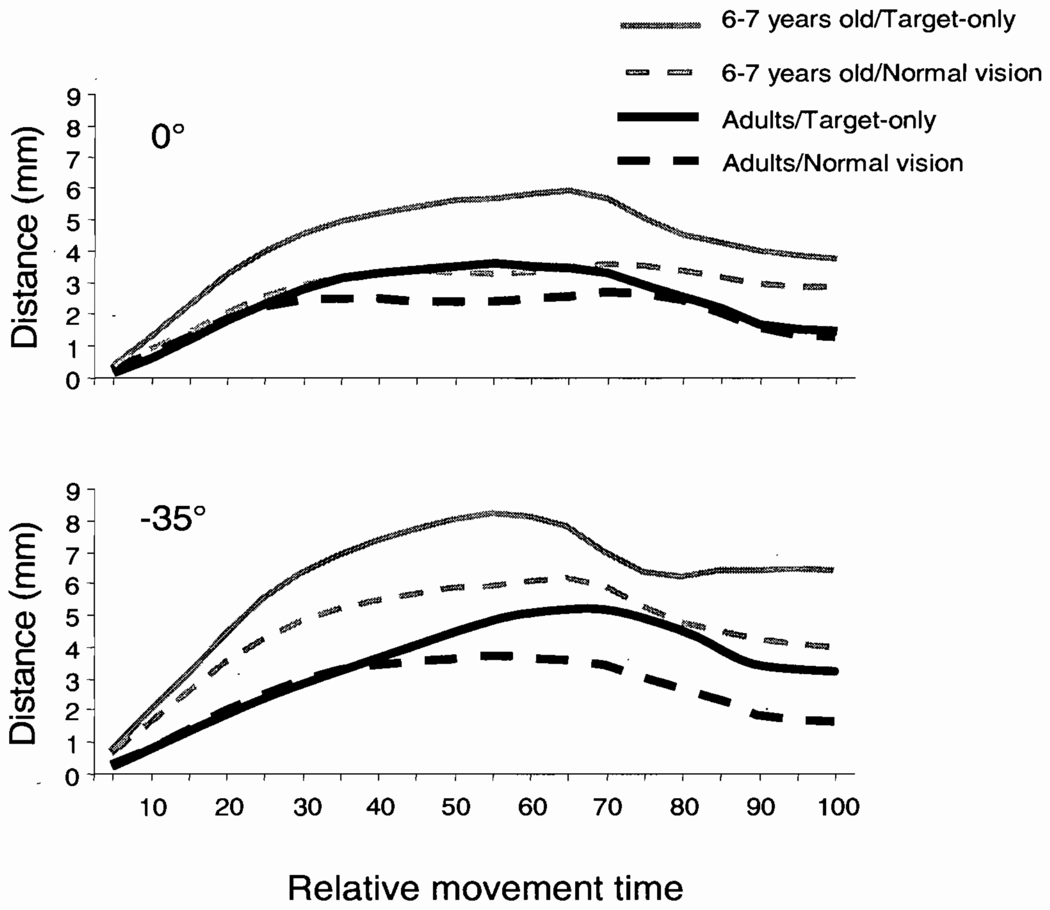

6-7 years old/Target-only
6-7 years old/Normal vision
Adults/Target-only
Adults/Normal vision
0°
-35°
Distance (mm)
0
1
2
3
4
5
6
7
8
9
10
20
30
40
50
60
70
80
90
100
Relative movement time

Figure 5

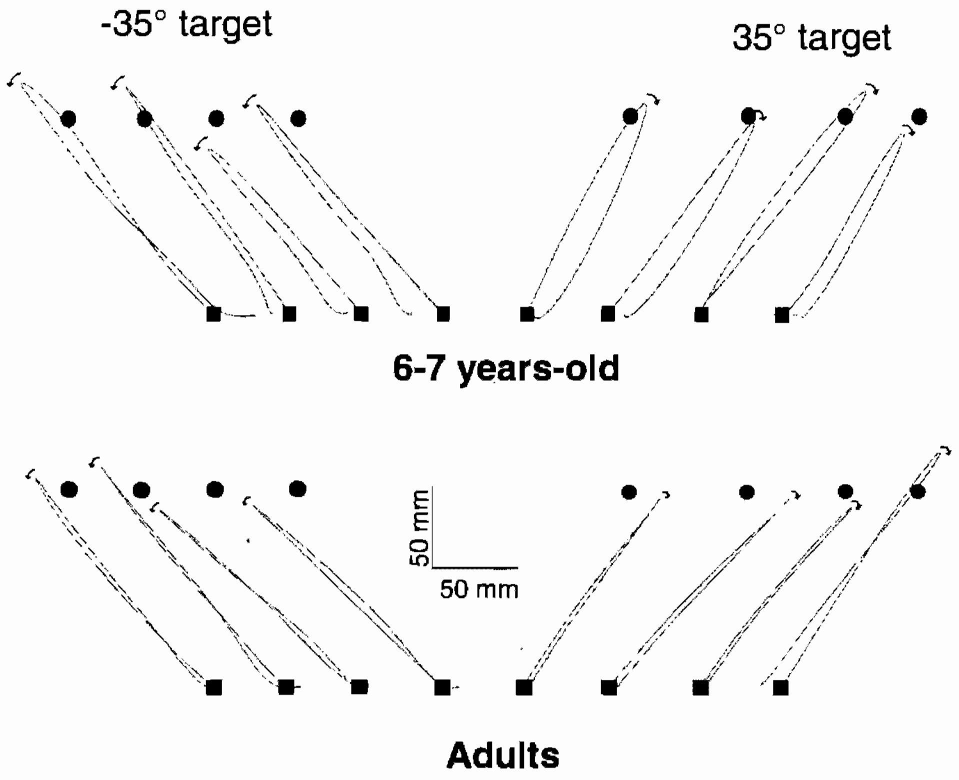
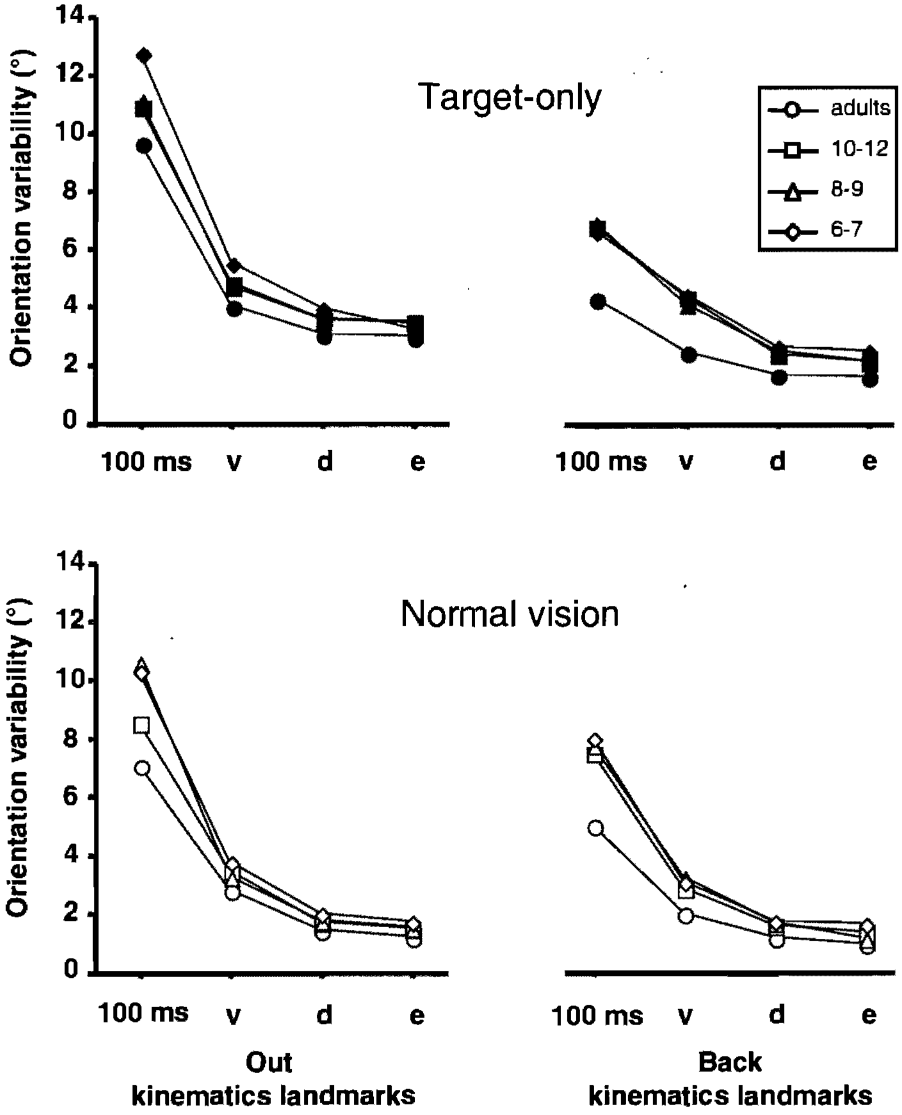


Figure 6


Target-only
Normal vision
Orientation variability (°)
0
2
4
6
8
10
12
14
adults
10-12
8-9
6-7
100 ms
v
d
e
Out
kinematics landmarks
Back
kinematics landmarks

ARTICLE SCIENTIFIQUE 3

Learning a new internal model of dynamic interfere with visual control

Isabelle Mackrous· Luc Proteau

Chapitre V

Learning a new internal model of limb dynamics interferes with the processing of visual information for movement planning and control

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Key words: movement planning, movement control, internal model, dynamics, manual aiming, learning, proprioception, visual feedback

Abstract

In the present study, we wanted to determine whether visual feedback would facilitate learning a new internal model of limb dynamics when a well-established internal model of limb kinematics is available. Participants performed a video aiming task with a 1.5 kg mass attached 25 cm laterally to the forearm, requiring them to learn a new internal model of limb dynamics. Vision of the cursor was available or not during this acquisition phase. Then, in a post-test, participants performed the task without visual feedback with or without the lateral mass. Participants developed a new internal model of limb dynamics regardless of whether or not visual feedback was available in acquisition. An important new finding of the present study was the observation that acquisition of a new internal model of limb dynamics interfered with the role usually played by visual feedback for the planning and control of goal-directed movements.

Learning a new internal model of limb dynamics interferes with the processing of visual information for movement planning and control

Goal directed movements require that the CNS performs a series of transformations so that information about one's hand and the target could be used to plan appropriate motor commands. These motor commands become finely tuned with practice, at least partially because of the development of internal models of movement kinematics and of movement dynamics.

Internal models of movement kinematics define reference axes for direction accuracy and a scaling factor between a set of motor commands and movement extent. In manual aiming movements, internal models of movement dynamics anticipate the consequences of biomechanical factors affecting the behavior of the arm, forearm, and hand and adapt the motor commands accordingly. Recently, Krakauer et al. (1999) proposed that kinematics and dynamics internal models develop independently from one another and that visual feedback does not facilitate the learning of dynamics model. In that study, participants performed out and back video-aiming movements between a fixed starting base and multiple targets located around it. Participants were asked to perform straight and uncorrected movements. In a first condition, visual feedback of the cursor was rotated 30° counterclockwise. Through practice, participants learned a new rotated reference frame and performed straight movements toward the targets. In a second condition, the location of the center of mass of the participants' forearm was experimentally modified by attaching a 1.5 kg mass laterally to the longitudinal axis of their forearm (see Fig. 1). Through practice, participants learned to model the new limb's dynamics created by the added mass and generated appropriate motor commands to overlap the out and the back portions of their movement. Participants submitted simultaneously to the above two experimental conditions performed the task as well as those submitted to one or the other condition, which led Krakauer et al. (1999) to conclude that practice resulted in the simultaneous development of independent internal models of limb kinematics and of limb dynamics. Moreover, and of particular importance for the present study, practicing the task in normal vision did not enhance learning in the "loaded" condition (see also Tong et al. 2002 for similar observations).

Modifying the inertial characteristics of the forearm by attaching a lateral mass to a manipulandum clearly requires that participants learn a new internal model of upper limb dynamics, at least to eliminate the large initial movement orientation bias that the added load creates. However, in the presence of visual feedback, any remaining bias should be detected quickly after movement initiation. For instance, in many recent experiments, it was shown that a sudden lateral displacement of the cursor moved by participants was quickly corrected for even if this cursor-jump was never consciously detected by the participants (Proteau et al. 2009; Sarlegna et al. 2003, 2004; Saunders and Knill 2003, 2004). Moreover, in Proteau et al. (2009; see also Körding and Wolpert, 2004) the cursor-jump occurred while the cursor was seen relatively far in the periphery of the retina (25° of visual angle). They showed that seeing the cursor for as little as 57 ms following the jump was sufficient to ensure quick and efficient correction for the cursor jump. This observation coupled with Saunders and Knill's (2003) finding that the delay to initiate a correction is constant regardless of the cursor-jump occurring at 25% or

50% of the movement trajectory suggests a near continuous monitoring of visual feedback. Because visual feedback generally results in better aiming accuracy than proprioceptive feedback alone (see Proteau, 1992 for a review), it is surprising that it played no role whatsoever in eliminating the bias caused by the added mass in Krakauer et al. (1999), eventually improving learning of a new internal model of limb dynamics.

Because participants had to learn simultaneously a new internal model of limb kinematics to counteract the 30° counterclockwise rotation of the visual feedback, Krakauer et al. (1999) observations might indicate that visually-based error detection and correction mechanisms might not be optimal for a new internal model of limb kinematics. Alternatively, these results might indicate that, although visual feedback can be used to ensure endpoint accuracy, learning of the new dynamical characteristics of the arm, ,because of the added mass, is solely based on the processing of proprioceptive feedback with no or minimal contribution of visual feedback. Our goal was to test the latter hypothesis.

To reach our goal, participants aimed at different targets while the inertial configuration of their arms was altered by attaching a 1.5-kg mass 25 cm laterally to the forearm (a "loaded condition"; see Fig. 1). This required that participants learned a new internal model of limb dynamics (Krakauer et al. 1999; Sainburg 2002; Sainburg et al. 1999), to reduce/eliminate initial movement orientation bias, but did not require learning of a new internal model of limb kinematics. Participants practiced this task in either a normal vision condition or in a target-only condition (only the starting base and target are visible). Following practice, participants performed two post-tests. In the first post-test, all participants performed the same task as in acquisition but in the target-only condition. Evidence of the processing of visual feedback by the normal vision group in acquisition would be obtained if: (a) they were more accurate/less variable in acquisition than the target-only group, (b) withdrawing visual feedback in post-test resulted in a significant increase in error/variability than late in acquisition. The second post-test was in all points similar to the first one, except that the participants performed the task in an unloaded condition. Withdrawing the load in this post test should result in large after-effects in the direction opposite to that created early in practice of the loaded condition, which is taken to represent that a new internal model of dynamics has been learned (Lackner and Dizio 1994; Shadmehr and Mussa-Ivaldi 1994). If learning of this new internal model of limb dynamics is not affected in any way by the presence of visual feedback then, the expected after-effect should not differ as a function of the availability or not of visual feedback during practice.

Method

Participants

Forty-eight participants aged between 20 and 30 years old took part in this experiment. They all reported normal or corrected to normal vision. They took part in a single thirty-minute experimental session. The Health Sciences Ethics Committee of the Université de Montréal has approved this study

Task and apparatus

The task was to move a computer's mouse-like device from a fixed starting position located close to the body toward a target located away from the body. The apparatus consisted in a table, a computer screen, a mirror, and a two-degree of freedom manipulandum. Participants sat in front of the table. The computer screen (Mitsubishi, Color Pro Diamond 37 inches) was mounted on a ceiling-support positioned directly over the table; the computer screen was oriented parallel to the surface of the table. Its image was reflected on a mirror placed directly beneath it and also parallel to the tabletop. The distance between the computer screen and the mirror was 18.5 cm while the distance between the mirror and the tabletop was 18.5 cm permitting free displacement of the manipulandum on the tabletop. The information presented on the computer screen was thus reflected on the mirror and was easily visible by the participant.

The tabletop was covered by a piece of Plexiglas. The manipulandum consisted of two pieces of rigid Plexiglas (43 cm) joined together at one end by an axle. One free end of the manipulandum was fitted with a second axle encased in a stationary base affixed to the tabletop. The other free end of the manipulandum was fitted with a small vertical shaft (length: 3 cm, radius: 1 cm), i.e., the stylus, which could be easily gripped by the participant. The participant's wrist was restrained and a Plexiglas sled supported his/her forearm (see Fig. 1). The sled had a rigid outrigger to which a 1.5 kg mass could be attached 25 cm laterally to the forearm. The starting base consisted of a piece of Plexiglas glued to the tabletop such that when the sled was positioned at the starting position, the stylus was located directly in line with the lateral center of the computer screen and the participant's midline. Each axle of the manipulandum was fitted with a 13-bit optical shaft encoder (U.S. Digital, model S2-2048, sampled at 500 Hz, angular accuracy of 0.0439°), which enabled us to track the displacement of the stylus online and to illustrate it with a 1:1 ratio on the computer screen. Moving the stylus away from the body in the frontal and sagittal planes resulted in an identical displacement of the cursor on the computer screen. The bottom of the stylus and of the optical encoder located at the junction of the two arms of the manipulandum was covered with a thin piece of Plexiglas. The working surface was lubricated at the beginning of each experimental session. It permitted participants to smoothly displace the stylus.

Procedures

Participants used their right dominant arm. They were asked to aim in a single motion (i.e., no stop and go or voluntary corrections) at a target located in line with their midline (0° target) or at 40° to its left (-40° target). The cursor (black, 3 mm in diameter) and the targets (black, 6 mm in diameter) were presented on a white background. The targets were located at 320 mm from the starting base.

Participants were asked to initiate their movement as they pleased following presentation of a target but were required to complete it in a movement time ranging between 480 ms and 620 ms (550 ms +/- 12.7%). Movement initiation was detected when the cursor was moved by 2 mm, whereas movement end occurred when the cursor was not displaced by more than 2 mm for a period of 100 ms. The procedure use to define movement endpoint made it difficult for the participants to use a "stop and go" strategy. During the acquisition phase of the experiment (see below), when movements were completed outside the target movement time bandwidth, the Experimenter reminded the participant of the target movement time. A movement time bandwidth is used to eliminate the possibility of different speed-accuracy trade-offs between the different conditions (Fitts 1954). Thus, in acquisition, differences in performance between the different conditions should mainly be expressed on the spatial components of the movements.

Participants performed four experimental phases. In all phases, the order of target presentation was randomized with the restriction that each target (i.e., 0° and -40° targets) was presented eight times in each successive block of 16 trials. At the beginning of each trial, all participants could see the cursor they had to move resting at the starting position and the target to be reached. Participants could not see their hand and arm during the duration of the experiment; they were located beneath the mirror reflecting the image illustrated on the computer screen.

The first two experimental phases were pre-test phases. For each one of the two pre-test phases, all participants performed 16 trials in the Target-only condition with no knowledge of results (KR). For the first pre-test, participants performed the task without the 1.5 kg mass (pre-test unloaded), whereas the 1.5 kg mass was attached to the outrigger in the second pre-test (pre-test loaded).

The third phase was an acquisition phase performed by all in the loaded condition. For this phase, participants performed 64 trials toward each one of the two possible targets. Participants were assigned randomly to different groups depending on the source of afferent information available during this phase. For the normal vision (NV) group, vision of the cursor was permitted for the whole duration of the movement, whereas for the target-only (TO) group, vision of the cursor was occluded as soon as it left the starting base. Following all acquisition trials, all participants received KR. Specifically, they were shown on the computer screen a figure illustrating the target they were aiming for and their movement's path. Participants were also verbally informed of their movement time in ms when it felt outside the target movement time bandwidth.

The last experimental phase was a post-test phase. It was performed by all in the Target-only condition with no-KR. Half of the participants in each visual feedback condition (i.e., NV and TO) performed 16 trials in the loaded condition, whereas the second half of the participants performed 16 trials in the unloaded condition.

Data reduction

The tangential displacement data of the stylus over time were first smoothed using a second order recursive Butterworth filter with a cut-off frequency of 10 Hz. The filtered data were then numerically differentiated once using a central finite technique to obtain the velocity profile of the aiming movement. To provide a quick feedback to the participant during acquisition, movement initiation was detected once the stylus had been moved by 2 mm, whereas for the main analyses, movement initiation was defined as the moment at which the tangential velocity of the cursor reached 10 mm/s. The difference in procedures used to detect movement initiation during acquisition and in the main analyses explains why the movement times to be reported below are longer than the target movement time used during acquisition. Movement endpoint was detected when the cursor was not displaced by more than 2 mm in a time frame of 100 ms.

Dependent variables

To illustrate how movements progressed toward the target, movement length and orientation were determined at every 5% of normalized movement time. Movement length was the length of the vector joining the starting base and the cursor at each temporal landmark. Movement orientation was defined as the angular difference between a reference vector joining the starting base and the target and that joining the starting base and cursor at each temporal marker. A positive value indicates a bias to the right of the reference vector, whereas a negative value indicates a bias to the left of the reference vector. Wang and Sainburg (2004) have shown that performing a manual aiming movement in a condition much like our loaded condition created an orientation bias early after movement initiation. Within-participant variability was computed for movement length and movement orientation at each temporal landmark. This dependent variable represents the within-participant standard deviation of the cursor location at each temporal landmark.

Statistical analysis

To facilitate reading of this article, the statistical analyses that were computed are defined at the beginning of each subsection of the results presentation. Geisser-Greenhouse correction was applied when Epsilon value was less than 1. All significant main effects involving more than two means were broken down using Dunn's technique. Significant interactions were broken down by computing simple main effects, which were followed by post hoc comparisons when they involved more than two means. All effects are reported at $\underline{p} < .05$ (adjusted for the number of comparisons).

Results

Temporal data

To ensure that speed accuracy trade-off did not change as a function of the different experimental conditions, movement time data were submitted to 3 distinct ANOVAS. First, they were submitted to an ANOVA contrasting 2 visual conditions (normal vision vs. target-only) x 2 experimental phases (pre-test unloaded vs. loaded) x 2 targets (0° vs. -40°), using repeated measurements on the last two factors. The second and third analyses were similar to the first but with one exception. In the second analysis, the experimental phases were early vs. late acquisition, whereas in the third analysis they were late acquisition vs. post-test.

Significant effect of target location was observed in all three analyses. In all cases, movement time was significantly longer for the -40° target than for the 0° target. In pre-test, this difference was larger in the loaded (862 ms vs. 815 ms) than the unloaded condition (816 ms vs. 790 ms), F(1, 44) = 5.6. Acquisition in the loaded condition, F (1, 43) = 156.8, did not change significantly what was observed in the pre-test loaded (866 ms vs. 807 ms, respectively), Finally, going from the acquisition phase to the post-tests significantly reduced the difference in movement time noted between the -40° and the 0° targets: post-test loaded (892 ms vs. 857 ms), F (1, 21) = 16.0, and post-test unloaded (840 ms vs. 832 ms), F (1, 20) = 24.8, respectively.

Pre-test, acquisition and post-test loaded

Movement extent

To determine how the added mass affected movement execution prior to practice with KR, mean movement length as well as movement length variability in pre-test were individually submitted to an ANOVA contrasting 2 experimental phases (pre-test unloaded vs. pre-test loaded) x 2 targets (0^{o} vs. -40^{o}) x 19 landmarks (10%, 15%, 20%, ...100% of relative movement time), using repeated measurements on the last three factors.

At movement endpoint (Fig. 2a, left panel) the loaded condition resulted in significant longer movements than the unloaded condition. For the -40° target, this difference between the loaded and unloaded conditions was significant at all kinematic landmarks, whereas it became significant at 85% of movement time for the 0° target. This is supported by a significant experimental phases x targets x landmarks interaction, $\underline{F}$ (18, 792) = 7.7. Also, as illustrated in Fig. 2c, (left panel) movement length was significantly more variable for the loaded than the unloaded condition, $\underline{F}$ (1, 44) = 13.1.

Our next step was to determine how practice with KR in both the normal vision and the target-only conditions helped participants control their movements in the loaded condition. Movement length and movement length variability data were individually submitted to an ANOVA contrasting 2 visual conditions (normal vision vs. target-only) x 2 blocks of acquisition (first block vs. last block of acquisition) x 2 targets (0^{o} vs. -40^{o}) x 19 landmarks (10%, 15%, 20%, ...100% of relative movement time), using repeated measurements on the last three factors.

As illustrated in Fig. 2a (middle panels), movement endpoint did not differ significantly as a function of the feedback condition or practice, ps > 0.11. However, movement unfolded very differently in the two visual feedback conditions. First, up to a relative time of 45%, movement length (see Fig. 2b) was significantly longer in the normal vision than in the target-only condition, F (18, 774) = 3.7. Second (see Fig. 2c, middle panels), for the first part of the movement, movement variability increased with movement extent. Then, in the normal vision condition, there was a sharp and sudden decrease in movement variability that began at approximately 60% of relative movement time. This decrease in variability did not occur in the target-only condition. Rather, variability leveled-up at around 75% of relative movement time. This is supported by a significant vision conditions x landmarks interaction, F (18, 774) = 34.8. Both these observations suggest that visual feedback permitted participants to modulate the second portion of their movement.

The above interpretation would be supported if it was shown that withdrawing visual feedback in post-test result in a decrease in movement length accuracy and an increase in variability. To test this prediction the dependent variables were submitted to an ANOVA contrasting 2 visual conditions (normal vision vs. target-only) x 2 experimental phases (last block of acquisition vs. post-test loaded) x 2 targets (0° vs. -40°) x 19 landmarks (10%, 15%, 20%, ...100% of relative movement time), using repeated measurements on the last three factors.

Although we observed that participants who practiced in the normal vision condition overshoot the target by 12 mm when transferred in target-only condition, this difference was not significant ($p = 0.09$), and no significant difference was noted between the normal vision and target-only groups. However, the sharp decrease in extent variability that had been noted in acquisition for the normal vision group no longer took place in the post-test loaded. Rather, movement variability kept increasing up to 75% of relative movement time and leveled-off thereafter. At movement endpoint, for the normal vision group, extent variability was approximately 4 times larger (17.2 mm vs. 4.4 mm, respectively) in the post-test loaded than late in acquisition. In addition, endpoint variability of the normal vision group in the post-test loaded was significantly larger than that of the target-only group. Finally, withdrawing KR to the target-only group in post-test loaded did not have any significant impact on movement length variability (see right panel of Fig. 2c). These effects are supported by significant vision conditions x experimental phases x landmarks interaction, $F\ (18, 360) = 7.8$.

Movement orientation

We used the same statistical analyses as in the preceding section, but with one exception. Because the effects of the added mass on movement direction largely differed for the two target locations, separate analyses were computed for each target.

In the pre-test unloaded, movements slowly deviated to the left as they progressed toward the target. For both targets, movements ended approximately 3° to the left of the target. Adding a lateral mass in the pre-test loaded condition, resulted in an initial bias to the right of the -40° target (~ 4°) and to the left of the 0° target (~ 10°). This initial bias gradually dissipated as movement progressed so that by 75% of relative movement time, no significant orientation difference was observed between the two types of trials. This indicates that the initial biases caused by the added mass were eliminated during movement execution.

Movement orientation variability data are illustrated in the left panel of Fig. 3c. Orientation variability decreased for both the loaded and unloaded pre-tests up to 65% of movement time and leveled-off thereafter. This is supported by a significant main effect of landmarks, F (18, 792) = 209.5. Also, a main effect of experimental phases, F (1, 44) = 34.3 revealed that orientation variability was lower during pre-test loaded than unloaded.

Fig. 3a and b illustrate that practice in the loaded condition resulted in a significant reduction in the initial bias noted in pre-test for both the -40° and 0° targets. The biases noted soon after movement initiation were gradually corrected for as movement unfolded. For both the -40° and the 0° targets, this is supported by a significant experimental phases x landmarks interactions, F (18, 774) = 15.6, and 5.3, respectively. No effect of visual feedback was noted on orientation bias, F (1, 43) = 0.17, p = 0.7 and F(1, 43) = 2.6, p = 0.12, respectively. However, this null effect is misleading. The left panel of Figure 4 illustrates orientation bias for each participant. Clearly, visual feedback permitted all participants to end their movement close to the target. Endpoint bias ranged between -0.76° to 0.35° (SE: 0.06) for the normal vision group. On the contrary, most participants in the target-only group still showed a relatively large bias at movement endpoint; this bias ranged between -3.52° to 1.84° (SE: 0.25). A supplementary analysis computed on the absolute value of the orientation bias at each landmark revealed a smaller absolute bias for the normal vision group starting at 75% of relative movement time, F (1, 43) = 4.9.

As illustrated in Fig. 3c (middle panel), within-participant orientation variability gradually decreased as movement unfolded, F (18, 774) = 208.8. This decrease invariability was significantly larger for the normal vision than for the target-only group, F (1, 43) = 34.5. Going from late acquisition to the post-loaded condition did not modify how the orientation bias noted soon after movement initiation gradually decreased as movement unfolded. As illustrated in Fig. 3a and b (right panels), this was true for both the -40° and 0° targets, and for both visual feedback conditions, $p > .10$. However, as shown in Fig. 4 (right panel), the fine tuning of movement orientation that was observed for all participants of the normal vision group late in acquisition is no longer present in the post-test loaded condition. For this group, a supplementary analysis revealed a significant increase in absolute constant bias between 75% to 100% of relative movement time when going from late acquisition to the post-test loaded, $p < .01$. Participants in the target-only group behave similarly late in acquisition and in the post-test loaded. No difference in absolute constant bias was noted for this group when going from late acquisition to transfer, $p > 0.6$.

Concerning within-participant orientation variability, going from late acquisition to the post-test loaded had no significant consequence for the target-only group. However, for the normal vision group, the slow and gradual decrease in orientation variability noted late in acquisition no longer took place. Rather, within-participant variability gradually decreased from movement initiation to 50% of relative movement time and leveled-off thereafter. This resulted in larger orientation variability in post-test than in acquisition for the normal vision group. This is supported by a significant visual conditions x experimental phases interaction, F (1, 43) = 5.7.

Internal model of limb dynamics

As previously presented, adding the lateral load in pre-test resulted in a significant initial bias to the right of the -40° target and to the left of the 0° target. During acquisition, we noted a significant reduction of this initial bias for both targets, regardless of the visual condition. For the target-only group, in agreement with Krakauer et al. (1999), this reduction of the initial bias likely reflects the learning of a new internal model of dynamics. For the normal vision group, this reduction in the initial orientation bias also likely reflects learning of a new internal model of limb dynamics. This is so because the influence of visual feedback needs at least (100 ms or 20% of relative time in the present study; see Carlton, 1992 for a review of visual processing delay) to result in significant trajectory changes. However, in comparison to the target-only group, visual feedback permitted participants to reduce significantly their orientation bias and both their orientation and extent variability for the last half of the movement. Therefore, it could be that the internal model of limb dynamics developed through practice differed for the target-only and the normal vision groups. For the target-only group, this model might ensure that movement progressed as intended for its entire duration. For the normal vision group, this model might ensure that the movement is initiated as planned, whereas visual feedback ensures optimal endpoint accuracy. To test this hypothesis, the dependent variables were individually submitted to an ANOVA contrasting 2 visual conditions (normal vision vs. target-only) x 2 experimental phases (last block of acquisition vs. post-test unloaded) x 2 targets (0° vs. -40°) x 19 landmarks (10%, 15%, 20% ...100% of relative movement time) using repeated measurements on the last three factors. For the movement orientation data, separate analyses were computed for each target.

Movement extent

Withdrawing the lateral mass in the post-test unloaded had a significant impact on movement length and on movement length variability (see rightmost panel of Fig. 2a, b and c). For both the target-only and the normal vision groups, going from the last block of acquisition to the post-test unloaded resulted in a significant increase in movement length and in movement length variability. This is supported by a significant main effect of experimental phases, $\underline{F}$ (1, 20) = 23.1 and $\underline{F}$ (1, 20) = 11.4 for movement length and movement length variability, respectively.

Movement orientation

Unloading the manipulandum also had a significant impact on initial bias. This is illustrated in the rightmost panel of Fig.3a, b and c. Concerning the orientation bias, movements were initially biased to the left of the -40° target and to the right of the 0° target (-12° and +3°, respectively). These biases that are opposite in direction to those observed late in acquisition gradually decreased as movement unfolded. This is supported by significant experimental phases x landmarks interactions, $\underline{F}$ (18, 378) = 70.3 and 64.5, for the -40° and 0° targets, respectively. As illustrated by the initial orientation bias of 5 typical participants (in Fig. 5), withdrawing the lateral mass resulted in similar aftereffect for both normal vision group and target-only group, $\underline{p} > 0.12$.

Finally, within-participant variability (Fig. 3c) significantly increased between late acquisition and post-test unloaded for the normal vision group and for the target-only group, $\underline{F}$ (1, 22) = 13.3, $\underline{p} = 0.01$. However, the most striking aspect of these results is the similarity of the within-participant variability data for the normal vision and target-only groups in the post-test unloaded. For both groups, there was a large decrease in orientation variability up to approximately 70% of relative movement time, at which point in leveled-off, $\underline{F}$ (18, 396) = 105.7, $\underline{p} < 0.01$.

Discussion

Our first goal was to determine whether visual feedback intervenes when learning a new internal model of limb dynamics. To reach our goal we experimentally displaced the center of mass of the participants' forearm, thus altering movement dynamics. On early exposure to this experimental condition (pre-test loaded), the participants' initial hand path deviated significantly from that observed in a control condition (pre-test unloaded). Thus, participants had difficulties planning their movements to counteract the effect of the added mass (Krakauer et al. 1999; Sainburg et al. 1999; Sainburg 2002; Wang and Sainburg 2004) and a new internal model of dynamics had to be learned. To establish the contribution of visual feedback when learning this internal model of limb dynamics, participants who practiced the task in normal vision were compared to participants who practiced the task in a target-only condition.

Online control

The results of both the pre-test loaded and the acquisition phases concur to show that proprioceptive feedback alone permitted participants to correct their movement for the relatively large orientation error caused by the addition (pre-test loaded and acquisition) or the withdrawal (post-test unloaded) of the 1.5 kg mass attached to the manipulandum when vision was not available. Even in pre-test, the large orientation error noted soon after movement initiation gradually dissipated as movement unfolded to reach the level of that observed for the control condition (pre-test unloaded). Thus, our results concur with previous observations (Ghez and Sainburg 1995; Krakauer et al. 1999; Scheidt et al. 2005; Shadmehr and Mussa-Ivaldi 1994; Tong et al. 2002; Sainburg et al. 1995; Sainburg et al. 1999; Wang and Sainburg 2004) indicating that proprioceptive feedback alone is sufficient to correct for large planning errors associated with a non optimal internal model of limb dynamics. Practice with KR permitted participants to reduce this initial orientation error indicating that participants learned a new internal model of limb dynamics, or update a pre-existing one. The large after-effects noted in the post-test unloaded fully support this position.

Nonetheless, the results of the present study showed that visual feedback was used to refine movement execution during acquisition. Specifically, during the acquisition phase, we observed a sharper and larger decrease in extent and orientation variability for the normal vision than for the target-only group that started approximately at mid-movement (see also Bédard and Proteau 2004; Proteau and Isabelle 2002; Mackrous and Proteau 2007 for a similar observation). In addition, the absolute orientation bias data revealed that movement endpoint was significantly closer to the target location in the normal vision than in the target-only condition. The latter observations indicate that visual feedback was used more effectively than proprioceptive feedback to reduce the planning bias resulting from the added mass. Could this more accurate source of afferent information facilitate or interfere with the development of a new internal model of limb dynamics?

Visual feedback is not involved in the learning of a new internal model of limb dynamics

During the acquisition and the post-test loaded experimental phases, movement extent and orientation did not differ much for the first half of the movements performed in normal vision or in the target-only condition. This suggests that movement planning was based largely on the same information for these two conditions. These sources of information were the static visual information concerning the starting position and the target (see Desmurget et al. 1998, for a review). Also, this suggests that for both the normal vision and target-only conditions, movement planning was based on the internal model of limb dynamics that was developed during practice as supported by the decrease in the initial movement orientation bias with practice.

If visual feedback had resulted in improved learning of the new internal model of limb dynamics, the normal vision group should have outperformed the target-only group, which was not the case. More importantly, in comparison to the target-only group, withdrawing the added load in the post-test should have resulted: (a) in a larger after-effect for the normal vision group if vision had facilitated learning of this new internal model of limb dynamics, or (b) in a smaller after effect for the normal vision group if vision had masked or interfered in any way with the processing of proprioceptive feedback for the learning of such a model. The similarity of results of the normal vision and the target-only groups in the post-test unloaded phase strongly invalidates both these hypotheses.

Proprioception was weighted more heavily than vision

Although visual feedback in acquisition permitted participants to be more accurate and less variable than the target-only group, withdrawing visual feedback in transfer had smaller detrimental effects on movement accuracy than what has been observed in a series of recent studies in which withdrawing visual feedback in transfer resulted in an increase in movement planning error (Proteau 2005; Proteau and Isabelle 2002), reduced modulation of early (Mackrous and Proteau 2007) and late movement trajectory (Elliott and Lee 1995; Khan et al. 2002, 1998; Mackrous and Proteau 2007; Proteau 2005; Proteau and Isabelle 2002, Tinjust and Proteau 2009). In the present study, withdrawing visual feedback in transfer had no significant impact on movement planning as evidenced by the very similar performance of the normal vision and target-only groups for the first half of their movement both in acquisition and in post-test.

In the same vein, Mackrous and Proteau (2007) showed that in a normal vision condition, participants produced a significantly larger peak acceleration than in a target-only condition, but that at the occurrence of peak velocity (approximately 50% of relative movement time) their movement was shorter than in the target-only condition. This observation suggested that visual feedback was used to modulate the output of the movement planning processes very soon after movement initiation. When visual feedback was withdrawn in transfer, peak acceleration remained as in acquisition for both the target-only and the normal vision groups. For the target-only group, the length of the movement vector at peak velocity remained as in acquisition, whereas it significantly increased for the normal vision group. Therefore, the modulation thought to take place early after movement initiation in the normal vision condition did not take place in transfer, ultimately leading to a large overshooting of the target in the normal vision condition (13%) but not in the target-only condition. In the present study, for the first 45% of relative movement time, movement was significantly longer in the normal vision than in the target-only condition, suggesting that visual feedback at least was not used as in Mackrous and Proteau (2007) to modulate movement extent soon after movement initiation. Similarly, although movement extent in transfer was approximately 4% longer than in acquisition for the normal vision condition, this difference was not significant. It seems that in the present study, vision did not permitted participants to modulate their movement trajectory soon after movement initiation.

Finally, as in previous work (Khan et al. 2002; Mackrous and Proteau 2007; Proteau 2005; Proteau and Isabelle 2002, Tinjust and Proteau 2009), during the acquisition phase of the present study we observed a large reduction of movement variability in the normal vision condition, most notably for the second half of the movement. This decrease in variability totally disappeared after the withdrawal of visual feedback. This indicates that visual feedback was used to modulate the late portion of the movement to ensure optimal endpoint accuracy.

Taken collectively, these results add to previous observations (Ghez and Sainburg 1995; Krakauer et al. 1999; Scheidt et al. 2005; Shadmehr and Mussa-Ivaldi 1994; Tong et al. 2002; Sainburg et al. 1995; Sainburg et al. 1999; Wang and Sainburg 2004) suggesting that visual feedback « *is unnecessary and does not enhance proprioceptive learning of the new internal dynamic model (Krakauer et al. 1999)* ». Specifically, we suggest that modifying movement dynamics as we did in the present study, modified the role usually played by vision for movement planning and control. Visual feedback no longer played an important role for updating movement planning processes and modulating one's movement during its first half. Rather, visual feedback was used only for updating the second half of the movement.

A likely explanation of these findings, which is line with recent observations (Contreras-Vidal 2006; Körding and Wolpert 2006; Sainburg et al. 2003; van Beers et al. 1999; van Beers et al. 2002), is that modifying movement dynamics resulted in the contribution of vision and of proprioception for movement planning and control to be weighted differently in the present study than in previous research (Körding and Wolpert 2006; Mackrous and Proteau 2007; Proteau 1992; Soucy and Proteau 2001; Tremblay and Proteau 1998; van Beers et al. 2002). Sober and Sabes (2003, 2005) suggested that the weighting of sensory signals depends on coordinate transformations that have to be performed by the CNS. Thus, when movement dynamics is not perturbed experimentally or otherwise, having the target and the cursor visible at all time results in vision being weighted more heavily than proprioception for movement planning and control. This would be so because the cursor and the target are presented in the same allocentric frame of reference. However, because the added (or withdrawn) load and its consequence on initial movement trajectory were likely detected more directly, earlier and perhaps even more accurately through proprioception than through vision (that would require transformation from an allocentric to an egocentric frame of reference), a minimization transformation hypothesis explains why proprioception was likely weighted more heavily than vision in the present study.

Conclusion

As in previous research, we showed that visual feedback is unnecessary for learning a new internal model of limb dynamics. A key finding of the present study is that, at least early in practice, learning of such a new internal model of limb dynamics reduces the reliance on visual feedback for movement planning and early control processes. A likely explanation of this finding is that the CNS weights more importantly the afferent information needing less transformation before it could be interpreted and acted upon movement execution.

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Figure captions

Figure 1 Participants performed the task from a starting position located in line with their midline. A sled, on which a 1.5 kg mass could be attached 25 cm laterally to the forearm, supported the participant's forearm. Small filled circles represent targets.

Figure 2 Movement length and movement length variability as a function of visual feedback, experimental phases and target location. *a)* and *b)* Practice with KR resulted in both the normal vision (open circle) and the target-only (filled circle) groups performing accurate movements. Withdrawing visual feedback and knowledge of result in post-test did not have any significant impact on movement length for both the normal vision and target-only groups. *c)* Movement length variability was larger in the target-only (filled circle) than in the normal vision (open circle) condition. Withdrawing visual feedback and KR in post-test resulted in an increase in variability for the normal vision group (open circle) but not for the target-only group (filled circle) during the post-test loaded. During the post-test unloaded, movement variability increased for both the normal vision and the target-only groups.

Figure 3 Orientation bias and orientation variability as a function of visual feedback, experimental phases and target location. *a)* and *b)* In pre-test, adding a lateral mass caused a large orientation bias that was eliminated during movement execution. With practice, participants reduced their initial bias. In the post-test loaded, withdrawing visual feedback and KR had no significant impact on orientation biases for both the normal vision (open square) and target-only (filled square) groups. In the post-test unloaded, large and equivalent aftereffects are observed for the normal vision and the target-only groups. *c)* Orientation variability decreased during movement execution, and more so for the normal vision than for the target-only groups. Orientation variability was larger for normal vision than the target-only group in the post-test unloaded.

Figure 4 Absolute orientation bias of all participants as movement unfolded during acquisition and post-test loaded. Visual feedback permitted all participants to converge accurately to the target.

Figure 5 Orientation bias of five typical participants as movement unfolded during acquisition and post-test unloaded. Withdrawing the lateral mass had similar impact on both normal vision and target-only group

Figure 1

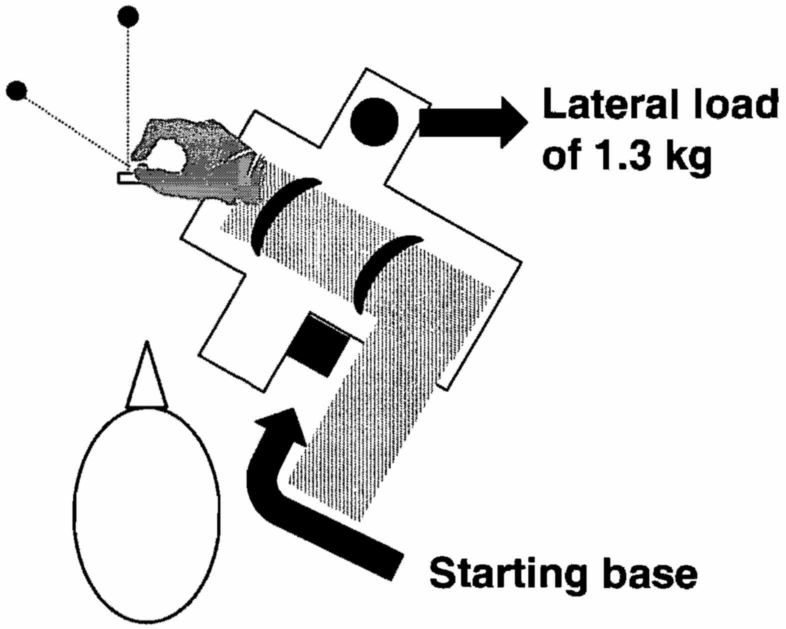


Figure 2

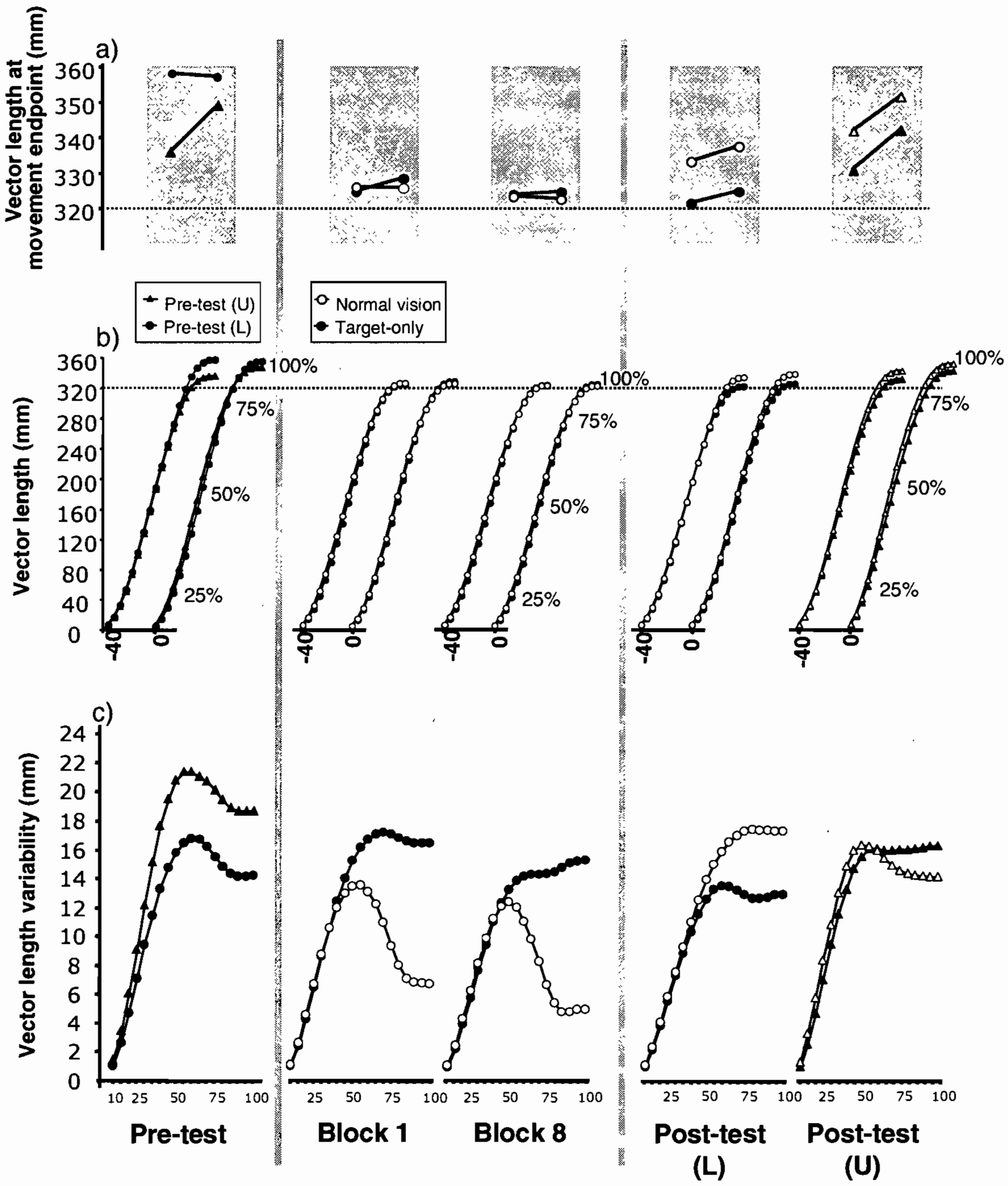

a)
Vector length at movement endpoint (mm)
360
350
340
330
320
Pre-test (U)
Pre-test (L)
Normal vision
Target-only
b)
Vector length (mm)
360
320
280
240
200
160
120
80
40
0
-40
0
100%
75%
50%
25%
c)
Vector length variability (mm)
24
22
20
18
16
14
12
10
8
6
4
2
0
10 25 50 75 100
25 50 75 100
Pre-test
Block 1
Block 8
Post-test (L)
Post-test (U)

Figure 3

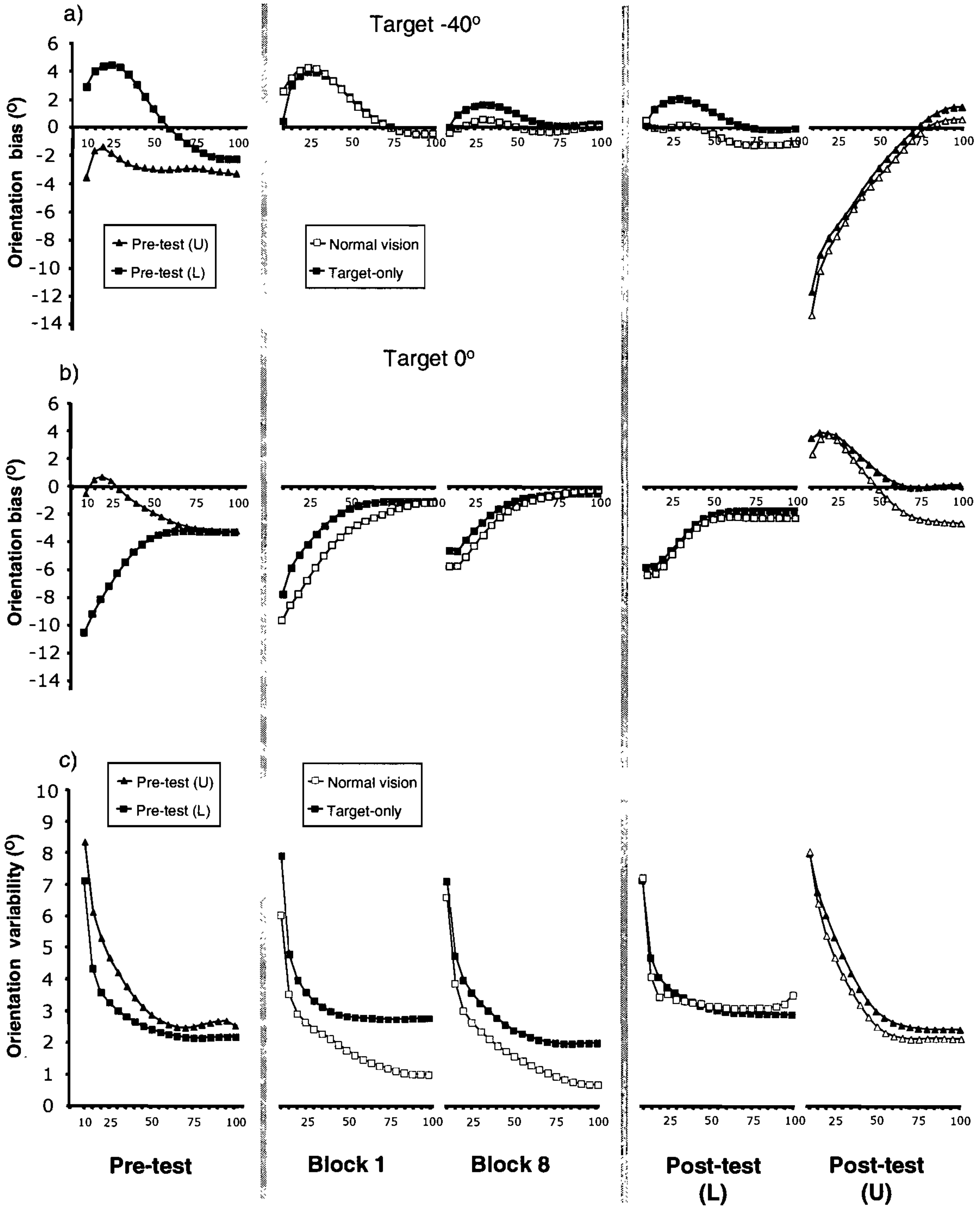

a)
Target -40°
Orientation bias (°)
6
4
2
0
-2
-4
-6
-8
-10
-12
-14
10
25
50
75
100
Pre-test (U)
Pre-test (L)
Normal vision
Target-only
b)
Target 0°
c)
Orientation variability (°)
10
9
8
7
6
5
4
3
2
1
0
Pre-test
Block 1
Block 8
Post-test (L)
Post-test (U)

Figure 4

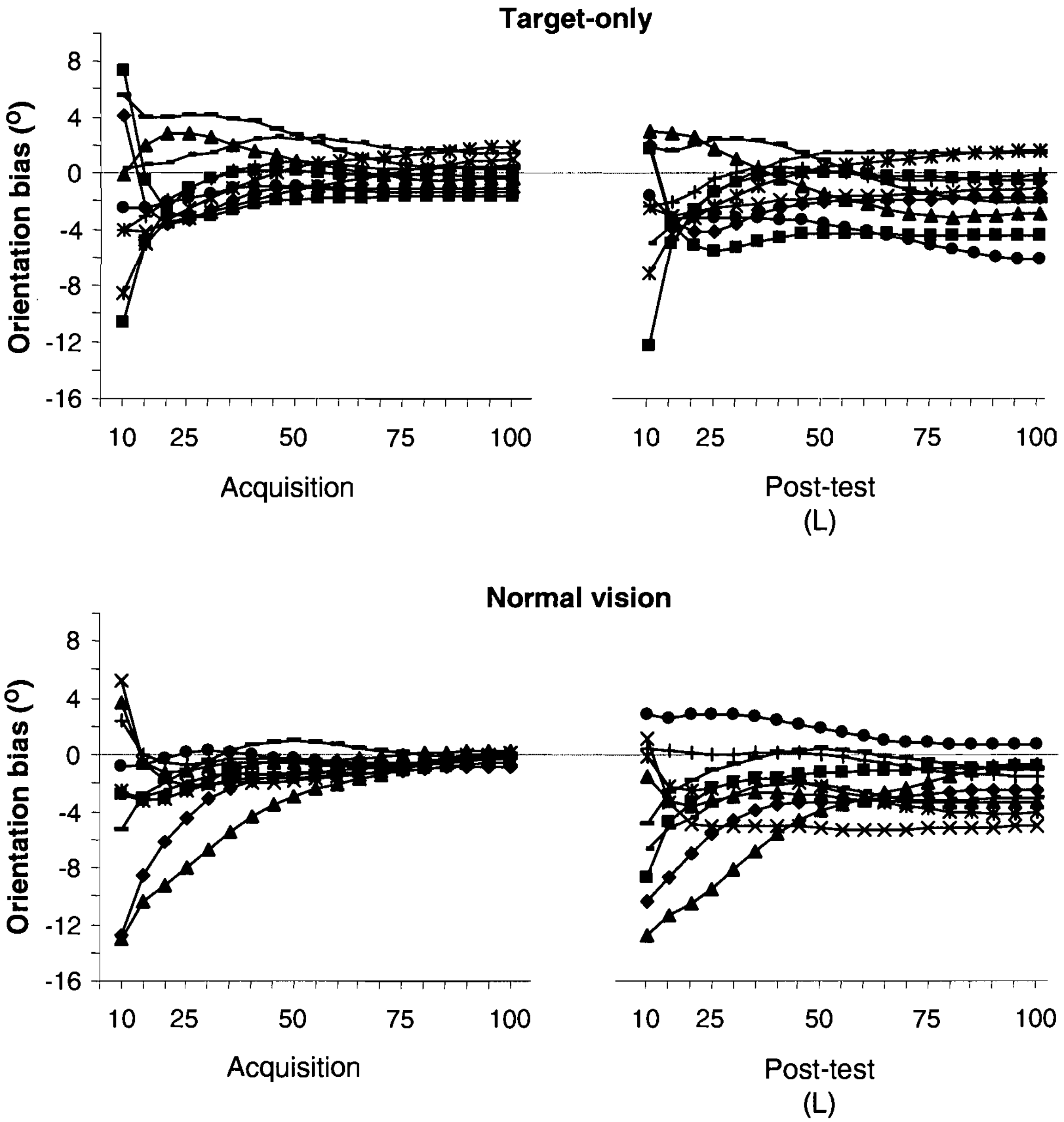
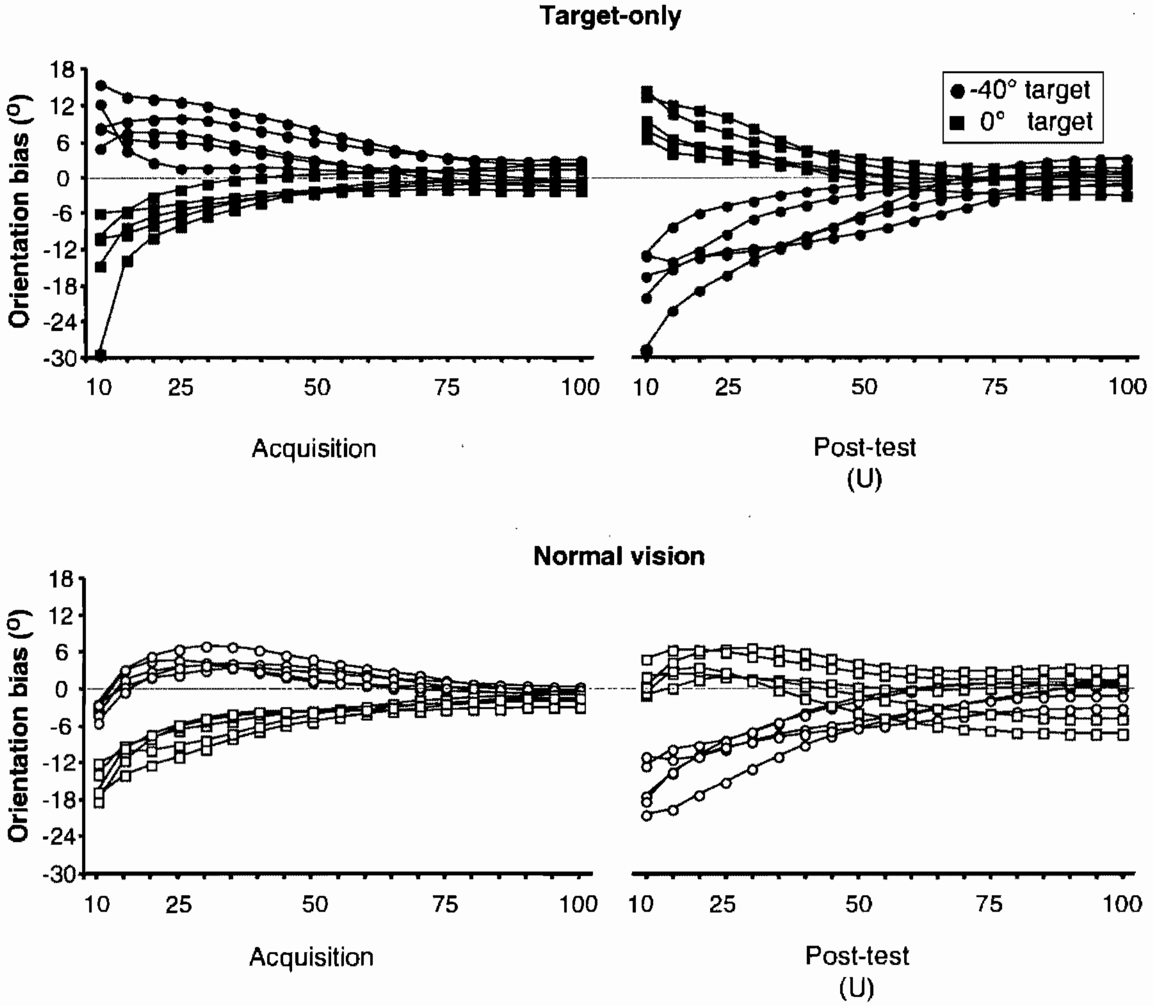

Target-only
Orientation bias (°)
8
4
0
-4
-8
-12
-16
10
25
50
75
100
Acquisition
Post-test
(L)
Normal vision
Orientation bias (°)
8
4
0
-4
-8
-12
-16
10
25
50
75
100
Acquisition
Post-test
(L)

Figure 5


Target-only
Orientation bias (°)
18
12
6
0
-6
-12
-18
-24
-30
10
25
50
75
100
Acquisition
Post-test
(U)
● -40° target
■ 0° target
Normal vision

Chapitre VI

Discussion générale

L'objectif général de cette thèse était de déterminer le rôle des informations visuelles pour le contrôle de la dynamique du mouvement. Plus spécifiquement, nous voulions déterminer s'il existait une interaction entre les mécanismes de modulation en ligne basés sur le traitement des afférences visuelles et ceux soutenant le contrôle de la dynamique du mouvement. La contribution des informations visuelles a été évaluée à l'intérieur de trois contextes dynamiques pour lesquels le modèle interne dynamique était bien établi ou en développement. Les mécanismes à l'étude étaient l'élimination des effets de l'anisotropie et l'apprentissage d'un nouveau modèle interne dynamique dans un paradigme d'adaptation ou de développement pendant l'enfance.

1 ÉTAT DE LA QUESTION

1.1 Sur la dominance des informations visuelles pour le contrôle du mouvement

Le vingtième siècle a été caractérisé par d'importantes découvertes quant à l'importance des afférences visuelles pour le contrôle du mouvement. Premièrement, les études ayant utilisé un paradigme de saut de curseur (Sarlegna et al. 2003; Saunders et Knill 2003; Sarlegna et al. 2004; Saunders et Knill 2004; Saunders et Knill 2005; Proteau et al. 2009) ont permis d'établir que la vision pouvait être utilisée rapidement pour corriger ou moduler la première impulsion de mouvement. Deuxièmement, plusieurs études ont démontré que la vision de la main ou d'un curseur lors de la réalisation d'un geste de pointage manuel favorisait une précision spatiale optimale comparativement à la vision de la cible et de la base de départ (Proteau 1992; Chua et Elliott 1993; Khan et

Franks 2003; Proteau 2005). Proteau et collaborateurs ont observé que l'avantage retiré de l'utilisation des informations visuelles (meilleure précision spatiale) résultait en une dépendance des participants à cette source d'afférence. Conséquemment, une grande détérioration de la précision spatiale était notée en transfert lorsque les afférences visuelles étaient retirées suite à une pratique modérée ou prolongée. Étant donné que les informations proprioceptives ne permettaient pas de préserver une bonne performance en transfert, ces auteurs ont proposé que les informations visuelles étaient traitées de façon prioritaire pour le contrôle du mouvement, et probablement au détriment du traitement des autres sources d'information sensorielle.

De récentes évidences neurophysiologiques supportent ce point de vue. Ainsi, Bernier et al. (2009) ont mis en évidence qu'un mécanisme d'atténuation/ suppression des informations proprioceptives prenait place lors de l'apprentissage d'une nouvelle représentation visuomotrice. Tôt dans l'apprentissage, ces auteurs ont observé une suppression substantielle des informations proprioceptives au niveau du cortex somatosensoriel primaire. Cette suppression de l'information proprioceptive permettrait de diminuer le conflit entre l'information provenant des systèmes visuel et proprioceptif (ces informations diffèrent lors d'une tâche d'adaptation visuomotrice). Dans la même veine, Hagura et al. (2007) ont observé qu'une dominance des informations visuelles – en vue de résoudre le conflit visuo-proprioceptif lors d'une perturbation- s'instaurait au niveau du cortex pariétal postérieur. Ultimement, le mécanisme de suppression de l'information proprioceptive favoriserait le contrôle visuel. Une question importante à l'étude dans cette thèse était d'évaluer si ce traitement prioritaire était réalisé à l'exclusion du traitement des informations proprioceptives lorsque la dynamique du mouvement est une caractéristique importante de la performance.

1.2 Sur le contrôle de la dynamique

Notre compréhension des mécanismes relatifs au contrôle de la dynamique du mouvement est basée sur des études ayant utilisé un paradigme d'adaptation à une perturbation dynamique (Shadmehr et Mussa-Ivaldi 1994; Ghez et Sainburg 1995; Krakauer et al. 1999; Shadmehr et Moussavi 2000). Ces auteurs ont démontré que pour contrer les effets d'une perturbation dynamique, les participants avaient développé un nouveau modèle interne de la dynamique du mouvement. Dans la même veine, Sainburg et al. (1995) proposaient que le contrôle des forces transmises lors d'un mouvement d'aller-retour (mouvement non perturbé) était basé sur un modèle interne dynamique. Les études effectuées chez des patients souffrant d'une neuropathie sensorielle (Sainburg et al. 1993; Ghez et al. 1995; Sainburg et al. 1995) ainsi que les études ayant évalué la généralisation de l'adaptation dynamique à différents espaces de travail (Sainburg et al. 1999; Shadmehr et Moussavi 2000) ont mis en évidence un rôle important des informations proprioceptives pour le développement ou la mise à jour du modèle interne de la dynamique.

1.3 Sur les modèles internes dynamiques chez l'enfant

La littérature chez l'enfant propose que l'intégration des conséquences biomécaniques d'un geste pour le contrôle de la dynamique du mouvement débute tôt pendant l'enfance (Konczak et al. 1995; Konczak et al. 2003). De plus, selon Jansen-Osman et al. (2002), le contrôle de la dynamique du mouvement chez l'enfant serait assuré par un modèle interne, tel qu'observé chez l'adulte. Cependant, ces auteurs suggèrent que ce dernier est imprécis et instable chez l'enfant.

1.4 Sur les afférences visuelles et le contrôle de la dynamique

La contribution des afférences visuelles pour le contrôle de la dynamique a été peu étudiée à ce jour. Toutefois, Ghez et al. (1995) ont démontré une amélioration de la performance chez des patients atteints d'une neuropathie sensorielle lorsque les afférences visuelles étaient disponibles. Outre la précision spatiale, ces auteurs ont mis en évidence que le contrôle de la dynamique était facilité en présence de vision chez ces patients. Il semble que la vision peut se substituer à la proprioception lorsque cette dernière est dégradée. Toutefois, l'utilisation des informations visuelles pour le contrôle de la dynamique, et plus particulièrement pour l'apprentissage d'un nouveau modèle interne, ne semble pas prioritaire chez les participants sains (Krakauer et al. 1999). Dans l'étude de Krakauer et al. (1999), les participants devaient apprendre un nouveau modèle interne dynamique afin de contrer les effets d'une masse latérale ajoutée au niveau de l'avant bras. Pour l'une des conditions expérimentales, les participants devaient simultanément apprendre ce nouveau modèle interne dynamique ainsi qu'un nouveau modèle interne cinématique (rotation de 30° de l'information visuelle). Les résultats ont révélé que la présence d'informations visuelles ne facilitait pas l'apprentissage du nouveau modèle interne dynamique, ce qui incita les auteurs à proposer que la vision n'intervenait pas dans l'apprentissage de ce type de modèle interne (voir Franklin et al. 2007, pour une observation similaire). Cependant, les évidences à cet égard étaient rares et peu convaincantes dans une situation où l'information visuelle n'était pas grandement sollicitée pour éliminer les biais dus à la rotation du feedback visuel.

2 APPORTS PRINCIPAUX DE CETTE THÈSE

2.1 Le traitement des afférences visuelles ne s'effectue pas au détriment du traitement des afférences proprioceptives

En premier lieu, nous nous sommes intéressés aux tâches dites plus naturelles (non perturbées), pour lesquelles le développement d'un nouveau modèle interne dynamique n'était pas requis. Contrairement aux prédictions antérieures sur la dominance des informations visuelles, nous avons démontré que le traitement de cette source afférence ne s'effectuait pas au détriment du traitement des informations proprioceptives. Plutôt, l'information proprioceptive restait entièrement disponible pour assurer le contrôle de la dynamique lors que l'exécution du mouvement. Nous proposons que pour des modèles internes cinématiques et dynamiques stables et bien établis, le mécanisme de suppression ou d'atténuation de l'information proprioceptive en présence de vision –du moins au niveau du cortex somatosensoriel primaire- ne prend pas place. Autrement, une détérioration du contrôle de la dynamique du mouvement sur la seule base des informations proprioceptives (condition de non vision ou de cible seulement) aurait due être observée en présence de vision. Tel n'était pas le cas chez l'adulte ainsi que chez l'enfant. La divergence entre nos résultats et ceux de Bernier et al. (2009) et Haruga et al. (2007) suggère que ce mécanisme de suppression ou d'atténuation est un mécanisme spécifique aux situations pour lesquelles un conflit émerge entre l'information provenant des systèmes visuel et proprioceptif, comme c'est le cas dans les tâches d'adaptation visuomotrice.

L'un des points majeurs soulevés dans cette thèse est l'observation d'un traitement distinct et simultané des informations visuelles et proprioceptives par le système nerveux central pour le contrôle de la cinématique et de la dynamique du mouvement, respectivement. D'une part, une importante modulation de l'étendue du mouvement sur la base des informations visuelles a été observée tôt après son amorce (expérience 1) et aussi pour favoriser une meilleure superposition des trajectoires d'aller et de retour (expérience 2). En plus des ajustements fins réalisés en fin de mouvement (Khan et al. 2002; Proteau et Isabelle 2002; Tinjust et Proteau 2009), cette modulation précoce sur la base de la vision semble suffisamment importante pour assurer une précision spatiale optimale. En fait, nous avons observé qu'en l'absence de contrôle visuel tôt dans l'exécution du mouvement (expérience 3) aucun avantage n'était retiré de la présence des informations visuelles sur le biais directionnel ainsi que sur l'étendue du mouvement.

D'autre part, nous avons observé que le contrôle des aspects dynamiques du mouvement s'effectuait largement sur la base des informations proprioceptives. Ainsi, dans la première expérience, l'élimination des effets de l'anisotropie était basée sur le traitement des informations proprioceptives même lorsque la vision était utilisée pour le contrôle en ligne de l'étendue du mouvement. Le retrait des informations visuelles en transfert n'a eu aucun impact sur le mécanisme responsable de l'élimination des effets de l'anisotropie. Dans la deuxième expérience, nous avons démontré que le contrôle des forces intersegmentaires était basé sur le traitement des informations proprioceptives et que ce mécanisme d'anticipation s'effectuait de concert avec le contrôle de la cinématique (basé sur le traitement de la vision).

Finalement, ce traitement simultané des informations visuelles et proprioceptives pour le contrôle de la cinématique et de la dynamique du mouvement, respectivement, est établi tôt pendant l'enfance. En effet, la disponibilité des informations visuelles n'a pas permis un meilleur contrôle des forces intersegmentaires chez l'enfant (expérience 2), mais a contribué de façon significative à la modulation en ligne de la trajectoire de retour.

Bien qu'au niveau neuroanatomique, les aires corticales responsables de cette ségrégation des informations sensorielles en fonction de la cinématique ou de la dynamique du mouvement ne soient pas bien connues, Filimon et al. (2009) ont observé que des régions différentes du cortex pariétal postérieur -et plus spécifiquement au niveau du *«parietal reach region»*- étaient associées au traitement des informations visuelles et proprioceptives. L'imagerie par résonance magnétique fonctionnelle a démontré que la région precuneus antérieure était prioritairement associée aux afférences proprioceptives tandis que la région supérieure au sulcus pariéto-occipital était associée au traitement des informations visuelles lors de l'exécution du mouvement. De plus, lorsque les différentes informations sensorielles correspondent bien l'une à l'autre , Hagura et al. (2008) ont noté une activation de l'hémisphère gauche du cervelet. Couplé avec l'activité du cortex pariétal droit, le cervelet participerait à l'intégration continue de l'information extéroceptive (visuelle) et intéroceptive (proprioceptive) pour la perception des mouvements de la main.

2.2 Le contrôle de la dynamique est basé sur le traitement de la proprioception

Tel que mentionné précédemment, nous avons observé un rôle important des informations proprioceptives pour le contrôle de la dynamique du mouvement. Qui plus est, nous n'avons trouvé aucune évidence attestant d'une contribution significative des informations visuelles pour ce type de contrôle, ce qui supporte les résultats antérieurs (Krakauer et al. 1999; Franklin et al. 2007). Ainsi, pour nos tâches plus naturelles, la présence des informations visuelles n'a pas interagit ou nuit à l'utilisation des informations proprioceptives pour le contrôle des forces intersegmentaires ou pour l'élimination des effets de l'anisotropie. De plus, nous avons mis en évidence que l'information visuelle ne contribuait pas au développement d'un nouveau modèle interne dynamique. La similarité des effets consécutifs observés pour les groupes « vision complète » et « cible seulement » supporte cette proposition. Bien que la vision ne contribue pas au développement d'un nouveau modèle interne dynamique, cette dernière était utilisée en cours de mouvement comme en témoignent les chutes de varaibilité notées à la fin du mouvement (voir Kranklin et al. 2007 pour une observation similaire). Toutefois, son rôle semble avoir été transitoire; la vision assurait une performance optimale, mais n'était pas intégrée dans la structure stable du mouvement.

Pour que la vision contribue de façon significative au contrôle de la dynamique, nous proposons que l'information proprioceptive doit être sévèrement dégradée tel que chez les patients déafférentés (Ghez et al. 1995; Sainburg et al. 1993, 1995) ou lors de l'observation (Mattar et Gribble 2005). Lors de l'observation d'un mouvement effectué dans un nouvel environnement dynamique, la proprioception n'étant pas sollicitée, il semble que l'information visuelle puisse assurer l'apprentissage d'un nouveau modèle interne dynamique. Toutefois, et tel qu'observé chez l'enfant, un traitement légèrement moins précis des informations proprioceptives ne semble pas suffisant pour permettre à la vision d'avoir un impact significatif sur le contrôle et l'apprentissage d'une nouvelle dynamique.

2.3 L'apprentissage d'un nouveau modèle interne engendre un changement dans le poids relatif des modalités sensorielles

Lors l'exécution du mouvement, le système nerveux central favorise le traitement de l'information sensorielle la plus pertinente en fonction de la demande de la tâche (Ghahramani et al. 1997; Legon et Staines 2006; Proteau et al., 1987; Staines et al. 2000; Tremblay & Proteau, 1998). Particulièrement, Legon et Staines (2006) proposent que l'importance accordée au traitement des afférences sensorielles les plus pertinentes est augmentée, tandis que l'importance accordée au traitement des afférences sensorielles moins pertinentes est atténuée. Dans notre manipulation (ajout d'une masse latérale, expérience 3), perturber les caractéristiques dynamiques du membre semble avoir augmenté l'importance attribuée au traitement des informations proprioceptives pour le développement d'un nouveau modèle interne dynamique, possiblement parce ce que c'est cette source d'afférence qui procure l'information la plus précise et la plus directe sur les interactions intersegmentaires (Sober et Sabes 2003, 2005). De plus, l'absence d'une modulation de l'étendue du mouvement tôt après son amorce sur la base de la vision suggère que le développement d'un nouveau modèle interne engendre un changement dans le poids des modalités sensorielles. L'information proprioceptive étant la source d'information la plus pertinente pour répondre à la demande de la tâche, son importance relative serait augmentée. Inversement, une moins grande importance serait accordée aux informations visuelles. Nous proposons que ce changement dans le poids relatif des modalités sensorielles interfère avec le contrôle visuel, dans une certaine mesure.

Conclusion

En conclusion, les paradigmes de perturbation semblent optimaux pour identifier la modalité sensorielle la plus pertinente au développement d'un nouveau modèle interne. Pour des tâches dites plus naturelles, notre analyse suggère que l'intégration multi sensorielles et la ségrégation des différentes sources d'information par le système nerveux central permet de prendre en charge plusieurs mécanismes en parallèle, sans interférence. Cet aspect du contrôle moteur est établi tôt pendant l'enfance.

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