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Executive Abilities For The Planning Of Sequential Motor Actions Performed Under Time And Space Constraints: A Visuo-Spatial Tapping Task

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Abstract (1684 characters)

In a constantly changing environment, executive abilities allow us to organize sensory information of multiple sources and to adapt to diverse situations while at the same time inhibiting inappropriate behaviors. Research on the executive functions (EFs) have historical roots on neuropsychology, with the description of frontal patients that were showing disruptions in organizing their daily behaviors independently of any impairment in long-memory, language or general intelligence. A wide range of neuropsychological tools is used today to evaluate executive abilities: Tower of London for planning, go-no-go for inhibition, etc. However, the classical tasks often present methodological limitations and they lack of correspondence between process and behavior. Furthermore, the field lacks of a compelling theory that make links between the EFs themselves. The present PhD work was an attempt to propose a novel task to assess the EFs in the place of the classical batteries of neuropsychological tasks. After offering an overview of the EF literature and presenting simple motor tasks that seem to target similar EFs to those described in neuropsychology (CH1), I present the spatial-tapping task as a challenging paradigm to understand the relationships between the different EFs (CH2), and its potential to be used in clinical settings (CH3). Then I show how a similar approach can be used to investigate how EFs intervene in the control of more complex motor sequences, e.g. bi-manual tasks (CH4). Overall, the results presented here support an embodied perspective of cognition with mental organization reflecting the way one plans motor sequences for adaptive behavior.

Keywords: timing, synchrony, spatial trajectory, attention, executive functions, pathology, bi-manual coordination, new technology

Résumé (1669 caractères)

Dans un environnement en constant changement, les fonctions exécutives (FE) nous permettent d'organiser l'information en provenance de sources multiples, de s'adapter à des situations sociales complexes et d'inhiber les comportements inappropriés. Les recherches sur le fonctionnement exécutif ont été initiées en neuropsychologie, après avoir observé chez des patients frontaux, des difficultés à organiser leurs comportements quotidiens sans pour autant présenter des difficultés de langage ou de mémoire. Un grand nombre de tests neuropsychologiques sont disponibles afin d'évaluer les FE. Cependant, ces tests sont souvent critiqués pour leur complexité et leur manque de validité de construction. Le champ des FE manque en réalité de modèles théoriques précis qui permettraient de décrire ces fonctions et leurs potentielles interactions pour le contrôle de comportements complexes. En conséquence, les tâches sont souvent construites de manière intuitive. Dans le présent travail de thèse, après revue d'un état de l'art sur les FE (CH1), je propose une nouvelle tâche, le spatial-tapping, qui pourrait être utilisée en remplacement des tâches classiques complexes (CH2). Je promeus également le potentiel de cette tâche à être utilisée dans des contextes cliniques (CH3). Je présente finalement comment les analyses réalisées pour le spatial-tapping afin d'étudier les FE peuvent être transférées à des situations motrices plus complexes, comme la coordination bi-manuelle (CH4). En conclusion, les résultats présentés dans ce travail de thèse sont en faveur de l'idée selon laquelle notre organisation mentale reflète la manière dont on organise nos mouvements.

Mots clés: temps, synchronie, trajectoire spatiale, attention, fonctions exécutives, pathologie, coordination bi-manuelle, nouvelles technologies

Résumé substantiel en français

Le fonctionnement exécutif peut être défini comme l'ensemble des fonctions mentales qui permettent la planification, la coordination et l'exécution de nos actions et activités quotidiennes. Dans la littérature, un nombre important de processus mentaux ont été proposés comme étant de potentielles fonctions exécutives, par exemple : le raisonnement logique, l'attention, la mémoire de travail, l'inhibition, la flexibilité mentale, etc. En parallèle, un grand nombre de tâches cognitives ont été développées pour mesurer l'un ou l'autre de ces processus mentaux. Cette multiplicité dans la définition des fonctions exécutives et des tâches qui sont censées les évaluer révèle un manque de cohérence dans la discipline, tant au niveau théorique, qu'expérimental.

Au cours de ce travail de thèse, plutôt que de suivre une approche déductive par laquelle une hypothèse concernant les mécanismes potentiellement impliqués dans la planification des activités est proposée est ensuite testée, j'ai adopté une approche inductive. Plus précisément, j'ai étudié comment les fonctions exécutives les plus admises dans la littérature intervenaient dans la planification et l'exécution d'actions simples produites les unes après les autres, selon des contraintes temporelles et spatiales. Ce travail a abouti à l'élaboration d'un paradigme expérimental unique permettant l'évaluation des fonctions exécutives principales, c'est à dire les fonctions de mise à jour en mémoire de travail, d'inhibition et de flexibilité mentale. Un résumé de l'état de l'art, ainsi que les résultats principaux obtenus sont proposés dans le présent synopsis.

Etat de l'art

L'étude du fonctionnement exécutif a débuté après avoir observé chez des patients souffrant de lésions cérébrales au niveau du cortex frontal, des difficultés à organiser leurs activités quotidiennes et à réaliser des tâches complexes, sans pour autant présenter des difficultés de mémoire, de langage ou de diminution de leur quotient intellectuel (Damasio, 1994; Harlow, 1868; Shallice & Burgess, 1991). Ces altérations subtiles ont permis de suggérer l'existence de fonctions mentales dédiées à l'organisation des activités complexes.

Les premières études scientifiques visant à comprendre le rôle des lobes frontaux dans la cognition humaine utilisaient les méthodes d'extirpation chirurgicale et de stimulation chez les animaux (chiens, singes), d'observation clinique chez les êtres humains. Ces études princeps décrivaient les lobes frontaux comme les régions “silencieuses” du cerveau (voir Luria, 1966). En effet, les changements comportementaux observés après extirpation ou stimulation chez les animaux n’étaient pas significatifs. Dans d’autres études des changements subtils avaient cependant été notés : après extirpation, certains chiens n’étaient plus capables de reconnaitre leurs maitres, étaient distrait par n’importe quel objet externe, ou se mettaient à tourner en rond sans raison (Bianchi, 1895, 1920, Bekhterev, 1907, Franz, 1907, tous cités par Luria, 1966, voir également Compston, 2012). Ces méthodes invasives ne permettaient pas vraiment de conclure quant au rôle précis joué par les lobes frontaux du cerveau. En effet, les changements observés chez les animaux pouvaient être interprétés comme étant la conséquence de l’extirpation d’une quantité significative de matière cérébrale. Par opposition, on pouvait également suggérer que les zones frontales permettaient de se concentrer sur des tâches précises sans se laisser distraire. Les premières observations cliniques de patients souffrant de lésions cérébrales frontales ont amené à des conclusions similaires. Il était difficile de savoir si les patients étaient plus impulsifs et moins attentifs parce qu’il leur manquait une quantité importante de matière cérébrale, ou si les lobes frontaux étaient en fait le siège permettant les fonctions d’attention.

Afin de faire évoluer ce champ de recherche, Luria (1966), a proposé d’adopter une méthode scientifique plus rigoureuse. Une série de tests neuropsychologiques très simples étaient réalisés par les patients. L’idée principale de ce chercheur était de proposer que les lobes frontaux permettraient la réalisation d’actions complexes plutôt que simples. Pour tester cette hypothèse, il proposa par exemple à des patients frontaux de répéter des phrases simples ou des séries de phrases, d’identifier des objets uniques ou d’identifier plusieurs objets les uns après les autres, de produire des rythmes simples ou des séquences de rythmes. En général, les patients étaient en difficulté dès que la tâche devenait plus complexe. Il se mettaient la plupart du temps à “persévérer”, c’est à dire à répéter la même action ou la même phrase indéfiniment sans être capable de passer à l’événement suivant (voir Luria, Pribram, & Homskaya, 1964). Ces observations ont permis à Luria de poser de premières hypothèses concernant le fonctionnement exécutif, hypothèses qui pour la première fois étaient soutenues par des résultats expérimentaux. Plus précisément, il suggéra que les lobes frontaux seraient le lieu de résidence de programmes ou de plans d’action, verbaux de nature, qui seraient utiles au contrôle, à la vérification et à la régulation des actions complexes. Les actions réalisées de manière habituelle seraient en fait constamment corrigées et optimisées par comparaison aux programmes activés au niveau des lobes frontaux. En d'autres termes, les lobes frontaux pourraient contenir un système d'autorégulation ou de feedback par lesquelles les formes de comportements complexes seraient élaborées à partir des actions habituelles.

L'approche neuropsychologique de Luria (1966), a fourni une base scientifique rigoureuse à l'étude du fonctionnement exécutif. Cependant les résultats obtenus ont été critiqués. En effet, Luria ne comparait pas les performances obtenues par ces patients frontaux à d'autres patients qui par exemple auraient subi des lésions de même envergure mais à d'autres localisations dans le cerveau (Shallice, 1988). De plus, les patients décrits présentaient des lésions qui n'étaient souvent pas circonscrites aux lobes frontaux. Finalement, chez certains patients présentant des lésions plus focalisées, les résultats n'étaient pas retrouvés (Canavan, Janota, & Schurr, 1985; Hécaen & Albert, 1978). Malgré ces défauts méthodologiques, des études utilisant d'autres tâches neuropsychologiques et les contrôles méthodologiques appropriés ont permis de confirmer les hypothèses initiales (Derouesné, Seron, & Lhermitte, 1975; Lhermitte, Derouesné, & Signoret, 1972). Un consensus a donc émergé autour de l'idée selon laquelle les lobes frontaux interviendraient dans la planification et la régulation des actions complexes. Ce consensus a notamment motivé Norman et Shallice (1986) à proposer un modèle de traitement de l'information pour illustrer les idées de Luria.

Ce modèle se divise en deux composantes principales : le Système Attentionnel de Supervision (SAS), le Gestionnaire d'Ordonnancement des Contraintes (GOC). Le GOC est le processus par lequel des routines d'action sont automatiquement activées, c'est-à-dire en fonction des stimuli présents dans une situation donnée. Par exemple, à la vision d'un verre empli d'eau, si j'ai soif, un comportement routinier pourrait être de saisir le verre et de le boire. Le SAS est le processus volontaire par lequel les routines peuvent être inhibées pour donner lieu à des comportements plus élaborés et adaptés au contexte social. Ce système est supposé avoir accès à une représentation générale de l'environnement, aux intentions de l'individu et à ces capacités cognitives. Si l'on reprenait l'exemple précédent, imaginons que le verre d'eau présent sur la table appartienne à mon interlocuteur. Je devrais donc inhiber une réponse motrice de saisie de ce verre et réorienter mes actions, par exemple, en allant chercher la bouteille d'eau présente dans mon sac. L'intérêt à utiliser un tel modèle réside essentiellement dans son pouvoir prédictif. En effet, indépendamment de nos connaissances en ce qui concerne le fonctionnement frontal, l'on pourrait se demander : que se passerait t-il en cas de défaillance du SAS? D'après Shallice (1988), deux prédictions peuvent être posées : (1) l'individu présenterait des difficultés à inhiber des comportements routiniers, en d'autres termes il serait distrait par n'importe quels objets présent dans son environnement, s'ils permettent de répondre à des demandes spécifiques de l'organisme, (2) l'individu présenterait des difficultés à activer un nouveau plan plus adapté à la situation. De manière intéressante ces deux difficultés sont retrouvées chez les patients frontaux : (1) de la distractibilité et de l'impulsivité, (2) des persévérations dans une règle donnée, sans possibilité d'en changer pour s'adapter à la situation.

Suite à la proposition de ce modèle, Shallice note que les difficultés liées aux persévérations ont été largement décrites et référencées dans la littérature. Des outils neuropsychologiques existent notamment pour tester ces fonctions (notamment le Wisconsin Card Sorting Test ou WSCT proposé par Grant & Berg, 1948; voir Milner, 1963 pour des études menées chez les patients frontaux). Par contre, très peu d'études ont été menées afin d'étudier la capacité des patients à élaborer et maintenir un plan verbal alternatif pour guider leurs actions, dans le cas où les routines comportementales doivent être inhibées. Pour parer à ce manquement, Shallice (1982) propose une nouvelle tâche, la Tour de Londres, adaptée du jeu de raisonnement logique la tour de Hanoï pour tester cette fonction. Dans cette tâche, trois sticks de bois dans lesquels des disques de différentes couleurs peuvent s'insérer sont disposés l'un à côté de l'autre et soutenus par une plateforme en bois. Les disques sont arrangés suivant une certaine configuration. La tâche du participant est de déplacer les disques pour atteindre une réalisation finale, en réalisant le moins de déplacements possibles. Afin de réaliser cette tâche, il est suggéré que les participants doivent construire par avance un plan stratégique verbal de nature, afin d'optimiser l'exécution motrice. Cette tâche a été testée chez un grand nombre de sujets souffrant de lésions cérébrales antérieures ou postérieures, droites ou gauches (Shallice, 1982). Les résultats ont révélé que les patients souffrant d'une lésion antérieure gauche uniquement présentaient des scores faibles dans cette tâche comparativement à tous les autres groupes. Ce résultat soutient donc l'hypothèse d'un déficit de planification de nature verbale (sachant que les capacités langagières sont connues pour être gérées par l'hémisphère gauche du cerveau) chez les patients souffrant de lésions frontales. Ce résultat, issu de prédictions posées à partir du modèle de Norman & Shallice (1982) confirme de par là même l'utilité de ce modèle pour la compréhension du fonctionnement exécutif. Cependant si l'on considère les tâches actuelles qui sont disponibles pour tester le fonctionnement exécutif, le WSCT pour les persévérations et la Tour de Londres pour les capacités de planification verbale, il apparait que l'une des fonctions clés proposée dans le modèle initial de Luria n'est pas testée. En effet, la capacité à vérifier et réguler l'information en temps réel par comparaison de l'action réalisée à une action planifiée (système de feedback) n'est pas évaluée. Dans cette perspective, le modèle de "mémoire de travail" proposé par Baddeley (Baddeley, 1986, 1992, 2012) apparait comme une version renouvelée du modèle de Norman et Shallice (1986).

Baddeley (1986) propose le modèle de mémoire de travail afin d'expliquer comment l'on pourrait traiter en parallèle plusieurs informations. Dans ce modèle, deux systèmes esclaves, le calepin visuo-spatial et la boucle phonologique permettraient un maintien à court terme de l'information. L'information en provenance de ces deux systèmes serait traitée, manipulée et coordonnée et au sein d'un système central d'exécution. Le paradigme clé utilisé par Baddeley pour tester les prédictions de son modèle est celui de la double tâche. Une tâche principale complexe (tâche de raisonnement, de compréhension ou d'apprentissage) est réalisée en même temps qu'une tâche secondaire de maintien de l'information à court terme et l'on mesure l'impact de la tâche secondaire sur la tâche principale. Cette approche a notamment permis de montrer comment le système central et les systèmes esclaves pouvaient agir conjointement pour la réalisation de tâches complexes (pour un exemple voir Robbins et al., 1996). Cependant, cette approche n'a pas permis d'en connaitre davantage sur le rôle joué par le système central d'exécution. Pour Baddeley, ce système agirait exactement à la manière d'un SAS (Norman & Shallice 1986). Baddeley lui même admet que les fonctions précises desservies par ce système restent imprécises. Ce système est un "fourre-tout" : tout ce qui n'est pas traité par les systèmes esclaves est traité au niveau du système central d'exécution, notamment, l'attention sélective, la coordination multitâche, l'inhibition des réponses dominantes, la récupération en mémoire de travail. Baddeley suggère également de remplacer le concept de "syndrome frontal" par celui de "syndrome dysexécutif" (voir Baddeley, 1996). Cette approche davantage fonctionnelle qu'anatomique permettrait notamment de laisser plus de liberté aux études centrées sur l'exploration du système central d'exécution, système dont le fonctionnement pourrait requérir d'autres régions cérébrales que les seules zones frontales.

L'étude plus spécifique des fonctions du système central d'exécution démarre avec

Miyake (2000). Une approche empirique basée sur l'analyse statistique des relations existant entre différents types de tâches exécutives est proposée. En effet, il existe désormais dans la littérature un grand nombre de tâches qui permettent de tester le fonctionnement exécutif, par exemple le WSCT, la Tour de Londres, ou la tâche de génération aléatoire de nombres proposée par Baddeley (voir Baddeley, 1996). Ces tâches sont impures dans le sens ou d'autres fonctions non-exécutives de nature sont nécessairement engagées (par exemple, les fonctions desservies par les systèmes esclaves) (Burgess, 1997; Phillips, 1997). De plus, ces tâches sont censées mesurer des aspects différents du fonctionnement exécutif, suggérant que le fonctionnement exécutif est modulaire de nature. Cependant, certaines fonctions semblent se chevaucher au travers des tâches. Par exemple, des chercheurs ont suggéré que l'ensemble des tâches classiques pouvaient engager une fonction d'inhibition (Goel & Grafman, 1995). Ainsi, le fonctionnement exécutif ne serait pas modulaire mais unitaire et les différences mesurées entre les tâches seraient principalement dues aux composantes non-exécutives qui diffèrent entre les différentes tâches. Afin d'aller plus loin dans la compréhension du fonctionnement exécutif, Miyake (2000) a proposé de réaliser une analyse statistique des variables partagées ou latentes entre différentes tâches. Trois types de tâches ont été prédéfinies : les tâches de mise à jour en mémoire de travail, d'inhibition et de flexibilité mentale. Des tâches "simples" sont dans un premier temps dissociées de tâches plus complexes. En effet, le problème de la complexité des tâches a également été montré dans la littérature (Rabbitt, 1997). Certaines tâches comme le WSCT pourraient être réalisées de plusieurs manières différentes : par exemple, via une stratégie centrée sur l'inhibition ou à partir d'une stratégie centrée sur les transitions entre règles consécutives (flexibilité). D'après les critères de Miyake (2000), les tâches simples n'engageraient que l'une des trois fonctions exécutives prédéfinies, alors que les tâches complexes pourraient en engager plusieurs. Pour chacune des trois fonctions exécutives, trois tâches simples sont réalisées par les participants (neuf tâches en tout), des tâches plus complexes sont réalisées dans un second temps. Les résultats de l'analyse des variables latentes a permis de révéler que les tâches simples censées mesurer la même fonction exécutive étaient bien corrélées entre elles et étaient significativement moins corrélées aux tâches constituant les autres ensembles, suggérant une indépendance entre ces trois fonctions exécutives. Cependant, l'analyse a révélé qu'un facteur commun était partagé entre les trois tâches. Finalement, les tâches complexes reflétaient bien la combinaison de plusieurs facteurs indépendants de nature. Ces résultats ont permis de conclure à une relative indépendance des fonctions desservies par le système central d'exécution, avec cependant le partage d'un facteur commun. A partir de ce travail, les recherches scientifiques ont été orientées vers la recherche de ces facteurs partagés par les trois principales fonctions exécutives de : mise à jour en mémoire de travail, flexibilité mentale et inhibition.

Des études supplémentaires menées par l'équipe de Miyake qui comparaient notamment des jumeaux dans neuf tâches exécutives simples (trois par fonction) ont permis de révéler que le facteur commun était largement héritable. De plus les fonctions les moins partagées par les jumeaux étaient les fonctions de flexibilité mentale et de mise à jour en mémoire de travail (Friedman, 2008). Des études longitudinales, dans lesquelles les capacités d'inhibition à l'enfance étaient comparées au développement des compétences exécutives à l'âge adulte ont permis de confirmer que ce facteur commun était l'inhibition. En parallèle, des positions ont été prises concernant l'implication de fonctions sous corticales dans le fonctionnement exécutif. Miyake (2012) suggère que le modèle "Cortex Préfrontal-Ganglions de la base-Mémoire de travail" (Prefrontal-cortex Basal-ganglia Working Memory, PBWM), proposé par O'reilly & Frank collègues (2012), pourrait être un modèle biologique plausible pour le fonctionnement exécutif. Des études en provenance d'autres champs de recherche, ont également mis en évidence, l'importance des ganglions de la base, et notamment du striatum dans la compréhension du fonctionnement exécutif (Cools, 2006, 2011). Plus précisément, à partir d'études génétiques (Colzato et al., 2010), et d'études cliniques de patients souffrant de la maladie de Parkinson (Cools, 2006), des corrélations inverses ont été révélées entre les compétences de flexibilité mentale et de mise à jour en mémoire de travail. Autrement dit, les sujets présentant de bonnes compétences en mise à jour en mémoire de travail présenteraient plus de difficultés à adopter un comportement flexible et vice versa.

En résumé, les connaissances théoriques concernant le fonctionnement exécutif ont évoluées de manière significative ces dix dernières années. Les études réalisées ont permis de révéler l'existence de deux fonctions exécutives indépendantes et opposées : la mise à jour en mémoire de travail, la flexibilité mentale. Ces fonctions partageraient à un certain degré une fonction générale d'inhibition. Des fonctions sous-corticales seraient également engagés dans le fonctionnement exécutif. Ces conclusions ont abouti suite à la mise en œuvre d'études de grande envergure, soutenues par des analyses statistiques poussées, mais également à partir d'études cliniques ou d'approches génétiques. Cependant, un problème persistant n'a pas été résolu : le problème de l'évaluation des fonctions exécutives à un niveau individuel. Même les tâches les plus simples (telles que définies par Miyake et al., 2000) restent impures, et engagent chaque fois des mécanismes non-exécutifs différents. Dès lors qu'il s'agit de comparer les compétences exécutives dans les trois principales fonctions exécutives, l'interprétation des résultats s'avère difficile (Voir Charlot et al. 2005, Clarys et al. 2009), avec une tendance dans la littérature à suggérer des déficits exécutifs globaux suite à l'évaluation neuropsychologique du fonctionnement exécutif. Par exemple dans le vieillissement normal ou dans la schizophrénie, toutes les fonctions exécutives seraient altérées. L'objectif principal de ce travail de thèse a été de proposer une nouvelle tâche qui ne serait ni complexe, ni impure afin de mesurer le fonctionnement exécutif.

Méthode et Résultats principaux

J'ai tout d'abord noté que des tâches très simples étudiées notamment dans le domaine du contrôle moteur pouvaient engager des fonctions de mise à jour en mémoire de travail et de flexibilité mentale, respectivement les tâches de production de rythmes (finger tapping) et de dessins de cercles (circle drawing). En effet, la production d'un rythme précis dans le temps, demande que l'on maintienne un référentiel de temps à suivre en mémoire à long-terme, que l'on maintienne de manière concurrente un représentation de l'intervalle de temps produit en mémoire de travail, et que l'on corrige finalement en retour les actions produites lorsqu'elles s'éloignent du référentiel à suivre (voir Treisman, 1963). Dessiner un cercle dans l'espace, par exemple dans le plan transversal et par un contrôle combiné du bras et de l'index, n'est pas une tâche motrice aussi simple qu'il pourrait paraître. Notamment, lorsque les contraintes de la tâche imposent la réalisation d'un mouvement continu. En effet cette action peut-être subdivisée en deux sous actions, c'est à dire, un premier mouvement d'extension, suivi d'un mouvement de flexion du bras (si l'on produit le cercle dans le sens antihoraire). Les mouvements de flexion et d'extension impliqués dans ce geste sont réalisés à partir de muscles différents, qui s'activent selon des patrons de forces et des délais neuromusculaires différents. Autrement dit, ils vont engager des programmes moteurs différents. Ainsi, afin de produire un geste fluide et gracieux dans l'espace, des stratégies cognitives vont être requises afin de grouper deux patrons d'action biomécaniquement distincts dans un schéma ou plan cognitif plus global.

Il a notamment été montré dans la littérature que l'acquisition d'un geste fluide dépendait de mécanismes d'anticipation qui pouvaient être visuels (fixer le point de transition entre les deux mouvements) ou musculo-squelettique (fléchir ou étendre par avance le poignet au moment de la transition entre les deux gestes) de nature (Roerdink, 2008). Nous suggérons ici que la tâches de "circle drawing" pourrait permettre l'évaluation de la flexibilité mentale, fonction qui requière de faciliter la transition entre des ensemble de règles qui diffèrent quant aux relations stimulus-réponse qu'elles imposent.

Dans le présent travail de recherche, j'ai proposé une tâche hybride de "finger tapping" et de "circle drawing". Notamment, six cibles qui formaient un cercle étaient présentées sur un écran tactile. Le sujet devait pointer ces cibles les unes après les autres en suivant le rythme d'un métronome. Ce rythme pouvait être très lent (plus d'une seconde d'intervalle entre les taps consécutives) ou très rapide (300 ms d'intervalle entre les taps consécutives). Dix essais étaient réalisés en tout à des tempi différents, du tempo le plus lent de 1200 ms au tempo le plus rapide de 300 ms, avec une augmentation du tempo de 100 ms à chaque essai. Dans une première étude (Chapitre 2, Etude 1) j'ai pu montré que cette tâche de "spatial-tapping" partageait les même propriétés que les tâches de finger tapping dans les tempi lents (entre 1200 et 900 ms), alors qu'elle ressemblait davantage au circle drawing dans les tempi rapides (entre 500 et 300 ms), avec la mise en évidence de la réduction d'un coût lié à la transition entre les mouvements d'extension et de flexion au niveau spatial et temporel dans les tempi rapides. Une phase intermédiaire (entre 800 et 600 ms) a également été révélée dans laquelle les participants subissaient une pression temporelle plus importante qui les poussait anticiper les événements suivants. Cependant, ils inhibaient leur action motrice afin de rester précis dans le temps. Dans une seconde étude (Chapitre 2, Etude 2), j'ai pu révéler les liens existants entre les processus psychologiques que sont l'attention focalisée et la conscience perceptive et la tâche de spatial-tapping. En effet, l'attention sélective était requise pour produire des actions discrètes précises dans le temps, alors que la production d'actions fluides dépendait plutôt de la capacité à grouper les différentes composantes de l'action dans un schéma global. J'ai donc montré que cette tâche simple pouvait engager des mécanismes mentaux complexes. De plus, afin de confirmer que la tâche pouvait être utilisée pour mesurer le fonctionnement exécutif, j'ai dans une troisième étude (Chapitre 2, Etude 3) proposé à des participants de réaliser trois tâches neuropsychologiques "simples" et le spatial-tapping. Une analyse de régression multiple a révélé des corrélations spécifiques entre les trois phases de la tâche de spatial-tapping et chacune des fonctions exécutives. Notamment, l'erreur de performance temporelle dans les tempi lent du spatial-tapping était corrélée aux scores obtenus dans la tâche de mise à jour en mémoire de travail uniquement. Les temps de contact dans les tempi intermédiaires étaient corrélés aux scores obtenus dans la tâche d'inhibition uniquement. L'erreur spatiale dans les tempi rapides, était corrélée aux scores obtenus dans la tâche de flexibilité mentale uniquement. Ainsi, le spatial-tapping permettrait de mesurer chacune des trois fonctions exécutives de manière spécifique (sans complexité), tout en évitant les problèmes d'impureté (contenus visuo-moteurs toujours identiques pour mesurer chacune des fonctions). La tâche de spatial-tapping nous a également permis de poser de nouvelles hypothèses concernant le rôle du fonctionnement exécutif dans le vieillissement normal (Chapitre 3, Etude 1) et dans la schizophrénie (Chapitre 3, Etude 2). Plutôt qu'un déficit exécutif global nos résultats ont révélé un déficit spécifique de l'inhibition lors du vieillissement normal. En ce qui concerne la schizophrénie, une fois encore, plutôt que de suggrer un déficit exécutif global, nos résultats ont révélé une tendance chez les patients à produire toujours des mouvements continus altérant leur performance notamment dans les phases lentes de la tâche (c'est-à-dire lorsque les actions sont réalisées de manière discrète). Ces résultats suggérent un déficit des processus de mise à jour en mémoire de travail dans cette pathologie, compensé par la mise en place d'une stratégie de flexibilité mentale dans cette pathologie. Dans une série d'études un peu différentes, nous avons démarré un travail de recherche sur la complexité dans les FE, notamment en demandant à des sujets de réaliser des actions plus complexes que dans le spatial-tapping (coordination bi-manuelle). Nos résultats ont révélé que des processus similaires à ceux trouvés dans la tâche de spatial-tapping, notamment les processus d'attention sélective et de groupement perceptif, étaient engagés. L'ensemble de ces résultats nous amène à proposer la tâche de spatial-tapping comme une tâche pertinente et innovante pour évaluer le fonctionnement exécutif, et cela en remplacement des tâches classiques largement considérées dans la littétature comme complexes et impures de construction.

D'un point de vue plus théorique, nos résultats nous ont amené à postuler l'existence de deux types d'inhibition : l'inhibition motrice, qui consiste à retenir la production d'une action motrice discrète, et l'inhibition cognitive, qui consiste à retenir le passage d'un stratégie cognitive (mise à jour en mémoire de travail) à une autre (flexibilité mentale). Aux vues de nos résultats (voir Chapitre 3, Etude 1), nous suggérons que le facteur commun partagé entre les trois fonctions exécutives soit la fonction d'inhibition motrice uniquement. L'approche adoptée nous a aussi permis de mettre en avant le rôle crucial du cervelet (une fonction sous-corticale) dans le fonctionnement exécutif, et de poser l'hypothèse l'existence d'une dissociation entre les fonctions desservies par le cervelet et le striatum. Alors que le striatum serait engagé dans les situations requérant de la flexibilité mentale, le cervelet serait engagé dans les situations nécessitant une mise à jour en mémoire de travail. Cette dissociation de fonctions est déjà reconnue dans les tâches motrices de circle drawing et de finger tapping, mais n'est pas admise dans le cadre théorique relatif au fonctionnement exécutif. Il pourrait être très intéressant pour des recherches futures de tester les performances de patients souffrant de déficits cérébelleux ou du striatum dans la tâche de spatial-tapping afin de confirmer cette hypothèse.

Pour conclure, j'espère que le travail réalisé au cours de cette thèse participera à l'évolution des connaissances et des méthodes d'évaluation relatives au fonctionnement exécutif.

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Chapter I

General introduction

1.1 Presentation of the topic

The executive functions can be seen as the cognitive mechanisms that allow organizing, planning, coordinating and executing our daily activities and behaviors. An important number of cognitive mechanisms have been proposed to subserve action planning, e.g. logical thought, reasoning, anticipation, concentration, attention, working memory, cognitive flexibility, cognitive stability, inhibition, task-set switching. Accordingly, a broad number of cognitive tasks have been developed to describe some or others of the concepts related to the executive functioning. Hence, the field lacks a compelling model that would define what might be the elementary executive functions, their relationships to each other, and their potential interactions to enable the performance of complex tasks. The field also lacks of an illustrative paradigm that could summarize the roles served by each specific executive function for action planning. The absence of such model and the lack of specificity and construct validity reported within the classical tasks constitute barriers today in the understanding of the role played by the executive functions in human cognition and render the interpretation of research results difficult.

In the present thesis work, rather than using a deductive method, by which assumptions about the potential cognitive mechanisms required for action planning guide the elaboration of cognitive tasks, we adopted an inductive approach. We proposed to study how the executive functions the most widely described in the literature intervene in the planning and execution of simple motor actions produced the one after the other, according to pre-specified temporal and spatial constraints. In the present chapter, I present: (1) an historical overview of the models and tasks used to define and assess the executive functions, (2) the limitations associated to the classical neuropsychological tasks, and I describe (3) potential motor tasks developed in the motor control domain that could be used in replacement of classical tasks to overcome their limitations.

1.2 Historical overview

In this section, an historical overview of the most influential and precursor models underlying the executive functioning is presented. The study of the executive functions starts with the observation of patients showing disturbances to plan their daily activities, independently of any long-term memory, language or IQ difficulties. Based on neuropsychological testing, cognitive models were then developed (Luria, 1966) and enriched through the years (Baddeley, 1986; Norman & Shallice, 1986). The most influential and up to date model describing the executive functions remains the model of Working Memory proposed by Baddeley in 1986 (see Baddeley, 2012).

1.2.1 Executive deficits following frontal lobe damage

Patients with frontal lobe damage were the first to demonstrate disruptions in the control and the organization of daily activities independent of any language or memory disorders (Damasio, 1994; Harlow, 1868; Shallice & Burgess, 1991). For example, the case of patient Phineas Gage, who was described by Harlow in 1868, was depicted before injury as a smart and energetic businessman, reasonable in his habits, and persistent in executing all of his plans of actions. This "efficient and capable man" who was employed as a construction foreman in a railroad company was able to deal with dangerous and complex tasks such as handling and preparing detonations in order to remove stones off of the future railroad. Such tasks required observing a number of well-defined steps while remaining cautious and concentrated for long periods of time. After frontal injury, this same person became impatient, impolite, obstinate, capricious, vacillating in his humors, and unable to carry through an action plan. This radical change led acquaintances to state that "Gage was no longer Gage", as if after brain damage, this person had a personality modification. More generally, impulsivity, disinhibiting, perseverations, decision-making and planning difficulties, emotional deregulation are the typical disruptions observed in patients following a frontal lobe damage (see Blumer & Benson, 1975). Clinical observations of frontal patients have constituted an historical basis for defining and studying the roles played by the "frontal functions" in human cognition.

1.2.2 First clinical observations and animal studies

Experimental research on the frontal lobes has been initiated through the surgical methods of stimulation and extirpation (1870–1890) in animals (see Luria, 1966). First results led to consider these brain areas as "silent", with the absence of significant changes found in animal behaviors after extirpation or following stimulation. In some studies, it was nevertheless seen that animals presented subtle changes in their behaviors after lesion, e.g. they were unable to recognize their master, they were distracted by any external object, they presented a number of strange automatic behaviors such as walking in circles without reason (Bianchi, 1895, 1920, Bekhterev, 1907, Franz, 1907, all cited by Luria, 1966, see also Compston, 2012). These observations led to state two distinct hypotheses: (1) the behavioral changes observed in animals could be the consequence of general disturbances in the functioning of the whole brain due to the extirpation of a significant quantity of brain matter, (2) frontal regions could be the seat of higher-level cognitive processes, such as “active attention”, “abstract intelligence” or “apperception” (contemporary view of the role of the frontal functions in psychology of Hitzig (1874), Ferrier (1876) and Wundt (1873-1874) respectively, all cited by Luria, 1966). From the single extirpation or stimulation methods, it was not possible to conclude in favor of the first or the second assumption. Similar conclusions were drawn from the clinical observation of patients suffering from frontal lobe damage: some findings led to conclude that the frontal lobes were the brain regions providing complex mental constructs to support the performance of complex adaptive behaviors as compared to more automatic ones (social behaviors, personality, emotional style, action sequences), and other findings led to conclude to a general decrease in intelligence due to a significant loss of brain matter. Hence, the initial observational methods were not sufficient to draw clear assumptions about the potential roles played by the frontal lobes in human cognition.

1.2.3 From observation to experimentation: the neuropsychological approach of Luria

The approach taken by Luria was in rupture with the initial clinical and neurosurgical methods (Luria, 1966). Luria was in fact the first to use an experimental approach (neuropsychological testing) and to propose a functional model to describe the role of the frontal lobes in cognition. He sincerely thought that the use of a scientific method would provide the means to overcome the confusions set within the previously mentioned interpretations, i.e., those seen with the initial surgical and descriptive methods. Luria’s approach was inspired by the rigorous experimental methods used by Pavlov and continuators in dogs and monkeys. The frontal lobes were first extirpated and animals were then conditioned to provide specific responses in the presence of particular stimuli. With this method, it was shown that after extirpation of frontal lobes in dogs, it was possible to condition a response to a single stimulus, while it was impossible to condition two distinct responses to two distinct stimuli (Anokhin, 1949, Shumilina, 1949, cited by Luria, 1966). For example, if two stimuli were presented while a response to only one stimulus was reinforced by food (response to S1= food, response to S2 = no food), dogs without frontal lobes were unable to present a selective response for the relevant signal (absence of reinforcement). Responses were provided in a random manner towards the two stimuli. These results suggest that frontal lobes enable the production of complex adaptive behaviors as compared to simple ones. This specific assumption that was supported for the first time by quantitative results, was then tested in Luria's patients through of a range of neuropsychological tests that varied in terms of complexity. For example, the patient "Zav" a 43 years-old female affected by a left frontal lesion (Luria, Pribram, & Homskaya, 1964), showed a relatively normal speech, without disturbances in articulation or in the grammatical constructions used, but showed significant echolalia and perseverations. She was able to repeat words and phrases without difficulty but showed difficulties to repeat a series of words and sentences, with the presence in this case of perseverations. She was also able to identify single objects presented to her, but was perseverating when more than one objects had to be identified within a sequence. She was able to reproduce single movements without difficulties, e.g. closing her eyes, pointing to her nose, etc. But she was impaired in the task of producing a series of distinct movements and especially when the same movement was to be reproduced several times, e.g. shake hands three times and then close eyes two times. In this specific task, while she was however aware of the instructions (shake your hands three times...), she perseverated on the first instruction and showed difficulties to stop repeating the gestures. This patient was also unable to repeat a rhythmic sequence according to verbal instruction, but was able to perform the task following visual instructions. Difficulties were however found when she was asked to produce a sequence of different rhythms. Thus, as soon as the individual events need to be organized as a sequence, with specific relationships with each other, the verbal and motor responses of this patient were inadequate. Vision helped overcoming some of the difficulties, which suggested a verbal basis of disturbances.

Overall, the experimental results obtained in patients confirm the view that frontal lobes could be the seat of the creation of complex programs or plans of behaviors. According to Luria, in humans at least, voluntary movements and actions could arise on an unconditioned biological basis, i.e. on the basis of a verbal plan that formulates the goal of the actions and the basic schemes required to perform them. Within the frontal lobes, the performance of these programs would be constantly monitored and checked by comparison of the actions performed to the original programs. Thus, habitual actions would be corrected and optimized through the use of a novel explicit plan that is more adapted to the current situation. Hence, the frontal areas could contain a self-regulating or feedback system by which complex forms of behavior are organized, compared and checked, as well as regulated for the performance of adapted social behaviors (Luria, 1966).

1.2.4 An information processing model for the frontal functions: the System of Attentional Supervision (SAS)

The neuropsychological approach of Luria provided a scientific and rigorous basis to define and describe the functions played by the frontal lobes in human cognition. However, the first results he got from neuropsychological evaluations were criticized because his patients often presented lesions that extended the frontal lobes (Canavan, Janota, & Schurr, 1985; Hécaen & Albert, 1978). Moreover, these patients were not compared to controls (Shallice, 1988) and in certain groups of patients, especially those characterized by more focused frontal lesions, an absence of impairments for the same tasks were reported (Canavan et al., 1985). Although the initial work proposed by Luria (1966) had some methodological issues, the idea of a deficit impacting the preparation phase of a complex action in frontal patients was confirmed in other studies using different neuropsychological tasks (Derouesné, Seron, & Lhermitte, 1975; Lhermitte, Derouesné, & Signoret, 1972). For example, in a study comparing four frontal patients showing a more or less severe frontal damage, the patient showing the most severe damage (Patient L2) was able to copy the Figure of Rey, a complex geometrical figure designed to assess constructional skills and memory, only when the figure was presented following six separate steps, with a small subsection of the figure to be added at each step of the copy. By contrast, when the entire figure was presented, he was unable to copy the figure, with scores being significantly lower as compared to the other patients (Lhermitte et al., 1972). The presence of these difficulties in frontal patients well fits with the hypothesis of a deficit in the programming of complex activities. These consistent results motivated Shallice and colleagues (Norman & Shallice, 1986; Shallice, 1988) to propose a conceptual information-processing framework to support the initial work of Luria.

The model proposed by Norman & Shallice (1986) is based on two main assumptions. First, the selection of routine operation is decentralized. Routines are automatically activated as a function of the inputs they received. Once, activated, a routine remains activated until the goal is reached. However, as a function of the inputs present in the situation, multiple routines may be activated. In this case, routines compete for selection, with the one or the other being dominant depending on the availability of the processing systems they require to be executed. The process by which routines are selected is named “contention scheduling”. Second, a system for attentional supervision (SAS) that possesses a planning component and learns from its mistakes, operates by modulating the contention-scheduling system, i.e. by activating or inhibiting specific routines as a function of task demands. This system has an access to both a representation of the environment, and to the organism’s intentions and cognitive abilities. This system that enables the production of willed actions is required when routines are inadequate, i.e. to deal with novelty, with danger, or in decision-making. Damage to this system is expected to give rise to the deficits encountered in frontal patients. One important advantage to use a cognitive model is the possibility to make predictions about the precise tasks that are expected to be impaired if the one or the other component of the model is disrupted. According to Shallice (1988), in the absence of SAS, two main types of disruptions are expected: (1) perseverations, when only one trigger is available in the situation with no possibilities in the absence of SAS to voluntary activate another schema, (2) distractibility, when multiple triggers are present and when there is no possibilities to voluntarily inhibit the competing routines to keep the relevant action plan running. Interestingly, these two deficits are the more consistent deficits encountered after frontal lobe damage.

While it has been well established that perseverating errors are specific to frontal lobe disruptions, in particular by the results obtained with the Wisconsin Card Sorting Test (Grant & Berg, 1948; Milner, 1963), the ability to impose a specific plan in the presence of routine competitors was not so well established, i.e. through a tailored experimental paradigm. Hence a specific experimental paradigm was proposed to assess the planning functions, namely the Tower of London (Shallice, 1982). This task was built as a simplified version of the Tower of Hanoï, a complex reasoning game. In the Tower of London task, a wood platform composed of three aligned vertical rods and disks of different colors or labels that can slide on to the rods are presented. The disks are first presented in an initial configuration. The participants' task is then to move the disks to reach a final configuration using the smallest number of moves. Sixty-one brain-damaged patients and twenty control subjects were tested with this task. Patients were placed in the anterior group when their lesion involved the frontal lobe with more than half of the lesion affecting regions anterior to the bisector of the line joining the nasion and the inion. Other patients were placed in the posterior group. Patients were finally divided into groups as a function of the side of their lesion, right or left. Results revealed that left anterior patients had significantly lower scores than all other patients and control subjects. The fact that deficits were shown in the left anterior group and not in the right anterior group suggested that some form of verbal process was required to perform the task. This interpretation was confirmed by the fact that no significant differences were reported in groups in a control task, the Block design sub-test of the WAIS, which required visuo-spatial and motor skills but no verbal plan to guide the actions. Overall, these results promoted the Tower of London as a relevant task to assess the planning function of the SAS and put forward the verbal aspect related to this function. Hence, at this point, two distinct paradigms, the WSCT and the Tower of London are proposed as exemplar tasks of the functions deserved by a SAS, i.e. respectively, (1) inhibiting an on-going routine and (2) activating a verbal or cognitive plan to control the production of a sequence of actions.

However, although these tasks allow testing the two main predictions of the model, it is hard to consider them as paradigmatic exemplars of the functions of the SAS, even if we consider that the SAS is modular in nature. Indeed, if we come back to the initial assumptions of Luria concerning the role of a potential SAS, it seems that the main function of real-time "self-regulation" of complex activity is not assessed in any of these tasks. Hence, it could be important to rethink the model and the related experimental tasks, by integrating at least the real-time regulation function of the SAS, and potentially by distinguishing between these processes that are executive in nature (regulation, control, inhibition) from others that are more focused on the content of the representations needed to guide the action sequences, e.g. the verbal plan. In this view, the model of Working Memory proposed by Baddeley (Baddeley, 1986, 1992, 2012) has been proposed as an updated version of the model proposed by Shallice and colleagues.

1.2.5 Working Memory: a multicomponent model for the executive functions

The multicomponent model of working memory proposed by Baddeley (1986) is one of the most actual and influential models of executive functioning. This model was designed with the aim to develop the initial modal conception of short-term memory (Atkinson & Shiffrin, 1968). The main prediction of the initial model suggested that short-term memory (STM) was the main entry towards long-term memory (LTM) encoding, with the capacity to encode information in LTM depending upon the time of residence of an item in STM. This assumption has been challenged in several ways. For example, in a study by Craig and Watkins (1973), a long sequence of words was presented with the instruction to recall the last word beginning with a pre-specified letter, e.g. with the letter B and the following list of items: ball, cabbage, blue, apple, cloud, basin, etc., the response would be basin. At the end of the task, subjects were asked both to answer the initial instruction, and to recall all words beginning by the specified letter. While they had no particular problem to recall the last word beginning with a pre-specified letter, they showed a poor level of performance to recall the other words of the sequence, which were thought to be held in STM during a certain amount of time. Moreover, no relationships were found between the time of maintain of the words in STM and the final performance. This result suggested that learning in LTM is not directly dependent upon the time of residence of an item in STM but could rather depend upon the manner items were processed to achieve a given task. Hence, relationships between STM and LTM seem more complicated than those predicted by the initial predictions geared from modal views of STM.

A more explicative view was taken by the “levels of processing” approach (Craik & Lockhart, 1972). Accordingly, LTM learning rather depends upon the nature of the processes of encoding than on the time of residence of an item in STM. The memory trace durability is assumed to be larger when the encoding processes are deeper. A continuum of levels of processing starting with a superficial and peripheral level of processing to an elaborated semantic level was proposed. For example, processing a word at a visual level only (peripheral level), was not expected to lead to an efficient LTM encoding, while processing the meaning of a word was expected to lead to a durable trace in LTM (semantic level). This effect was found in a number of studies using incidental learning procedures that required to process items in a pre-specified way and then to recall or recognize the words (Hyde & Jenkins, 1969; Johnston & Jenkins, 1971). For example, in one of these studies, when subjects were asked to estimate the number of letters present in a word, LTM encoding was more superficial than when they were asked to rate a word according to its pleasantness (Hyde & Jenkins, 1969). Although such conception of memory is more compelling than those proposed in initial models, some assumptions of the models were challenged. In particular, the levels of processing were conceived according to a linear view, for example a word will be processed first visually, second, phonologically, and finally semantically. However, this assumption did not fit with some of the behavior patterns observed in deep dyslexic patients (Marshall & Newcombe, 1966, 1973). These patients were able to process the meaning of a word without being able to derive its phonological features, e.g. they read the word prayer as church. These findings and many others (see Baddeley, 1986 for more details) argue against the idea that levels of processing are linear and are in favor of a parallel distribution of these processes. Hence, to learn about a given stimulus, many dimensions of the stimulus can be processed at the same time or independently as a function of task demands.

These assumptions are summarized in the model of working memory proposed by Baddeley (1986, 1992, 2012). In this model, two slaves systems, the visual sketchpad and the phonological or articulatory loop allow storing short-term information of different nature (respectively visuo-spatial imagery vs. speech based information) and in a concurrent manner. The information coming from these two sources are processed, manipulated and coordinated through a central executive. The main paradigm used by Baddeley and continuators to test the predictions of the model was the dual-task paradigm. In these tasks, two concurrent sources of information had to be stored and processed at the same time. For example a series of digits had to be maintained in mind until the end of the task while a concurrent task of learning, reasoning or comprehension was performed. In all cases, the performance obtained on the main task was dependent on the load (number of digits) on the maintaining task. However, the degree of disruption was always lower than predicted, which suggested a relative independency between the central executive and the maintaining slave systems. For example, when playing chess, it was shown that a second task involving the visual sketchpad (manipulation of a keypad) or the central executive (by random letter generation) had a significant impact in the player's performance while secondary tasks involving the phonological loop (articulatory suppression) had no impact (Robbins et al., 1996). The model of multi-component working memory fits very well with the main assumptions of Luria concerning the roles played by the frontal lobes in human cognition: a self-regulating system or a real-time "feedback" system that constantly check, monitor and regulate the subject's performance on complex tasks (such as learning, comprehension, reasoning) by comparing the actual performance to programs or plans that are maintained active in memory. Furthermore, the central executive system of Baddeley was assumed to play the same role than the SAS proposed in the model of Norman & Shallice (1986).

However, it is important to note that according to Baddeley, without refuting the fact that the frontal lobes may subserve executive functioning, he suggested to maintain a functional conception of the central executive and to replace the common concept of "frontal syndrome" by the more functional concept of "dysexecutive syndrome" (see Baddeley, 1996). Indeed, in his terms, "restricting the understanding of the functions served by the central executive to an anatomical perspective could be damaging to the evolution of the concept". Moreover, Baddeley admitted that the precise functions served by the central executive are yet very unclear. He employed himself the term of "ragbag" to define the role potentially played by the central executive, i.e. all the functions that are not deserved by the slave systems are potential functions for the central executive, e.g. selective attention, multi-tasking coordination, retrieval in LTM, inhibition of a dominant response (see Baddeley, 1996).

1.3 Complexity and impurity issues in executive tasks

While important advances have been done to make the initial assumptions of Luria's evolving within a well defined information-processing framework (Baddeley, 2012; Norman & Shallice, 1986), the concept of central executive remains vaguely defined. In spite of this vagueness, there was a need in research and clinical settings to assess executive functioning. The position taken by neuropsychologists and researchers interested in assessing the executive functions have been to use batteries of multiple tasks known to have an impact on the executive functioning, e.g. the Tower of London (Shallice, 1982), the WSCT (Grant & Berg, 1948; Milner, 1963) or random generation tasks (Baddeley, 1996). Many issues have been examined using batteries of multiple tasks that have nevertheless allowed considerable advances in the understanding of the executive functioning since the last fifteen years.

1.3.1 Multiplicity of the executive functions, multiplicity of executive tasks

Using batteries of multiple tasks implicitly comes down to consider that the executive functions assessed by the different tasks are independent in nature. According to the theoretical contexts in which the tasks were developed, it really seems that the tasks tap independent executive functions. For example, the Tower of London was initially developed to assess the "planning function", i.e. using a verbal plan to prepare all the moves to do in advance and then, execute the strategy (Shallice, 1982). This task was developed in order to put forward the existence of this function that emerged as a prediction of the model proposed by Norman & Shallice (1986). Indeed, at this time the prevailing task related to executive dysfunctions was the Wisconsin Card Sorting Test (WSCT). In this task, four cards are placed in front of the subject. Then, a pack of response cards is provided to the subject. Each card may contain a distinct symbol (geometrical figures), colors, and numbers of items. The subjects' task is to classify each card according to a certain rule, by placing each response card, one at a time with one of the four cards initially displayed. The classifying rule is known by the experimenter but is not explicitly instructed to the participant. In fact, after each placement, the subjects are told whether they placed the card correctly or not. Hence, the subjects must infer the correct sorting rule. After the subjects have followed the correct rule during a certain number of trials, the rule is changed. Then, the subjects are required to adapt their response to the new rule. The number of times the subjects respond in accordance to a previously correct rule while the current rule has changed is measured as a perseverative response. Hence, the task assesses the subjects' capacity to inhibit a routine behavior, to impose a novel S-R mapping according to changing contingencies. This function can be seen as fundamentally different of the "planning" function assessed by Shallice (1982) with the Tower of London.

The model further proposed by Baddeley (1986) integrates the assumptions drawn by Norman & Shallice (1986) concerning the executive functioning but adds the real-time checking component that was at the core of the initial model of Luria (1966). This function is especially assessed in the random number generation task (see Baddeley, 1996; Robbins et al., 1996). In this task, participants are asked to produce series of digit numbers that is "as most random at possible" during a certain amount of time (e.g. two seconds). Hence, the task requires (1) to maintain active in memory the series of digit numbers that were already generated, (2) to update these series according to memory span (on average, seven items at a time can be maintained in short-term memory), and (3) to select a number that is sufficiently distant from the previous numbers generated according to the routine counting rule (1-2-3-4). Hence, a constant checking of the current behavior according to a pre-specified rule is required in this task. It is thus the case that according to the logic following which the models of executive functions were developed and to the evolution of the theoretical models, novel tasks were each time proposed.

From these diverse tasks and various models, it seems today that at least three functions have been identified with, e.g., the functions of planning, inhibiting a routine behavior, and real time adaptation. Furthermore, the hypothesis of independency between the executive functions has been supported by clinical observations, which revealed dissociation in the performance of patients in various contrasting executive tasks. For example, some patients revealed poor performances in a planning task (such as the Tower of London) but were not impaired when they were asked to perform a task in which responses were dependent upon contingencies (such as in the WSCT), and vice versa (Koechlin, Corrado, Pietrini, & Grafman, 2000). A similar dissociation was found between a decision making task (in which impulsive behavior required inhibition) and a working memory task (Bechara, Damasio, Tranel, & Anderson, 1998). Hence, these results reflect the idea that the executive functions are multiple and independent in nature (Godefroy, Cabaret, Petit-Chenal, Pruvo, & Rousseaux, 1999). Another range of studies has examined the relationships between executive tasks through the use of correlation and regression analyses (Burgess, Alderman, Evans, Emslie, & Wilson, 1998; Lehto, 1996). On average, correlations between executive tasks were found to be low, hence confirming the multiple nature of the executive functions (see Miyake et al., 2000). Nevertheless, as suggested by Miyake (2000) at least two arguments may challenge the hypothesis of independency between the executive functions: (1) most of the tasks used are “frontal tasks”, in the sense that they were designed to target functions that were disrupted in frontal patients; Hence, there is no functional evidence that they assess the executive functions per se; (2) although the tasks were designed to target specific functions some redundancies in the functions they require are found. For example, it was suggested that all classical frontal tasks require the core function of inhibition (Goel & Grafman, 1995), e.g. the WSCT, the Tower of Hanoï (a more complex version of the Tower of London), the Delayed Alternation task. It was also often reported that these tasks are impure in the sense that they require cognitive processes that are not executive in nature, e.g. short-term memory (Burgess, 1997; Phillips, 1997). Accordingly, the absence of correlations observed between classical tasks could be to the presence of these non-executive processes that added noise within the performance scores of the tasks. This specific hypothesis has been tested in a study by Miyake (2000), and led to moderate the assumptions of a complete dissociation between the executive functions. Results of this challenging study are presented in the next section.

1.3.2 Independency and commonalities between the executive functions (Miyake et al. 2000, 2012)

Task complexity is a recurrent issue in the executive field that often constituted barriers in the interpretation of experimental results (e.g. Charlot & Feyereisen, 2005; Clarys, Bugaiska, Tapia, & Baudouin, 2009). Indeed, tasks are too complex in the sense that they involve both executive and non-executive processes (Burgess, 1997; Phillips, 1997). If we consider that the executive functions are independent, then some tasks are also too complex in the sense that multiple executive processes, such as inhibition and working memory updating, may be independently used to solve them. For example, the Tower of Hanoï, a more complex version of the Tower of London, could be solved through the use of two distinct cognitive strategies. While some participants may use the so-called verbal planning strategies (Shallice, 1982), also referred as goal-recursion strategies (Carpenter, Just, & Shell, 1990), others use a more “routine” or “intuitive” strategy according to which the next move or disk is spontaneously displaced towards the position that is the closest to the desired final configuration (Goel & Grafman, 1995). Such interpretation difficulties were also reported in the WSCT that was found to involve both working memory and task-set switching abilities (Sood & Cooper, 2013). In the same line, working memory tasks (e.g. N-back tasks) that were seen to require both inhibition and updating strategies (Hockey & Geffen, 2004; Jaeggi, Buschkuehl, Perrig, & Meier, 2010; Jonides & Smith, 1997). The main consequence of task complexity is obviously a lack of test-retest reliability in the tasks (Rabbitt, 1997).

With the objective to have a better understanding of the executive functioning while avoiding the problem of task complexity, Miyake (2000) proposed a latent variable analysis between a range of neuropsychological tasks. As compared to common regression or correlation studies, this specific statistical analysis asks whether common variability is shared across a range of tasks. First, three main functions were defined as being executive in nature according to research findings: the inhibiting function, the working memory function of updating and the switching function. The inhibition function was defined as the ability to voluntarily inhibit a dominant, automatic or prepotent response. The updating function was defined as the ability to revise the items hold in working memory as a function of the task demands, i.e. replacing old relevant information by new one. The switching function was defined as the ability to shift back and forth between multiple tasks, operations or mental sets. For each function, a set of three “simple” tasks were choosen. Simple tasks were impure but were simple in the way that they a priori tapped a unique executive function. For example, the stop-signal task was one of the task used to assess inhibition (Logan, 1994). In this task, participants are asked to produce fast motor responses to categorize whether a presented word corresponds to an animal or to a non animal. Then, when an auditory beep is emitted, the subjects’ task is to inhibit their motor response. The latent variable analysis was then conducted between these tasks in order to assess whether they were sharing common variances. A range of a priori complex tasks was also selected: the WSCT, the Tower of Hanoï, the random number generation task, the operation span task and a dual task. A second wave of analysis was then conducted to assess in a proper way whether these tasks were complex or not (according to the extent to which the three functions were considered to separable). Results revealed that: (1) the tasks selected to tap a unique executive function were significantly correlated between them, while correlations with the other tasks were lower, (2) the CFA analysis by which the data obtained were fitted to several models according to specific assumptions (e.g. the one-factor model that assumes the unity of all three functions or the two-factor model that assumes the unity of two of the executive functions) revealed that the three functions were clearly distinguishable but at the same time shared some commonalities, (3) tasks a priori expected as being complex in nature were often really complex, with a combination of multiple factors being the better model to explain the variance observed in the data.

Overall, these results confirm the complexity of classical neuropsychological tasks but provides the means to better define how these tasks are build (cf. validity construct issue) and they contribute to the understanding of the relationships between the three main executive functions after having statistically suppressed the issues related to task impurity. Hence, the three functions are clearly separable although they share some commonalities. Thus, now the question is naturally turned to the description of the potential sources of commonalities between the tasks or functions measured. Two speculative hypothesis were proposed by Miyake to answer the question according to the tasks demands that may be shared between the nine used tasks. The common factors shared between all executive tasks could be: (1) the maintenance of goal and context information in working memory, as well as (2) the presence of inhibitory mechanisms (respectively to ignore irrelevant information in updating tasks, or to suppress an old mental set to transition to a novel one in switching tasks).

It is the case that in the past decade a focus has been set on determining the commonalities and differences between the executive functions, mainly through an attempt to specify the biological underpinnings of the executive functions (Miyake & Friedman, 2012), with a genetic approach in healthy subjects (Colzato, Waszak, Nieuwenhuis, Posthuma, & Hommel, 2010; Friedman et al., 2008). Executive deficits have also been considered in other patients than frontal patients, i.e. Parkinson's patients and their related striatal deficits (Cools, 2006, 2011). This work illustrates the most actual considerations for the executive functions and is presented in the next final section.

1.3.3 Relationships between the executive functions: neurobiological underpinnings

Since the research work by Miyake et al.(2000), a focus has been set on determining the commonalities rather than the differences between the three main executive functions of *updating, switching and inhibition*. Studies were carry on in Miyake's group through the use of a behavioral genetic perspective, according to which twin brothers and sisters were assessed in a range of nine executive tasks assessing the three executive functions (Friedman et al., 2008). Results indicated that commonalities in the executive functions were due to a highly heritable common factor (99% heritable), while diversities were due to substantial differences in the updating and switching functions that were also genetic in nature (56% vs. 42% of heritability, respectively). The switching function only showed variances that were attributable to environmental factors (14%). The variance of the inhibiting variable was completely shared with the common variance of the two other executive functions without specific variances related to inhibition. This result suggests that inhibition could play the role of common factor between the two more specific updating and switching EFs. Such hypothesis was confirmed in a longitudinal study in which twin brothers and sisters were tested during childhood (before 36 months of age) on their self-restraint abilities to not touch an attractive toy during 30 s (inhibition abilities), and in late adolescence in the three executive functions (Friedman, Miyake, Robinson, & Hewitt, 2011). Results revealed that the less-restrained children had lower scores on the common factor and larger scores in the switching-specific factor, while no changes were reported with age in the updating ability. Hence, they confirm the role of inhibition as a common factor in the executive functioning. They further suggested some opposition between the abilities to inhibit a dominant response in order to maintain a single task goal and the abilities to switch flexibly from a task goal to another. One of the most current direction taken by Miyake's group (see Miyake & Friedman, 2012) is to try getting a better understanding of the neural mechanisms underlying the executive functioning. The prefrontal-cortex basal-ganglia working memory (PBWM) model developed by O'Reilly and colleagues (O'Reilly & Frank, 2006), has been proposed as a plausible biologically model for the executive functioning. In particular, this model could explain the opponent computations going on between the common factor of inhibition and the switching function. Indeed, it is proposed that prefrontal regions could bias sub-cortical regions (basal ganglia) through their connections to posterior regions to help maintaining and manipulating tasks goals (updating function). In absence of this cognitive bias, prefrontal regions and the basal ganglia would collaborate to improve cognitive flexibility in the context of dopaminergic reward learning contingencies (switching function).

These assumptions have found large echoes in recent neurobiological and behavioral studies that have attempted to clarify the roles played by the dopaminergic system on cognitive control (Colzato et al., 2010; Cools, 2006, 2011). These studies were initiated after having observed opposite effects (positive or negative) of dopamine therapy on executive abilities in patients suffering of Parkinson's disease. Parkinson's disease is characterized primarily by motor symptoms (such as tremor, rigidity, bradykinesia) and L-DOPA medication is well known to improve these specific symptoms. According to Cools (2006), the more contrasting effects that were found at the cognitive levels following L-DOPA treatment may reflect the spatiotemporal depletion of dopamine, which is most severe in the dorsal striatum in early stages of the disease and progresses later to the ventral striatum. Hence, at early stages L-DOPA medication could improve certain functions associated with the dorsal striatum (that predominantly projects to the dorsolateral prefrontal cortex) and at the same time impair through an overdosing the cognitive functions served by the relatively intact ventral striatum (that predominantly projects to the orbitofrontal cortex). While the dorsal striatum may subserve the establishment of abstract stimulus-response associations (updating-like function), the ventral striatum should subserve more concrete stimulus-outcome associations (switching-like function). On the same set of patients using the same drugs, the performance on updating and switching task was shown to differ on opposite ways. While some patients had normal scores in switching tasks, their performance was significantly impaired in updating tasks (Kimberg, D'Esposito, & Farah, 1997; Mehta, Manes, Magnolfi, Sahakian, & Robbins, 2004). The reversal pattern of result was also observed (Kimberg & D'Esposito, 2003). These opposite patterns of results were revealed to depend upon the frontal/striatal dopamine (DA) levels. While high frontal DA levels are beneficial for updating performances, they lead to a reduced ability to perform switching tasks. While low frontal DA levels are beneficial for switching performances, they lead to a reduced ability to perform updating tasks. These cross-talk of benefits/impairments in relationships to DA levels in the PFC was confirmed in genetic studies in which distinct genotypes related with these frontal

DA levels showed similar patterns of performance in switching vs. updating abilities (Colzato et al., 2010). Overall, these findings confirm the potential contribution of the striatum (a structure of the basal ganglia) in the performance of executive tasks and for this specific reason corroborates the PBWM framework (Miyake & Friedman, 2012; O'Reilly & Frank, 2006). However, an opposition between the switching strategies and the updating strategies are stated. This assumption does not fit the initial assumptions of Miyake who rather opposed these two functions. The common factor between these functions was again said to be the inhibition function. Interestingly, in the studies conducted in the cognitive control domain, the function of inhibition has been completely left out. Hence, one could argue that the core deficit shown in Parkinson's patients (Cools, 2006) and the individual differences reported in the two executive tasks (Colzato et al., 2010) were dependent upon the inhibition factor only, impacting as a consequence the two other functions.

In conclusion, great advances have been made in the past decade to gain a better understanding of the roles played by the executive functions in human cognition, their potential interactions, and the potential neural substrates subserving these functions. These advances were supported by large-scale twin studies involving over 150 participants, neurobiological studies involving patients, as well as genetic approaches. Nevertheless, the field still lacks of a compelling experimental paradigm that could be used both in academic and in clinical settings to assess the two executive functions of switching and updating as well as their relationships to inhibition, at an individual level (to avoid group designs). Another key issue is the need of using a single task to evaluate these key functions in order to avoid impurity issues. The development of such task was the main objective of the present thesis. Theoretical basis underpinning the choices made to develop such a task is presented in the next sections.

1.4 The present endeavor: using simple rather than complex tasks to assess the executive functions

It is interesting to note how the tasks became more and more complex with the evolution of the theoretical models underlying the executive functioning. In Luria's first neuropsychological tests, patients were asked to repeat singles sentences or series of sentences, to identify single objects or series of objects, to reproduce single patterns of movements or series of patterns, to repeat a motor rhythmic sequence or to produce a series of different rhythms (Luria et al., 1964). Hence, Luria's tasks were often motor and single actions were systematically compared to series of embedded actions. With Shallice (1982), the tasks became significantly more complex. Indeed, the Tower of London was inspired from a complex mathematical reasoning game, the Tower of Hanoï. This task was visuo-motor in nature, i.e. participants had to produce moves of disks from a wood stick to another, and from an initial configuration of disks to a final one. By designing this task, the main author's intention was to target a planning function based upon verbal thought. Baddeley (1986) introduced dual-task paradigms and multi-tasking situations. Here, two or more cognitive tasks, often verbal, sometimes visual or phonological had to be produced on the same time. Hence there are some important questions we could ask ourselves here: do we need complex mental functions to deal with complex tasks? Do we use complex and unitary mental constructs such as "reasoning" to solve complex reasoning games or is the apparent complexity in the functions served by the complementarity and coordination of more simple modules? Is it necessary to use a "verbal" plan to produce a series of actions (e.g. in the Tower of London)? What are the relationships between cognitive planning and motor planning? Are the cognitive planning tasks dependent upon the activation of motor areas in the brain or are they purely cognitive? Do we really need complex tasks to assess the executive functions? Here is the problematic of my research work. Without attempting to answer all these questions, I propose that simple motor tasks may involve high-level cognitive processes or executive functions dependent upon similar mechanisms and brain regions than those described in the neuropsychology domain.

1.4.1 Simple finger tapping tasks engage updating mechanisms

Finger tapping tasks are simple motor tasks in which taps of the index finger are produced on a platform repetitively, and following a pre-specified rhythm. In order to produce well-timed actions, classical models of timing assume the existence of an internal clock, a model that is based on the possible existence of a pacemaker, counter, store and comparator (Treisman, 1963). The pacemaker produces regular pulses. The counter records the number of pulses arriving during a given time interval, e.g. between the two clicks of a metronome, and transfers this measure to a referential memory. The counter then records the number of pulses relative to the produced interval of time and transfers this measure into working memory. The referential and the produced interval are then compared and a judgement can be made (e.g. the interval produced is shorter than the referential). If the deviation to the referential interval is significant, a correction can be made through successive adjustments, at a later point. Hence, from a theoretical point of view simple finger tapping tasks may involve updating-like mechanisms to match the timing of a current action to a referential interval of time. The involvement of working memory mechanisms in finger tapping tasks has also been seen in behavioural studies using the dual-task paradigm. These studies revealed significant effects of explicit timing mechanisms on the central executive, i.e. in complex tasks (mental arithmetic) as compared to more simple tasks requiring the visuo-spatial sketchpad (visual search and tracking tasks) (Brown, 1997), and on the phonological loop, i.e. in serial recall and articulation tasks (Saito & Ishio, 1998; Saito, 1994). Interestingly, both finger tapping tasks and working memory mechanisms were seen to depend upon cerebellar processes at the brain level (Chen & Desmond, 2005; Desmond, Chen, & Shieh, 2005; Desmond, Gabrieli, Wagner, Ginier, & Glover, 1997; Ivry & Spencer, 2004; Ivry, Spencer, Zelaznik, & Diedrichsen, 2002; Kawashima et al., 2000; Olmo, Cheeran, Koch, & Rothwell, 2007). The function of the cerebellum in these tasks could be to play the role of internal clock (Ackermann, Gräber, Hertrich, & Daum, 1997; Keele & Ivry, 1990; Trenkner, Smith, & Segil, 1984) or to provide the necessary circuitry to the sensory system to extract temporal information and to the motor system to learn to produce a well-time response (Penhune, Zatorre, & Evans, 1998). Hence, finger-tapping tasks appears as relevant tasks to assess the working memory mechanisms depending upon both the phonological loop and the central executive.

1.4.2 Circle drawing as switching tasks

In the motor timing domain, explicit timing is the mode of action control that requires maintaining active in working memory a representation of the timing interval in order to produce a well-timed action. Explicit or event-based timing is often opposed to another mode of action control, namely emergent timing (Huys, Studenka, Rheaume, Zelaznik, & Jirsa, 2008; Robertson et al., 1999; Zelaznik, Spencer, & Doffin, 2000; Zelaznik, Spencer, & Ivry, 2002). In emergent timing, the task goal is not focused on the needs to maintain accurate timing. Timing results from movement control processes that constrain a spatial trajectory. In other words, the primary task goal is to produce a movement from a departure point to an arrival point. Timing corrections are then applied, i.e. a posteriori, on the subsequent repetitions of a given action (Robertson et al., 1999). While explicit timing is required in motor tasks that are discrete in nature, i.e. with attention focused on each isolated action of the sequence; emergent timing is rather involved in continuous tasks such as in circle drawing tasks (Huys et al., 2008; Zelaznik et al., 2000). In circle drawing, circular movements of the finger, which is here under the control of the arm, are repetitively drawn on a platform according to a pre-specified tempo. To perform these particular tasks, it was shown that the cerebellum was not required (Ivry et al., 2002), by contrast, another subcortical structure, namely the basal ganglia seem to be particularly involved (Ivry & Spencer, 2004; Spencer & Ivry, 2005; Spencer, Zelaznik, Diedrichsen, & Ivry, 2003). Because in emergent timing tasks, the timing is corrected after having produced a motor response towards a specific location in space, the role played by the basal ganglia in these tasks could be to provide the necessary learning contingencies to reinforce or punish the production of a motor action performed within a specific spatiotemporal context (O'Reilly & Frank, 2006). Another potential role for the basal ganglia in emergent timing tasks such as circle drawing could be to group single action patterns into more global patterns or chunks (Graybiel, 1998). Indeed, circle drawing tasks can be seen as complex action patterns to produce in the sense that producing a circle with the arm can be divided upon two main sub-movements: an extension movement that is followed by a flexion movement. Flexion vs. extension movements of the arms are produced by different sets of muscles, with each muscles-set being activated following distinct neurotransmission time lags, requiring distinct force patterns to be activated, and then reacting differently to the environmental constraints (e.g. gravity). Hence, each specific sub-movement of the sequence may require a specific motor program (Schmidt & Lee, 2011; Schmidt, 1975). In order to produce a circular movement, it is the case that a specific task goal naturally emerges: the two distinct sub-movements involved in the sequence have to be smoothed within a more global action pattern (Beek, Turvey, & Schmidt, 1992; Hogan & Sternad, 2007; Hogan, 1987). These smoothing demands can be measured as a reduction in the spatial and temporal error at the location of the transition point between the two sub-movements involved in the action sequence. This reduction in the spatio-temporal errors at a precise spatial location are referred to as “anchor points” and were seen to depend upon the performer’s abilities to anticipate a transition point between two motor sub-elements, through visual (fixating the gaze at the transition point) or musculoskeletal strategies (flexing or extending in advance the movement at transition points) (Roerdink, Ophoff, Peper, & Beek, 2008). Hence, circle-drawing tasks could be relevant tasks to measure the switching abilities between two sub-elements of a sequence, resembling the executive function of transitioning between task-sets, which defines in fact the classical switching task (e.g. the WSCT, also see Rogers & Monsell, 1995). Moreover, within neurobiological models, the production of such a circle-drawing task seems to depend upon the basal ganglia, as it is expected in the case of classical switching tasks (Cools, 2011; O’Reilly & Frank, 2006).

1.4.3 Motor preparation, attention and conscious perception

In the two previous sections (1.4.2, 1.4.1.) we proposed that repetitive finger tapping and circle drawing tasks could be relevant motor tasks to assess the executive functions of updating and switching. The remaining question is what kind of task to use to assess the inhibition function. Inhibition has been defined as the ability to retain a dominant or prepotent motor response in order to (1) keep running an adapted strategy, (2) propose another strategy more adapted to the task demands. Because inhibition has been prevailingly defined as motor in nature, it is the case that this function would be required both in finger tapping and in circle drawing tasks. Motor inhibition could be required in finger tapping tasks to retain the production of a too-fast action, in order to keep each action sufficiently discrete (or isolated of the subsequent action) to put in place the correct event-based timing strategy. Inhibition in circle drawing tasks is necessarily involved when the task’s demands are geared to the needs to produce accurate timing. Indeed, in this case, the subsequent actions require more control of the motor response to deal with the task constraints. Hence specific measures of inhibition could be inferred from both tasks in particular by manipulating the temporal constraints of the tasks.

One could also argue that finger tapping and circle drawing tasks are primarily under the control of subcortical functions and in this way do not require high-level cognitive functions to be produced. Here, I would refer the reader to action-based theories of selective attention, which suggest that attention completely overlaps with motor preparation (Rizzolatti, Riggio, & Sheliga, 1994; Tipper, Lortie, & Baylis, 1992). Indeed, any goal-directed movement requires the selection in advance of a specific endpoint. Such selective processes were invariably affected by the presence of distractors that automatically attract attention, and the same distractors were shown to affect the subsequent eye or arm movement trajectories (Pratt & Abrams, 1994; Sheliga, Riggio, & Rizzolatti, 1994; Van der Stigchel, 2010; Welsh & Elliott, 2004, 2005). Hence, the mere goal-directed movement requires focused spatial attention. Interestingly, another high-level construct have been recently presented as performing similar roles than spatial attention but through the opponent computation in order to deal with distinct constraints, i.e. conscious perception (Boxtel, Tsuchiya, & Koch, 2010; Hohwy, 2012; Tsuchiya & van Boxtel, 2013). More specifically, when it is not possible to focus attention on discrete events, e.g. because too many task-relevant elements are present in the internal and external environment to solve a given issue, conscious perception could enter into play to bind the several task-relevant items within a more global structure of control. Hence, while attention can be seen as an “analyser” that provides specific resources on discrete events to facilitate the corresponding S-R relationships, conscious perception could be envisaged as a “synthesizer” that binds together multiple relevant information and then allow defining the global task context to act upon (Boxtel et al., 2010). These two opposite computations have been also recently proposed as the main high-level mechanisms intervening to coordinate complex sequences of bi-manual actions (Swinnen & Wenderoth, 2004). Overall, we argue here that simple motor tasks such as repetitive finger tapping and circle drawing tasks could be used in replacement of complex neuropsychological tasks in order to assess the well-running of the executive functions (i.e. switching, updating, inhibition) at an individual level (e.g. for clinical purposes), and in a more specific way than the actual tasks do (the two tasks did not overlap in terms of the functions and associated brain regions they involve).

1.4.4 Presentation of the thesis work program

The hypothesis whereby simple motor tasks could be used in replacement of traditional executive tasks to assess the high-level executive functions was tested through a series of experimental studies that are presented in the next chapters. In chapter II, we present a novel paradigm, namely the spatial-tapping task, which was designed as a hybrid of finger tapping and circle drawing tasks (Study 1). In this task, it was shown that both attention and conscious perception were required as a function of the task constraints (Study 2). Moreover, correlations between scores observed in classical neuropsychological tasks and scores derived from the spatial-tapping task were obtained (Study 3). In chapter III, two studies are presented in which elderly individuals (Study 1) and schizophrenia patients (Study 2) were tested in the spatial-tapping task. In chapter IV, I present a series of experiments in which the concept of spatial tapping was transferred towards more complex settings, i.e. bi-manual coordination (Study 1). Limits, perspectives and potential impact of the present research work are finally discussed in closing chapter V.

Chapter II

A unique task to assess the executive functions: the spatial-tapping task

Chapter's overview

In the present chapter, we present a novel paradigm, the spatial-tapping task, which was designed as a hybrid of finger tapping and circle drawing tasks. More precisely, in **Study 1**, participants were asked to produce repetitive taps of the index finger on six discrete visual targets that were arranged around a virtual circle following distinct tempi (from slow to fast tempi). This task was shown to share similar properties than finger tapping tasks at slow tempi (between inter-taps periods of 1200 to 900 ms), than circle drawing tasks at faster tempi (periods of 500 to 300 ms). At intermediate tempi (periods of 800 to 600 ms) a specific phase of transition of control strategies was revealed.

In **Study 2**, we show that both attention and conscious perception were required to optimize the well production of an action sequence as a function of the task constraints, i.e. attention at slow tempi to help rendering the actions more discrete and well-timed and conscious perception at faster tempi to enable the production of circular movements.

Finally, correlations between scores observed in three classical neuropsychological tasks (updating, inhibiting and switching tasks) and scores derived from the spatial-tapping task are presented in **Study 3**. Results revealed that the performance scores in the updating task were correlated to the timing errors in the slow phase of the spatial-tapping task only. The scores obtained in the inhibiting task were correlated to the contact times in the intermediate phase of the task only. The scores obtained in the switching task were finally correlated to the spatial error in the faster phase of the task only. These results suggest that the spatial-tapping task is able to target independently the three main executive functions, with the cognitive task goal being changed as a function of the task demands.

S1: Dione, M., Ott, L., Delevoye-Turrell, Y. (submitted). Arguments in favour of the coexistence of the two distinct timing modes of action control in a single task performed with a unique effector: the spatial-tapping task.
S2: Dione, M., Ott, L., Delevoye-Turrell, Y. (in prep). Abrupt onsets to modulate selective attention and conscious perception in a circle-tapping task.
S3: Dione, M., Ott, L., Delevoye-Turrell, Y. (2013). Planning ahead through space and time: from neuropsychology to motor control. In M. Knauff, M. Pauen, N.Sebanz, & I. Wachsmuth (Eds.), Proceedings of the 35th Annual Conference of the Cognitive Science Society (pp. 2207-2212). Austin, TX: Cognitive Science Society.

Study 1

Arguments in favour of the co-existence of the two distinct timing modes of action control in a single task performed with a unique effector: the spatial-tapping task

Abstract

The control of rhythmic action sequences may involve two distinct timing processes, i.e. event-based and emergent timing. They are usually revealed through finger tapping and circle drawing tasks, respectively. In the present study, we asked whether a single task in which finger taps are produced along a circular trajectory at distinct tempi could reveal the two timing modes. Sixty-eight participants performed the spatial-tapping task at ten distinct tempi (periods of 1100 ms to 300 ms). Using both autocorrelation analyses on timing variables and analyses of the trajectory information in space, we show that the timing mode used in the spatial-tapping task was predominantly event-based at slow tempi ($\geq$ 900 ms), emergent at faster tempi ($\leq$ 500 ms) and hybrid at intermediate tempi. We discuss the possibility to use the spatial-tapping task as a novel experimental paradigm to explore different timing modes and their role in executive functioning.

1.1 Introduction

There is growing evidence that two distinct modes of timing are involved in the control of rhythmic action sequences, namely event-based timing and emergent timing (Huys, Studenka, Rheaume, Zelaznik, & Jirsa, 2008; Robertson et al., 1999). They have been revealed through two distinct experimental paradigms, finger tapping and circle drawing tasks, respectively (Zelaznik, Spencer, & Doffin, 2000; Zelaznik, Spencer, & Ivry, 2002). While the task goal in finger tapping is to maintain accurate timing with, e.g., a metronome (Wing & Kristofferson, 1973a, 1973b), the task goal in circle drawing is more specifically to produce smooth and regular action patterns in space, i.e. without interruption in the spatial trajectory between the distinct movements involved in the action sequence (Beek, Turvey, & Schmidt, 1992; Hogan & Sternad, 2007; Hogan, 1987; Roerdink, Ophoff, Peper, & Beek, 2008). In such a case, timing emerges as a consequence of the control dynamics of the hand trajectory (Robertson et al., 1999; Turvey, 1977).

In the present study, we propose to combine the demands of both tapping and circle drawing tasks within a unique spatial-tapping task to be performed at distinct tempi. We suggest that this approach will help gain a better understanding of the constraints that lead to transitions from one cognitive strategy of action control to another (a series of discrete actions vs. a continuous sequence of movements). Because most of our daily activities require spatio-temporal preparation, we propose furthermore that this spatial-tapping task is an ecological paradigm enabling the study of the effects of time constraints on action planning and execution through space. After an overview of the timing literature suggesting the existence of two modes of timing for motor control, we will report the findings obtained using the spatial tapping task. Classic analyses of timing variables (e.g. autocorrelation functions of the inter-response intervals and asynchronies) will be presented in combination with analyses of space performances (endpoint error distributions in space) to suggest that action control modes may coexist and become more or less predominant as a function of task constraints. In a final section, we will discuss the possibility that the spatial tapping task may be used as a simple neuropsychological task to evaluate the executive functions related to action planning, i.e., updating, inhibiting and switching in patients but also in healthy individuals planning to perform rhythmic actions of various complexities.

1.1.1 Planning ahead through time

Most of our daily activities, e.g. musical activities, require the planning of actions through space and time. Nevertheless, the task goal can be geared towards the needs to produce actions at a precise moment in time. For example, practicing a piano piece requires a player to set and focus on the time intervals needed between successive key presses to perform a given rhythmic pattern. In this case, an explicit internal representation of the intervals of time separating the successive actions is needed. In order to produce well-timed actions, e.g. repeated finger taps at a precise and regular rhythm, classical models of timing assume the existence of an internal clock, a model that is based on the possible existence of a pacemaker, counter, store and comparator (Treisman, 1963). The pacemaker produces regular pulses. The counter records the number of pulses arriving during a given time interval, e.g. between the two clicks of a metronome, and transfers this measure to a referential memory. The counter then records the number of pulses relative to the produced interval of time and transfers this measure into working memory. The referential and the produced interval are then compared and a judgement can be made (e.g. the interval produced is shorter than the referential). If the deviation to the referential interval is significant, a correction can be made through successive adjustments, at a later point.

This mechanism of time control through discrete event coding, referred to in the literature as event-based timing, can be revealed through time series analyses of the successive intervals of time, produced during a simple finger tapping task (Vorberg & Wing, 1996; Wing & Kristofferson, 1973a). Classically, inter-response intervals (IRIs) are measured as the difference in time between the onsets of successive taps. A given series of IRIs are staggered at one or more positions (In is compared to In+1) and correlation measures are performed. When timekeeping processes act to maintain a regular rhythm between successive actions, negative autocorrelation values (AC) are revealed at lag-1 while the values at greater lags are equal to zero (Wing & Kristofferson, 1973b), suggesting that a short interval is followed by a longer one, and vice versa. According to the W-K model, this negative AC-1 does not reflect immediate compensation of timing errors, but rather subtends low variability of the pacemaker to produce regular pulses. Indeed, the W-K model assumes the existence of two sources of variances to explain the variability observed in series of produced IRIs: a central source of variance related to the clock mechanism and a peripheral source of variance that reflects the motor implementation of the response, i.e. neuromuscular transmission lags. As it has been revealed through heartbeat interval patterns, when the variability of the pacemaker increases (e.g. in patients showing atrial fibrillation as compared to healthy subjects), negative dependencies in the heartbeats intervals significantly decreased at lag-1 (Ten Hoopen & Reuver, 1967). Hence, according to this biological model, the negative interdependency in series observed at lag-1 might reflect the stability of the pacemaker to produce regular pulses while a decrease in the negative AC-1 indicates an increase in the pacemaker instability. The measure of AC-1 values of IRIs are largely used today as an indicator of the involvement of event-based based timing in motor timing tasks (see Repp & Su, 2013; Repp, 2005, for reviews on motor timing tasks, methods and measures).

1.1.2 Planning ahead through space

Another important task goal in motor behaviour is to produce smooth patterns of successive movements through space (Hogan & Sternad, 2007; Hogan, 1987). For example, dancing may require producing movements across distinct directions and with distinct limbs without abrupt changes or interruptions in the spatial trajectory, in order to keep fluency and grace across the entire action pattern. Anticipatory mechanisms have been identified as the psychological mechanism that enables the control of movement smoothness through space and time in the context of cyclic actions (Roerdink et al., 2008). When cyclic actions are produced such as in continuous circle or line drawing, anchor points, which can be defined as reductions in spatial and/or temporal errors at specific locations along the trajectory path, are commonly observed (Beek et al., 1992). Anchor points are often detected around reversal points, e.g. transition points between flexion/extension movements and are described as “intentional attractors” at which critical information is available for the organization of the cyclic movements (Beek et al., 1992). This role of anchor points has been highlighted for example in a task in which participants were asked to alternate continuously between flexion vs. extension movements of the wrist (continuous line drawing). It was further shown that orienting the gaze or flexing/extending the wrist in advance in regards to the anchor point reduced significantly both the spatial and the temporal variability at this point (Roerdink et al., 2008). Thus, the production and sequencing of biomechanically distinct movements involves a switching cost that is measurable in space and time, and which can be reduced by anticipating through visual or musculoskeletal strategies the specific points of transitions between successive movements of a motor sequence, for the production of smooth and graceful motor patterns.

1.1.3 Finger tapping and circle drawing tasks reveal two distinct timing modes

Circle drawing tasks have been suggested as a valuable paradigm in the motor timing domain to reveal emergent timing, a mode of time control which is fundamentally different from the clock-like timing mode described above, i.e. the event-based mode (Huys et al., 2008; Robertson et al., 1999; Studenka & Zelaznik, 2008; Zelaznik et al., 2000, 2002). While event-based timing is involved in tasks that require maintaining an explicit representation of the timing interval to produce such as finger tapping along with a metronome (Semjen, Schulze, & Vorberg, 2000; Treisman, 1963; Wing & Kristofferson, 1973a), emergent timing is assumed to result from movement control processes that constrain a spatial trajectory for movement fluency (Turvey, 1977) and as such, have been studied using drawing tasks that require smooth production of cyclic actions (Zelaznik et al., 2000, 2002).

The first experimental evidences to distinguish between the two timing modes were reported by Robertson et al. (1999), who compared variance measures of the IRIs between different sorts of drawing and tapping tasks and found that temporal precisions in tapping tasks and drawing tasks were not correlated. Correlations were in fact not observed between distinct tasks involving similar tempo but did emerge when similar dynamics were required. More interestingly, the autocorrelation values of IRIs suggested different modes of time control: negative AC-1 values were revealed in finger tapping tasks while they were positive in circle drawing tasks. Authors suggested that, in discrete tapping tasks, participants need to estimate when to bring the finger down on the surface device without any particular trajectory constraints, while in continuous drawing tasks information about the entire space trajectory is crucial to produce consistent and stable intervals of time. These results have now been replicated (Studenka & Zelaznik, 2008; Torre & Delignières, 2008; Zelaznik et al., 2000). Importantly, clinical studies are now providing converging evidence that distinct neuronal systems are engaged according to each specific timing mode (Ivry, Spencer, Zelaznik, & Diedrichsen, 2002; Spencer & Ivry, 2005, 2007; Spencer, Zelaznik, Diedrichsen, & Ivry, 2003). Abnormalities in event-based timing are reported in patients with cerebellar damage whereas distortions of emergent timing are seen in Parkinson's disease, i.e., in patients with basal ganglia abnormalities.

1.1.4 Coexistence of the two modes of motor timing using two effectors

While event-based and emergent timing are usually conceived as mutually exclusive modes of timing, it has been suggested in the literature that the two modes could in fact coexist in a dual task situation (Repp & Steinman, 2010). Participants were asked to tap with their left hand and to draw circles with their right hand. After introducing phase shifts in the metronome series, phase correction responses (PCRs) were measured as the difference between the asynchrony associated with the phase shifted tone and the asynchrony associated to an estimate of when the response event should have occurred in the absence of phase shift. This measure was used as an indicator of the timing mode used to control sequence production, with larger mean PCR expected in the case of event-based timing (in this case, several taps are usually required to correct for the error) as compared to emergent timing (in this case, the timing stability is assumed to be poorly disturbed by a phase shift because the actions are not controlled through pure timing processes, see Repp, 2008). Results revealed that in this dual task, the tapping activity of the left hand was event-based in nature (large PCRs) while the drawing activity of the right hand was emergent (small PCRs). However, it was shown through an interaction effect that the circle drawing activity inhibited the PCR of the tapping activity especially at faster tempi, suggesting that the two tasks were in fact coordinated together, at least at fast tempi. Thus, authors concluded that the two modes of timing may coexist, i.e. be used simultaneously and be coordinated together when speed constraints are important. They took the results one step further by suggesting furthermore that the two timing modes could in fact coexist within a same task under any constraints, with however a predicted predominance of one or the other mode as a function of task demands. Suggestions were then proposed indicating the importance in future studies to find a motor task that would combine event-based and emergent processes under a single task situation and involving a unique effector.

The possible existence of such a hybrid task containing an event-based component and an emergent component with complementary contributions that would vary as a function of task demands has recently been challenged (Delignières & Torre, 2011). For these authors, the two modes of timing are necessarily exclusive and the idea of a mix of timing processes is not sustainable. Indeed, while the event-based mode suggests an abstract or effector-independent representation of the time intervals to produce, the second mode involves an effector-dependent representation of time. Thus, the two modes cannot conceptually be superimposed within a single task and furthermore, using a unique effector. According to these authors, the actual debate reflects ambiguities that remain in the interpretation of the tasks variables, e.g. autocorrelation values, which are used to demonstrate the existence of both modes of timing. Indeed, close to zero AC-1 values of IRIs are often interpreted as reflecting emergent processes while they could in fact result from (1) the simple increase in variability of the pacemaker, or (2) a hybrid strategy which consists in alternating rather than combining the two timing modes. The second assumption was tested by these same authors through the use of the air tapping task and specific instructions that encouraged participants to use event-based timing (maintain the timing accuracy) or emergent timing processes (optimise the smoothness of finger trajectory changes - Spencer et al., 2003). Through autocorrelation measures averaged across the group, results confirmed the authors' hypothesis and showed that the timing was event-based for the tapping task (negative AC-1), emergent for the oscillation task (positive AC-1), and hybrid for the air-tapping task (close to zero AC-1). However, by analysing AC values during the course of a trial for each participant, results revealed that participants were in fact alternating between the two modes of timing. Hence, it was proposed that other dependent variables are today needed in the field of motor timing in order to distinguish and to clearly reveal the specificity of each timing mode. In the present study, we propose to consider the anchoring points in space and the autocorrelation values in time to nourish the actual debate of two distinct coexisting timing modes for motor control. In the next paragraph, we describe the spatial-tapping task to test the possible co-existence of the two timing modes within the same action-sequence, using a unique effector.

1.1.5 The spatial-tapping task to suggest coexistence using a unique effector

The spatial tapping task was designed as a hybrid of finger tapping and circle drawing. In this task, participants are asked to produce finger taps on six distinct visual targets that are displayed around a virtual circle. The rhythmic tapping was to be performed following distinct tempi that were indicated by an auditory metronome. This design provided a task that is a mix of tapping and drawing demands under various speeded constraints: discrete events for the finger (on the six targets), with control of the spatial trajectory for the arm (around the circle). Using this task, we will test the hypothesis that tapping actions will be more discrete at slower tempi because time allows for the individual coding of each target; tapping actions should be more continuous at faster tempi because the timing pressure will force participants to simplify the complexity of the workspace in order to still perform the task even under extreme speeded constraints. Hence, we predict that event-based timing should be more involved at slower tempi and emergent timing should be more involved at faster tempi. In order to assess this hypothesis, we measured both time and space dependent variables. First, autocorrelation (AC) values of the IRIs and asynchronies were used to reveal event-based timing at slow tempi. As reported in other studies (Repp & Steinman, 2010; Torre & Delignières, 2008), AC values of asynchronies are generally positive and become stronger when the timing is emergent rather than event-based, suggesting fractal or long-term memories across the series, i.e. an error produced at the start of the trial is propagated until the end of the cycle. Hence, we predict that the AC values will be more negative for IRIs and less positive for asynchronies in the slow trials as compared to fast trials (Repp & Steinman, 2010; Torre & Delignières, 2008; Wing & Kristofferson, 1973b). Second, the area of the endpoint spatial distribution was measured as a function of target position. We predicted that we would find the emergence of anchor points in the spatial trajectory (reduction in spatial and timing errors) at the specific points of transition from extension to flexion, at faster tempi especially; this would be an indicator of the emergent timing processes.

In order to get more information about the trajectory information relevant for our participants, we further computed the orientation of the main axis of each spatial ellipse. These orientations were then contrasted to the referential/expected orientations (computation of an angular error). Similar measures have been used in previous studies to reveal the context in which hand pointing actions are planned in space (Desmurget, Jordan, Prablanc, & Jeannerod, 1997; Desmurget, Pélisson, Rossetti, & Prablanc, 1998; Rossetti & Régnier, 1995). Indeed, spatial ellipses have been shown to be oriented according to the preceding spatial position of the hand when participants are required to point from a starting point to a visual target without visual feedback of hand position (Gordon, Ghilardi, & Ghez, 1994). When the explicit instruction to"follow the straight path" linking a starting point and a target was given, the spatial ellipses measured at the target point were elliptical in shape and oriented towards the starting point, while they were roughly circular (and none oriented) when no specific instructions were provided to the participants (Desmurget et al., 1997). In another study, the spatial ellipses were oriented according to the global spatial configuration of the visual display (an arc or a line array of targets) only when movements were planned in reference to a memory-based stimulus, i.e. movements were executed 8 seconds after presentation of the target (Rossetti & Régnier, 1995). Hence, there is evidence that the orientation of the main axis of spatial ellipses can provide information about the psychological processes that guide the planning of hand pointing actions.

Because in the present spatial tapping task, multiple actions were required to be sequenced, one after the other in space and in time, we suggest that anticipation of the future motor element to perform is required more when time pressure is increased. Hence, we suggest that: (1) the ellipses will not demonstrate any specific orientation when attention is allocated to each discrete target (at slower tempi); (2) with increasing temporal pressure, the next target will be anticipated and in such case, the ellipses will be oriented as a function of the future target location (at intermediate tempi); (3) at the fastest tempi, the ellipses will be oriented as a function of the global arrangement of targets, here the contextual representation of a circular path and may be oriented in reference to the tangent to the circle. These results will furthermore be contrasted to the timing modes inasmuch that none oriented ellipses should be found for slow tempi when targets are considered as independent events; oriented ellipses should be observed at fast tempi when the global trajectory is predominantly considered under an emergent mode of time control.

1.2 Method

1.2.1 Participants

Sixty-eight right-handed students between 18 to 29 years of age and recruited from the University of Lille 3 participated voluntarily in the study. All participants received an information letter and provided written informed consent. All participants performed the task with their right hand and reported having normal or corrected-to-normal vision. The protocol received approval of the ethics committee in Human Sciences of the University of Lille 3.

1.2.2 Material & stimuli

A picture composed of six black targets was displayed on a touch screen Elo Touch 19” 1915L. The targets (10 mm diameter, 100 mm apart) were placed around a virtual circle of 100 mm radius. The participants were invited to stand in front of the screen that was placed upon a table and oriented parallel to the table (see Figure II.1).

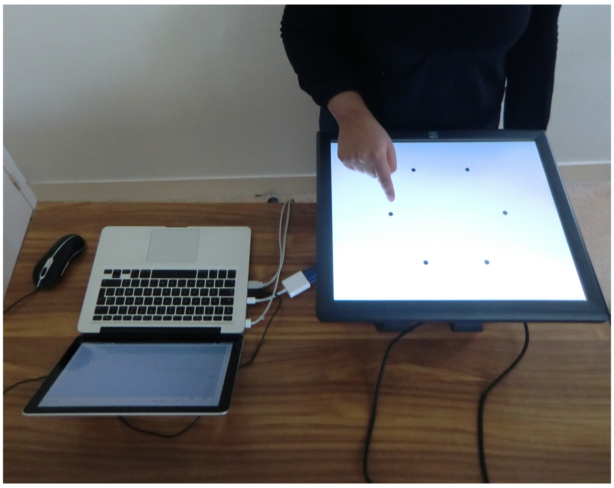

Figure II.1: Schematic representation of the experimental protocol

1.2.3 Task and procedure

The subjects’ task was to touch each visual target one after the other, starting from the bottom right target, and moving counter-clockwise using the right index finger (fist closed). Participants were instructed to synchronize each pointing action to a series of regular auditory tones (beep duration = 100 ms) that was played through computer speakers. Participants were encouraged to let their left arm hang relaxed along the body side. They were clearly instructed that the goal of the task was to be synchronized with the metronome. Each subject performed a total of nine trials. The initial tempo was an inter-onset interval (IOI) of 1100 ms. The temporal interval was increased by 100 ms after each trial with the fastest tempo having an IOI of 300 ms. Participants were required to produce sixty taps for each trial. The total duration of the session was 10 minutes, approximately.

1.2.4 Measured response parameters

Picture display, auditory tones, data collection and data analyses were controlled and conducted using Matlab software. The alpha level was set to 0.05 for all statistical procedures.

Autocorrelation measures. Inter-response intervals (IRIs) were measured as the time intervals between the onsets of successive taps. Asynchronies were calculated as the difference in time between the onset of a tap and the start of the nearest auditory tone. After omitting the first six IRIs and asynchronies of each trial, autocorrelation values were calculated up to six lags. Confidence intervals were used to assess whether the autocorrelation values were significantly different from zero (bounds $= 0 \pm Z_{(1-\alpha/2)}/\sqrt{N} = 0 \pm 1.96/\sqrt{68} = \pm 0.23$, see Box & Jenkins, 1976). These measures served as an indicator of the presence or absence of action control through an internal clock.

Timing and spatial errors. The $\mathrm{IRI}_{\mathrm{error}}$ was computed as the percentage of difference between each IRI and the reference inter-onset interval (IOI) of a given trial ($IRI_{error(i)} = (IRIi - IOI)/IOI * 100$). The IRI_{errors} were then averaged for each position, IOI and participant. This measure served as an indicator of the timing error. Asynchronies were also averaged for each position, IOI and participant and served as an indicator of synchronisation error with an external metronome. The endpoint distributions of the pointing actions were plotted for each target position (Figure II.2a). Using principal component analysis, spatial ellipses were then fitted to the movement endpoint distributions (Figure II.2b, for details on the calculations, see Gordon, Ghilardi, & Ghez, 1994). The confidence intervals were set to 95% on axis length. The area of spatial ellipses was then computed and used as an indicator of the spatial error.

Planning strategies. An aspect ratio was first measured for each ellipse as the square root of the ratio of the two axis lengths (the larger divided by the smaller) and was used as an indicator of the shape of the ellipses with an aspect ratio superior to 1 suggesting an elongated ellipse (see Van Beers, Haggard, & Wolpert, 2004, who used the same indicator for the characterisation of an elliptic shape). Second, the orientations of the main axis of each ellipse were computed. Finally, an orientation deviation (OD) was calculated as the angular difference between the orientation of the main axis of each ellipse and three referential orientations computed as the orientation of (1) the line linking the current target (n) to the next (n+1), (2) the line linking the current target (n) to the preceding one (n-1), (3) the tangent to the virtual circle computed for each target position (see Figure II.2c). These measures were used as indicators of the spatial planning strategies used to control hand trajectory.

Analyses of variance (ANOVAs) were performed for each variable with IOI; “target position” (TP) and “interval position” (IP) as repeated measures. Fisher LSD post hoc tests were used when required. The TP and IP position are presented in Figure II.3.

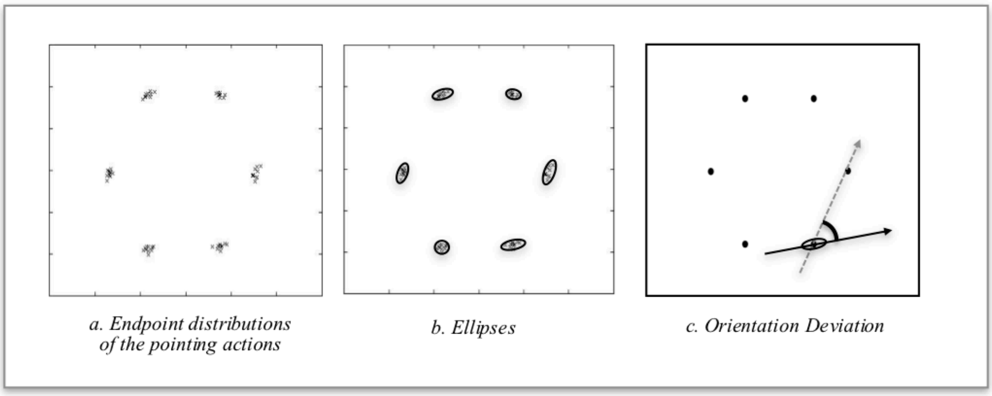

Figure II.2: Visual illustration of the three methodological steps that were implemented to calculate the orientation deviation (OD) of the endpoint scatterplots

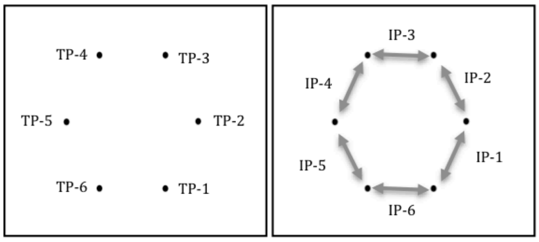

Figure II.3: Schematic description of the target positions (left) and the interval positions (right)

1.3 Results

1.3.1 Autocorrelation functions of the inter-response intervals and the asynchronies

The results obtained for the autocorrelation values (AC) of the IRIs and asynchronies as a function of IOI and for the six lags are presented in Figure II.4. Dependencies in the series were considered as significant when AC values were <- 0.23 or >+0.23 (see the methods section). ANOVA for repeated measures were then conducted as a function of IOI when dependencies in the series were revealed.

As expected, statistical analyses revealed the existence of negative dependencies in the series of IRIs at lag-1. The AC-1 values were negative between 1100 to 700 ms of IOI and not significantly different from zero at other IOIs. The ANOVA for repeated measures conducted as a function of IOI on the AC-1 values was significant (F(8; 536)=20.369, p<0.001). Post hoc tests revealed that the AC-1 values observed between 1100 to 800 ms of IOI (M= -0.28, SD= 0.14) were significantly larger than those observed between 600 to 300 ms of IOI (M= -0.15, SD= 0.16). No significant differences for AC-1 values were revealed at 700 ms of IOI (M= -0.25, SD= 0.15) and slower IOIs (M= -0.21, SD= 0.16). The AC-1 value reported at 300 ms of IOI was close to zero and significantly smaller than those observed at all other IOIs (M= -0.04, SD= 0.18).

Further dependencies in the series of IRIs were revealed at lag-6 only, i.e.

between successive cycles, with a cycle being composed of six successive IRIs. The values were positive between 500 to 300 ms of IOI and not significantly different from zero at other IOIs. The ANOVA for repeated measures conducted on the AC-6 as a function of IOI was significant (F(8; 536)=17.586, p<0.001). Post hoc tests revealed that the AC-6 values were significantly smaller between 1100 to 800 ms of IOI (M= 0.11, SD= 0.19) as compared to all other trials. From 700 to 600 ms of IOI, they were significantly larger than at slower tempi and significantly smaller than at faster tempi (M= 0.20, SD= 0.20). Finally, between 500 to 300 ms of IOI, the AC values were the largest as compared to all other trials (M= 0.30, SD= 0.19).

For the asynchronies, statistical analyses revealed the existence of positive dependencies in the series at lag-1. The AC-1 values were in fact positive across all tempi. The ANOVA for repeated measures conducted on the AC-1 values as a function of IOI was significant (F(8; 536)= 4.308, p<0.001). Post hoc tests revealed that the AC-1 values were significantly smaller between 1100 to 800 ms of IOI (M= 0.38, SD= 0.24) than between 600 to 300 ms of IOI (M= 0.48, SD= 0.22). Further positive dependencies were observed in the series at greater lags, here at lag-2. AC-2 values were positive between 800 to 500 ms of IOI and not different from zero at other IOIs. The ANOVA for repeated measures conducted as a function of IOI was however not significant (F(8; 536)= 1.822, ns.) indicating that the dependencies between asynchronies were similar across tempi.

1.3.2 Timing and spatial errors: asynchronies, $\mathrm{IRI}_{\mathrm{error}}$ and mean area of spatial ellipses

ANOVA for repeated measures were conducted as a function of IOI, target position (TP) and interval position (IP) for each dependent variable (asynchrony, $\mathrm{IRI}_{\mathrm{error}}$, area of spatial ellipses).

The ANOVA conducted on the asynchronies, revealed an absence of significant differences as a function of IOI (F(8; 536)=1.130, ns.) and an absence of interaction effect IOI*TP (F(40; 2680=1.171, ns.), see Figure 5a. A significant effect of TP was revealed (F(5; 335)= 5.243, p < 0.001). Post hoc tests confirmed that the asynchronies at TP-2 and TP-5 were not significantly different between them (M= -3 ms, SD= 128 ms) but were significantly different as compared to all other TPs (M= 4 ms, SD= 125 ms). The ANOVA conducted on the

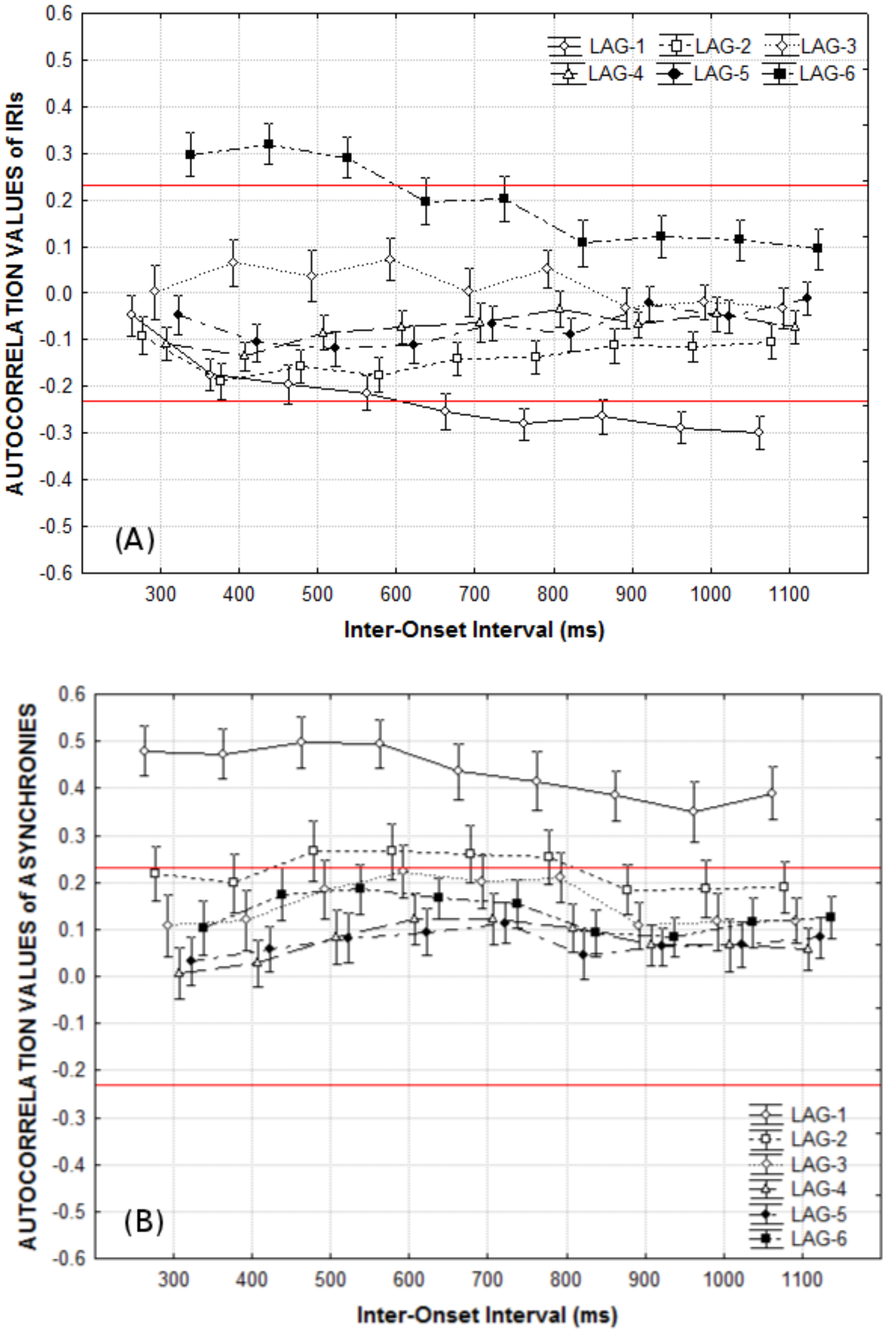

Figure II.4: Autocorrelation functions of the asynchronies and of the inter-response intervals (IRI) are presented as a function of the tempo (inter onset interval – IOI) imposed by an external metronome. The legends specify for each figure the considered time lags

$\mathrm{IRI}_{\mathrm{error}}$ revealed both significant effect of IOI (F(8;536)=12.413; p<0.001) and interaction effect IOI*IP (F(40;2680) = 6.607; p<0.001).

Post hoc tests relative to the effect of IOI revealed that $\mathrm{IRI}_{\mathrm{error}}$ was small and close to zero between 1100 to 400 ms of IOI (M= -0.2%, SD= 3.2%) and was significantly larger at 300 ms of IOI (M= 2.1%; SD= 6.4%) as compared to all other intervals (Figure II.5b), suggesting that the time intervals were accurately produced across most of the tempi.

Post hoc tests relative to the IOI*IP interaction revealed that at slower tempi, i.e. between 1100 to 800 ms of IOI, the $\mathrm{IRI}_{\mathrm{error}}$ was small and negative for IP-1 (M= -1.1%, SD= 2.8%) and IP-4 (M= -1.5%, SD= 2.6%), small and positive for IP-2 (M= 1.9%, SD= 3.1%) and IP-5 (M= 1.1 %, SD= 2.9%), and close to zero for IP-3 (M= -0.2%, SD= 2.4%) and IP-6 (M=-0.6 %, SD= 2.7%). Hence, at slower tempi, the timing intervals were shorter than the referential IOI before TP-2 and TP-5 as if these targets positions were being anticipated a little too much. At 700 ms of IOI, the $\mathrm{IRI}_{\mathrm{error}}$ increased significantly for most of intervals, i.e. IP-1 (M= -2.1%, SD= 3.4%), IP-2 (M= 2.3%, SD= 3.3%) and IP-5 (M= 2%, SD=3.2%), without changes in the sign of the error. From 600 to 400 ms of IOI, significant changes were revealed for all IPs and altered in some case the sign of the error. The error was in fact more negative for IP-3 (M= -1.4%, SD= 3%) and more positive at IP-2 (M= 3.2%, SD=2.9%) at 600 ms of IOI. For 500 and 400 ms of IOI, the error was further more negative at IP-4 (M= -3.8%, SD= 3.9%) and IP-5 (M= 1.42%, SD= 3.9%), while no changes were revealed for IP-6 and IP-1. These results suggest that from 600 to 400 ms of IOI, the $\mathrm{IRI}_{\mathrm{error}}$ was more negative just before the location of one of the potential anchor point. From 500 ms of IOI, the negativity was propagated for half of the virtual circle, and more positive for the other half. Finally, at 300 ms of IOI, the errors became more positive for all IPs. These results are presented in Figure II.5c.

For the spatial errors, the ANOVA conducted on the area of spatial ellipses revealed both a significant effect of IOI (F(8;536) = 216.620; p<0.001) and an interaction effect IOI*TP (F(40; 2680) = 6.666, p<0.001). These results are presented in Figure II.6. Post hoc tests relative to the effect of IOI revealed that the area was smaller at slower tempi, i.e. between 1100 to 900 ms of IOI (M= 36 mm^2; SD= 22 mm^2) as compared to 500 to 300 ms of IOI (M= 125 mm^2, SD= 76 mm^2). Between 800 to 600 ms, the area was significantly larger than that measured for slower tempi (M=51 mm^2, SD= 29 mm^2), but smaller than that measured for faster tempi (Figure 6a). Post hoc tests relative to the

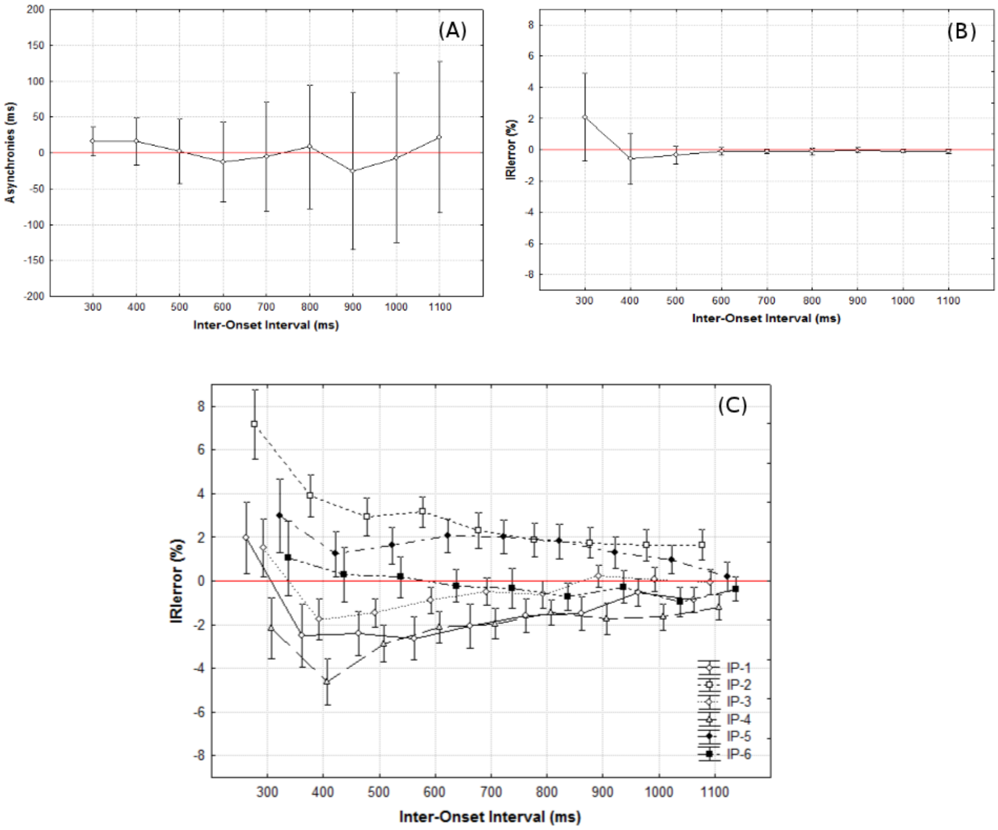

Figure II.5: Asynchrony errors (left) and temporal errors (inter response interval error – IRI, right) are presented as a function of the tempo (inter onset interval – IOI) imposed by an external metronome. The bottom panel reveals the temporal errors as a function of the tempo for each of the interval positions in space (IP) effect of IOI*TP revealed no differences as a function of TPs between 1100 to 900 ms of IOI. From 800 to 700 ms of IOI, the area was significantly smaller at TP-5 (M= 39 mm^2, SD= 36 mm^2) and TP-2 (M= 44 mm^2, SD= 24 mm^2) respectively, as compared to TP-6 (IOI= 800 ms: M=53 mm^2, SD= 36 mm^2, IOI= 700 ms: M= 57 mm^2, SD= 35 mm^2). From 600 to 400 ms of IOI, the area was significantly smaller at TP-4, and significantly larger at TP-1. For all other targets, the closer the TPs were to TP-4, the smaller was the area; the closer they were to TP-1, the larger was the area (Figure 5b). At 300 ms of IOI, the area was the smallest at TP-4 (M= 160 mm^2, SD= 126 mm^2) and the largest at TP-1 (M= 233 mm^2, SD= 125 mm^2), which was significantly larger than that measured at all other TPs. Overall, these results suggest the emergence of an anchor point in the spatial trajectory at TP-4 from 600 ms of IOI.

1.3.3 Orientation deviation according to the three models of motor planning

The aspect ratio was measured first to reveal whether the scatterplot of terminal pointing errors were elliptical in shape. ANOVA for repeated measures were then conducted on the orientation deviation of the principal axis of the ellipse (OD) as a function of the interaction IOI*MODEL and IOI*TP*MODEL.

For the aspect ratio, single t-tests conducted as a function of target position revealed that the aspect ratio was significantly different from 1 for all TPs and at all tempi (for readability purposes, t-values were not reported; M= 1.40, SD= 0.24). These results suggest that a main axis emerged to produce an oriented scatterplot of the endpoint spatial errors at all tempi and for all targets.

The ANOVA conducted on the OD revealed significant interaction effects of IOI*MODEL (F(16; 1072)= 9.697, $p<0.001$) and IOI*TP*MODEL (F(80; 5360)= 2.679, $p<0.001$) (see Figures 7 & 8, respectively).

Post hoc tests relative to the IOI*MODEL interaction suggested that the error to the models were the smallest for two of the models (previous target and tangent to the circle) across all tempi, except at 1000 ms of IOI for which no significant differences were revealed between the three tested models (see Figure 7). Mean ODs were overall significantly smaller at faster tempi than slower ones, i.e. from 700 ms of IOI for the OD from the previous target and from 600 ms of IOI for the OD from the tangent of the circle. These findings indicate that significant changes in the modes of planning control emerged around 700 ms of

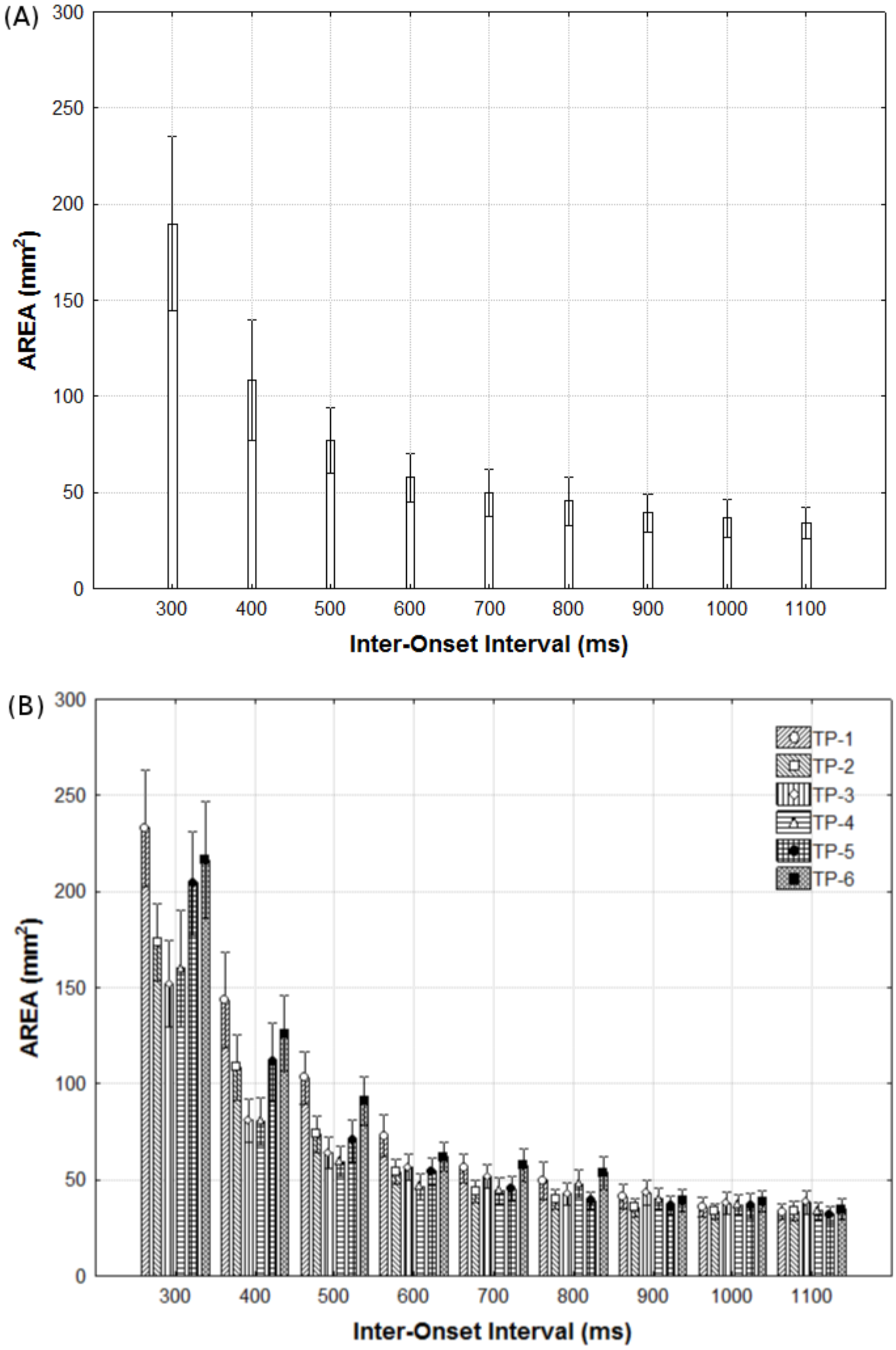

Figure II.6: Spatial errors (area of the endpoint scatterplots) are presented as a function of the tempo (inter onset interval – IOI) imposed by an external metronome. Results are specified for each specific target position (TP) in the bottom panel. N.B. in the top panel, those bars that are grouped with brackets are not significantly different from each other (alpha level set to 0.05).

IOI, movements becoming more continuous with less attention focused on each discrete target.

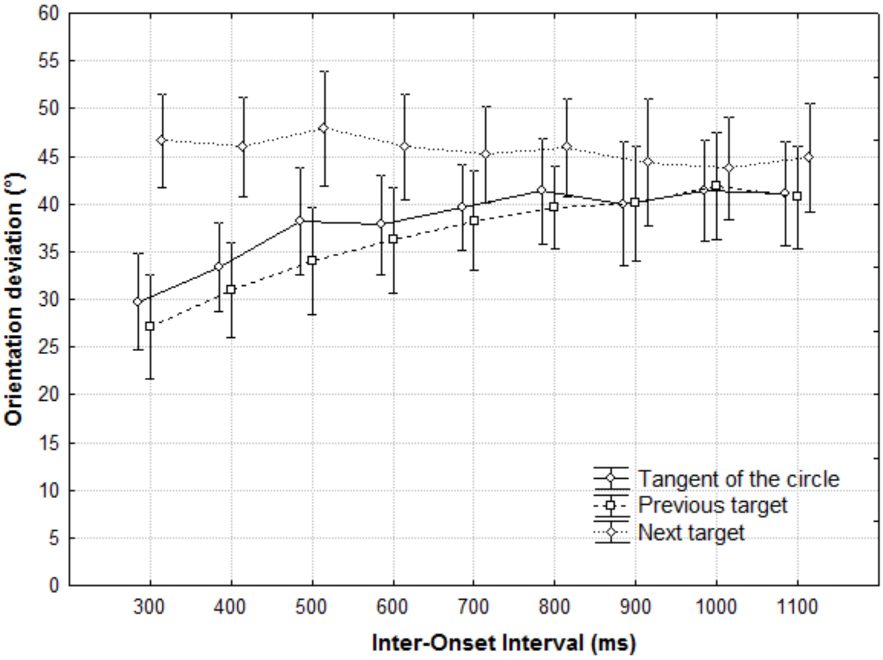

Figure II.7: Orientation deviations of the endpoint scatterplots are presented as a function of the tempo (inter onset interval – IOI) imposed by an external metronome for the three selected models: fit to the tangent to the circle (circles); fit to the previous target (squares); fit to the next target (diamonds)

Post hoc tests on the IOI*MODEL*TP interaction revealed that ellipses were significantly oriented towards future targets between 1100 to 600 ms of IOI for TP-1 and TP-4 only, with however a significant decrease in OD for TP-1 between 800 to 600 ms of IOI. Interestingly, between 500 and 300 ms of IOI, the ellipses at TP-1 and TP-4 became significantly less oriented towards future targets (i.e. TP-2 and TP-5), suggesting a change in control strategy from a predictive to a more reactive model due to time pressure. In fact, for tempi faster than 500 ms of IOI, the ellipses at TP-4 and TP-5 were significantly more oriented towards the tangent to the circle as compared to the two other models. For all other target positions, the best fit was obtained with an orientation towards the previous target position at all tempi. Note however, that the ellipses at TP-3 were significantly more oriented towards TP-4 (our anchor point) from 500 ms of IOI. These results suggests that significant changes in the planning strategies were revealed at 800 ms of IOI (less prediction available at TP-1), and at 500 ms of IOI (prediction of the anchor point with more circularity in the gesture).

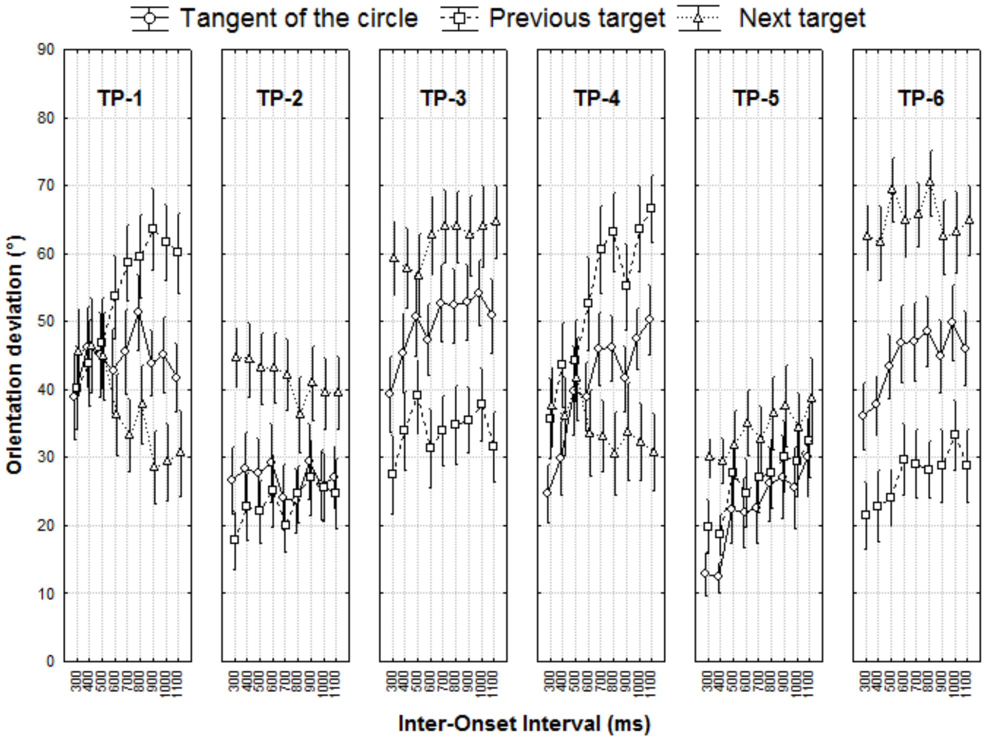

Figure II.8: Orientation deviations of the endpoint scatterplots are presented as a function of the tempo (inter onset interval – IOI) imposed by an external metronome for each target position (TP). The legends specify the three selected models that are considered: fit to the tangent to the circle (circles); fit to the previous target (squares); fit to the next target (diamonds).

1.4 General discussion

The objective of this study was to nourish the actual debate concerning the possible co-existence of the two timing modes of action control. Empirical studies have suggested the possibility to combine the two modes within dual task paradigms (Repp & Steinman, 2010; Studenka & Zelaznik, 2008). However, the possibility of such a combination within a single task using a unique effector was not tested. In the present study, we propose a novel task to assess the coexistence hypothesis - the spatial-tapping task that was designed as a hybrid task of finger tapping and circle drawing, the two prevailing paradigms used in the motor timing domain. More specifically, participants were asked to produce finger taps towards six distinct visual targets while moving their arm around a circular trajectory, at distinct tempi imposed by a regular metronome. An original analysis of the endpoint distributions in space was performed to provide additional dependent measures to the autocorrelation values classically used in the timing literature to support a transition from event-based to emergent processes as a function of increasing tempo.

As suggested by the results reported here, we found that the timing was predominantly event-based at slow tempi (periods of 1100 to 900 ms) and emergent at fast tempi (periods of 500 to 300 ms). A transition from event to emergent operated at intermediate tempi (periods of 800 to 600 ms). In this phase, the timing accuracy was progressively decreased with the emergence of an anchor point in space at 600 ms of IOI, i.e., a reduction in the spatial and timing errors at the transition point from extension to flexion movements. Hence, at the specific tempo of 600 ms, the two motor timing modes were coexisting, indicating that at this tempo, participants tried to maintain the timing accuracy but started to produce more circular trajectories in order to cope with increasing time pressure.

The findings presented here provide the means to reconsider up to a certain degree the question developed by Delignières & Torre (2011): while it is certainly not possible to guide the arm both with and without a timing representation of the rhythmic sequence, our results suggest that it is possible to guide arm movements using both a timekeeping mechanisms and a predictive control of the spatial constraints of trajectory. Thus, our findings argue in favour of the coexistence of the two motor timing modes, with a predominance as a function of task demands. But they furthermore infer the importance of considering time embodied within a task, i.e., interpreting spatial and timing errors within the theoretical context of action planning overall rather than to the motor timing domain per se. In the following discussion section, we first detail the general findings of the present study. Second, we present arguments in favour of the coexistence of action control modes, before proposing to relate these results to a three-component action planning model that is currently used in the neuropsychological literature of executive functions (Miyake & Friedman, 2012; Miyake et al., 2000).

1.4.1 Global performances in the spatial-tapping task

The statistical analyses of variance conducted on the asynchronies revealed that our participants tapped in synchrony with the regular metronome across all tempi with relatively small mean errors and variances close to ±100 ms at tempi slower than 600 ms, and ± 50 ms at faster tempi. The intervals of time were on average accurately produced across tempi, i.e. with $\mathrm{IRI}_{\mathrm{error}}$s close to zero, except for the fastest trials performed at 300 ms of IOI for which the $\mathrm{IRI}_{\mathrm{error}}$ significantly increased. The spatial error varied following three speed intervals: best performance in space was reached between 1100 to 900 ms of IOI; the spatial error was slightly but significantly increased (larger mean area) between 800 to 600 ms of IOI as compared to slower trials, and was finally the largest for trials performed at tempi of 500, 400 and 300 ms of IOI.

The analysis of the orientation of the endpoint scatterplots provided the means to consider whether actions were planned in a discrete or continuous way across tempi. Significant changes in the mode of planning control were revealed around 700 ms of IOI. From 700 ms of IOI, the ellipses were on average significantly more oriented towards preceding targets, suggesting that less attention resources were available to focus attention on discrete elements. From 600 ms of IOI, the ellipses were on average significantly more oriented as a function of the tangent to the circle, suggesting that from this specific IOI, the movements became more circular.

Hence, these results suggest that participants were able to follow the instructions, which was to keep at best the synchrony across all tempi. The spatial error was increased stepwise with changing tempi with maximum errors observed for tempi faster than 500 ms of IOI. As predicted, the trajectories of the pointing actions were discrete at slow tempi and became more continuous from 600 ms of IOI. In the next paragraph, we detail the results obtained for the autocorrelation values.

1.4.2 Autocorrelations analyses suggest that a transition from event-based to emergent timing occurred in the spatial-tapping task

Measures of both the asynchronies and the inter response intervals (IRI) were performed to reveal the timing modes used to perform the spatial-tapping task. The results for the IRIs revealed that the autocorrelation values at lag-1 were significantly more negative between 1100 to 700 ms of IOI as compared to faster tempi, suggesting as proposed by the W-K model (Wing & Kristofferson, 1973b) that slow motor sequences are planned and guided through a clock-like mechanism i.e. controlled through event-based timing. The IRI autocorrelation values at lag-1 remained negative at moderate tempi (600 ms to 400 ms of IOI) but the amplitude of AC-1 was none different from 0 at the fastest tempo of 300 ms of IOI, suggesting that here the timing mode used was emergent in nature.

The strategy to use changing tempi to lead participants to transition from a given mode of timing control to another has already been used in the literature (Huys et al., 2008; Repp, 2008). In the study proposed by Repp (2008), a finger-tapping task was performed under distinct tempi and a phase shift was introduced in the metronome series. Phase correction responses (PCRs) were used as an indicator of the timing mode used for motor planning and execution, with larger mean PCR expected in the case of event-based timing. Results revealed that timing control was more event-based between 1200 to 700 ms of IOI as compared to faster IOIs (300 to 600 ms), which were more emergent in nature. Hence, the results presented in the present contribution using the spatial-tapping task confirm those observed by Repp (2008), with a shift from one mode to the other occurring at the similar metronome speed of 700 ms of IOI. As reported in other studies (Repp & Steinman, 2010; Torre & Delignières, 2008), AC values of asynchronies are generally positive and become stronger when the timing is emergent rather than event-based, suggesting fractal or long-term memories across the series, i.e. an error produced at the start of the trial is propagated until the end of the cycle. In the spatial-tapping task, AC-1 values of asynchronies were positive across all tempi, but were significantly more positive when faster than 600 ms of IOI as compared to slower tempi, confirming that the timing was more emergent for rhythmic tempi faster than 700 ms of IOI. To note the fact that

Significant dependencies in the series of IRIs and asynchronies were also revealed at lags greater than 1. For IRIs, significant dependencies were revealed at lag-6; these dependencies increased in amplitude with increasing tempo. These autocorrelation values at lag-6 may reflect in fact dependencies between cycles, with a cycle being composed of the six successive intervals of times (6 visual targets composed the virtual circle). Here, AC-6 values were close to zero for slower tempi (1100-800 ms of IOI), significantly positivity between 700 to 600 ms of IOI, and the largest positivity between 500 to 300 ms of IOI. This pattern of results suggest that IRI variability propagated throughout a cycle in an increasingly fashion with increasing tempi, suggesting an emergent mode of control.

1.4.3 Anchor points to confirm the use of emergent timing

Classically, sensorimotor synchronisation tapping tasks require participants to produce a series of taps in synchrony with a metronome. This task explicitly requires the control of discrete timed events. In circle drawing tasks, participants are required explicitly to produce a smooth trajectory around a virtual picture. In the following, we will argue that the spatial positioning of the series of targets through the workspace, lead our participants to perform a true mix of tapping and drawing.

To reveal a temporal anchor, the $\mathrm{IRI}_{\mathrm{error}}$ was analysed as a function of spatial locations. $\mathrm{IRI}_{\mathrm{error}}$ reflected an alternation of negative/positive errors between 1100 to 700 ms of IOI, i.e., an alternation between relatively short and long intervals. Such patterns of results suggest the involvement of sequential error correction mechanism that take place when a timekeeping event-based mechanism is used to maintain timing accuracy (Wing & Kristofferson, 1973a, 1973b). Between 600 to 300 ms of IOI, the pattern of timing errors was different. Indeed, the $\mathrm{IRI}_{\mathrm{error}}$ was more negative just before TP-4, i.e. just before the point of transition between extension and flexion movements only, which suggests that an anchor point in time emerged from 600 ms of IOI. From 500 ms of IOI, timing errors were amplified with more negativity for those time intervals following TP-3 and more positivity following TP-6, suggesting the existence of long-term memories across the series of IRIs (within the semi-circle), i.e. an error produced at the start of the semi-cycle propagated throughout the cycle due to the absence of corrective mechanism in the timing domain (see Torre & Delignières, 2008).

To reveal a spatial anchor, we introduced an original analysis of the spatial endpoint distributions. Using principal component analysis (see Gordon et al., 1994), spatial ellipses were fitted to the endpoint distributions surrounding each target location. The spatial area of each ellipse was then measured as an indicator of the spatial error. Statistical analyses revealed an absence of differences as a function of spatial position between 1100 and 900 ms of IOI while between 800 to 700 ms of IOI, the spatial error was significantly smaller at TP-5 and TP-2 respectively as compared to other TPs. Statistical analyses further revealed that between 600 and 300 ms of IOI, a significant reduction in the spatial error was observed at TP-4, phenomenon that was observed for no other target position: under high speeded constraints TP-4 seemed to be used cognitively to anchor hand trajectory in space. Furthermore, the closest the TPs were located to TP-4, the smaller was the spatial error; The closest the TPs were to TP-1 (opposing target), the larger was the spatial error. These results suggest that for faster paced sequences, the task goal was predominantly spatial with a specific focus directed towards the critical point in space at which the transition between arm extension and flexion was necessary to ensure task performance.

Overall, these results suggest that anchor points emerged in space and in time from 600 ms of IOI and faster. While the task goal was to maintain timing accuracy between 1100 to 700 ms of IOI, the task goal may have transitioned towards the needs to smooth the flexion/extension movements involved in the sequence in order to insure the production of the circular shape for faster tempi. It is possible that a lack of attentional resources forced participants to focus on a unique point in space to implement corrections and the location at TP-4 was chosen due to its specific biomechanical properties (change from extension/flexion arm direction). Hence, our paradigm somehow revealed the fact that as a function of task constraints, different relationships can exist between movement trajectories and timing goals. In some situations, movement trajectories serve the timing goals by implementing timing error corrections, as in the case for slower tempi. In other situations, movement trajectories simply implement temporal regularity, with a cognitive focus that is now being set on the spatial trajectory and as such, the task is to perform synchronised oscillations in the shape of a circle. We further consider the question of trajectory shape in the next section.

1.4.4 Changes in planning strategies revealed through the analysis of arm trajectories

As a support to explain how the actions may have been planned through space, we analysed whether spatial ellipses were oriented towards the next target, the preceding target or in function of the tangent of the circle.

First, the analysis of the orientation of the ellipses indicated that the arm trajectory was controlled following three distinct strategies, with changes in strategies that followed the stepwise increase revealed for the spatial error (area of spatial ellipses) in function of tempi. Indeed, between 1100 to 900 ms of IOI, the spatial error was the smallest. Here, the spatial ellipses were oriented towards the next target at TP-1 and TP-4 only, to predict the spatial locations of TP-2 and TP-5. They were oriented in function of the two other models at other TPs. Note here that TP-2 and TP-5 were the TPs at which the better synchrony was reached across trials and towards which predictive timing mechanisms were oriented (the intervals of time were shorter than the referential just before these specific TPs). Second, between 800 and 600 ms of IOI, a slight but significant increase was reported in the spatial error. Here, the spatial ellipses were significantly less oriented towards the next target at TP-1 as compared to slower IOIs while no changes were reported at TP-4. Third, between 500 and 300 ms of IOI, the ellipses at TP-1 and TP-4 were not oriented anymore towards the next target, however, the ellipses at TP-3 were significantly more oriented towards the next target, i.e. TP-4, the anchor point. This suggests that a change in cognitive strategy occurred for tempi faster than 500 ms of IOI.

Hence, three task goals were here identified: time control at slow tempi, space control at fast tempi and an intermediate phase, during which the task goals were both temporal and spatial in nature. More specifically for the intermediate phase, i.e., between 800 and 700 ms, participants were trying to maintain temporal accuracy whereas the spatial constraints were becoming difficulty to control (gravitational effect on arm dynamics). Here, motor inhibition strategies may have been implemented in order to avoid performing a circular movement and maintaining the discrete aspect of the motor task. For 800-700 ms of IOI, this strategy was efficient: in spite increases in time and space variability, the AC-1 values of IRIs remained significantly negative. Nevertheless, at 600 ms of IOI, clues to coexistence were observed: the orientation of the ellipses further confirmed that the planning strategies remained focused on time, while an anchor point was revealed at TP-4. The IOI of 600 ms is often referred to in the literature of timing as the spontaneous tempo (Fraisse, 1982), i.e. a tempo for which a resonance phenomenon takes place between the natural internal beat and a preferred perceptual rhythm (Drake, Jones, & Baruch, 2000). At this tempo, participants often report optimal pulse sensation (Parncutt, 1994) and better tempo sensitivity (Drake & Botte, 1993; London, 2002). Further studies are now needed to know whether the spontaneous tempo codes for a functional frequency that signs the moment for which the cognitive system is able to co-activate those processes that are geared to the implementation of smooth trajectory and those that code for a precise control of event-based timing. This hypothesis could be tested using, e.g. a dual task paradigm to reveal the cognitive resources required for motor planning and execution (Delevoye-Turrell et al. 2006) and following the present data, reduced attentional cost should be obtained specifically when the spatial-tapping task is to be performed at the preferred motor tempo of 600 ms of IOI, the similar pace that codes for rhythmic preference (Kornysheva et al., 2010).

1.4.5 Timing, motor planning and executive functions

Let us now consider the spatial-tapping task as a simple visuo-motor planning task in which tapping actions are sequenced the one after the other in space and time. It is the case that in the neuropsychological literature, this complex rhythmic task would require three different executive functions. Indeed, at slower tempi, working memory mechanisms would be thought to be required to maintain and update the referential time interval for timing accuracy purposes. At faster tempi, one would consider the switching cost relative to the necessary transition between a motor schema related to arm extension and another motor schema needed for the arm flexion. It would then be considered that significant reduction in switching cost could be reached through the use of anticipatory strategies. Finally, at intermediate tempi, inhibitory processes would be thought to be required to favour (or combine) one or other of the control modes of action control with an equilibrium needed between switching and maintaining in order to obtain accurate performance levels both in space and in time. Interestingly, these functions of updating, inhibiting and switching are referred to in the literature as the main high-level executive functions that are involved in the planning of action sequences (Friedman et al., 2008; Miyake & Friedman, 2012; Miyake et al., 2000). Hence, we have suggested that the spatial-tapping task could be an exemplar (non-verbal) task that would provide the means to gain a better understanding of the executive functions themselves and a possible insight on their possible function for motor timing. It is the case that the actual tasks that are used especially in pathological populations suffer a number of validity problems leading to numerous misunderstanding and ambiguities in the domain of the neuropsychology of the executive functions (see Miyake et al., 2000). Hence, we have proposed in a recent study (Dione, Ott, & Delevoye-Turrell, 2013) the possibility to use the spatial-tapping task to assess execution functions by correlating results obtained in the spatial-tapping tasks with those obtained in the tests classically used to evaluate inhibiting, updating and switching. Multiple regression analyses revealed significant and specific relationships between (a) the $\mathrm{IRI}_{\mathrm{error}}$ in the slower phase of the spatial-tapping task and the scores obtained in a n-back task assessing the updating function, (b) the contact times in the intermediate phase of the spatial-tapping task (results not shown here) and a go-no-go task assessing the inhibition function, (c) the magnitude of the spatial area in the faster phase of the spatial-tapping task and a letter-number task assessing the switching functions. Hence, it may be possible to use the spatial-tapping task as a relevant neuropsychological test to assess the executive functions of motor planning in various healthy and pathological populations. For this purpose, we promote as a conclusion the importance of multidisciplinary research for the further understanding of the relevance of high-level cognitive functions in the timing and executive domains of motor control.

Acknowledgments

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Study 2

Abrupt onsets to modulate selective attention and conscious perception in a circle-tapping task

Abstract

Conscious perception and attention have been presented within the predictive coding framework as using similar brain functions: prediction error minimization through opponent computations. While conscious perception is seen as a synthethiser that binds together the multiple information presented to us in order to represent the world in a simplified manner, attention is thought as an analyzer that reduces the variability of discrete perception-action links for a better definition of the causal relationships between the events arising in the world. The predictive coding hypothesis remains a theoretical view about the brain functions and needs empirical examples in humans to support the hypotheses of the model.

In the present study, we asked participants to produce tapping actions of the hand following a circular trajectory at distinct tempi. In order to manipulate selective attention and the opposite computation, i.e. conscious perception, abrupt onsets were respectively displayed to orient the motor preparation towards the current visual target to tap, or in anticipation towards the next one. Results revealed that the action were more discrete and accurate in time when attention was focused on each discrete action (current condition), while actions were more variable in space and more circular in the second situation when attention was oriented towards the next event. Hence, we were able to favor selective attention and/or conscious perception in the spatial-tapping task according to specific task constraints and through the help of distractors attracting attention in an automatic way.

2.1 Introduction

2.1.1 Attention and conscious perception as perception/action mediators

It is often considered that our capacity-limited brain is not equipped to process the multiple information present in our environment in real-time. Therefore, attention is required to select relevant information from irrelevant sources in order to meet task goals (James, 1890). By definition, this implies a focus of processing resources for attended stimuli as compared to non-attended stimuli (Reynolds & Chelazzi, 2004). The effects of selective attention have been widely studied in humans through cueing paradigms (Posner & Petersen, 1990; Posner, 1980), in which a cue provides a prior information about the possible location of a future target to detect in the visual display. Whether the cue allows reliable predictions about the location of appearance of the future target (valid trials), facilitation effects are commonly reported, i.e. participants tend to respond faster and with higher accuracy as compared to invalid trials. Hence, attention could be defined as a cognitive mechanism that bias perception to enhance the subject's capacity to process and to act upon a given stimulus. Although nobody disputes the view that attention acts as a spatial spotlight that biases perception to optimize the processing of a given visual object or stimulus (Posner, 1980), there is increasing evidence that the primary role of attention is motor preparation, even when no motor execution is required. Indeed, according to action-based theories of selective attention (Rizzolatti, Riggio, & Sheliga, 1994; Tipper, Lortie, & Baylis, 1992), attention does not arise through the intervention of specific attentional circuits but overlaps motor preparation. This theory, namely the "premotor theory of attention" has been tested empirically in studies requiring themotor preparation of eye movements (Sheliga, Riggio, & Rizzolatti, 1994; Van der Stigchel & Theeuwes, 2007; Van der Stigchel, 2010). Indeed, an eye movement or a saccade brings the central focus of the eye from a starting point to an endpoint. Hence, a specific spatial location must be selected as an endpoint for the saccade, requiring necessarily selective attention for motor preparation. Thus, oculomotor settings appear as prevailing paradigms to reveal the relationships between attention and motor preparation. In a study proposed by Sheliga et al. (1994), the trajectory of the saccade was shown to be influenced by the spatial position of a precued imperative target which was displayed from five possible target locations and which indicated when to produce a vertical saccade from a fixation point to a dot located at the bottom of the screen. The saccades were typically deviated away from the spatial position of the imperative stimuli. This result suggests that focusing attention in a covert manner (i.e. the eyes and head are fixated) on a spatial position during the motor preparation of a saccade influences the saccade trajectories. These findings were broaden in another series of experiments that showed that the oculomotor system was activated wherever spatial attention was allocated (Van der Stigchel & Theeuwes, 2007) and support the idea that spatial attention is not dissociable from motor preparation. The premotor theory of attention was also recently tested within a motor task using upper limb movements (Brown, Friston, & Bestmann, 2011). In this study, participants had to produce flexion or extension movements of the wrist with the right or the left hand, in function of the information provided by a visual target. The target was preceded by valid or invalid cues, which informed the participant about the two dimensions manipulated. Reactions times were measured through EMG recordings of the right forearm flexor and extensor muscles. A significant interaction effect between the validity of movement and effector cues was revealed on reaction times suggesting that the same mechanisms that served to bias perceptual signals in the visual domain also biased proprioceptive signals in the motor domain. Hence, based on these findings, it is today thought that motor preparation and selective attention overlap, with attention being a mediator between perception and action.

It has been recently suggested that another kind of mental phenomenon could play the same mediate role between perception and action, in particular when multiple sensory information must be processed at the same time (Boxtel, Tsuchiya, & Koch, 2010; Hohwy, 2012; Tsuchiya & van Boxtel, 2013). This mental phenomenon is referred to in the literature as “conscious perception”. Here, the term of consciousness does not refer to the levels or states of consciousness such as wakefulness or coma, but rather to the content of consciousness, i.e. awareness. According to Boxtel et al. (2010), the function of conscious perception is diametrically opposed to the function of attention. Rather than selecting information, conscious perception summarizes relevant information pertaining to the current state of the organism in relation to its environment and in function of the task that is considered. Conscious perception may be operating at longer timescales than attention and at a different level of the cortico-visual hierarchy. This function, which may correspond to a binding function (Treisman & Gelade, 1980) may be implemented in order to build long-term plans, to support decision making, but also to enable theory of mind or logical thought (see Tononi, 2004, 2008). Hence, attention and conscious perception could play a similar cognitive role of mediation between perception and action but in two distinct manners: while attention would be to analyse, conscious perception would rather act as an information synthethiser to promote global contextual understanding (Boxtel et al., 2010).

2.1.2 Conscious perception and attention in the predictive coding framework

The integrative view that attention and conscious perception may both subserve the similar cognitive function for distinct task objectives has been recently proposed in the literature under the predictive coding framework (Hohwy, 2012). Accordingly, the core function of the brain is to represent the world so we can act meaningfully on it. Hence, the brain has to identify what events causes in the world its sensory inputs. Because one cause may have many effects and one effect can have many causes, the brain is assumed to act like a hypothesis tester which takes into account prior expectations about events happening in the world to minimize prediction errors to enable the production of adapted and/or optimized behaviour within the world (Friston, Mattout, & Kilner, 2011; Friston, 2010). Because sensory inputs have repeatable patterns, expectations can be drawn and bias the subsequent input, hence, with repeated experiences the prior expectation can be updated to get closer to the ideal hypothesis.

According to the predictive coding hypothesis, there are two levels at which prediction errors can be minimized: (1) by changing the predictive model itself, or (2) by keeping the model constant and then optimizing its accuracy by biasing the incoming input. While conscious perception is assumed to ensure the first function, selective attention is proposed to perform the second (Hohwy, 2012). Here, conscious perception may have the function of representing the world: the distinct sensory attributes or events constituing the world are bound together and define a priori the cognitive context to act upon. In contrast, attention is expected to act as an optimizer when the context is fully determined and when the subject experiences statistical regularities about the occurrence of more specific and precise causal relationships. In this case, an attentional bias can be introduced to test the causal model in an empirical and embodied way. Optimizing the causal model comes down to learning about the causal relationships between feelings and events arising in the world, hence, in this alternative way, the causal model would be updated. To illustrate these situations, let us take the example of a child trying to go cycling on a bike for the first time. This child can have a certain conscious perception or prior expectations about the posture to maintain on the bike and the way in which the movements have to be coordinated to ensure high-levels of performance. These prior expectations about the concept of bicycling can be enriched before ever having tried using the bike. Hence, the child's awareness about the situation is updated before the use of the bike. Through motor experience of cycling, another state of prediction error minimization becomes available. Now,the child knows specifically how to do rather than generally what to do: the predictive model is stabilized. The task goal can be now tuned through focused attention to the needs to optimize the motor predictions.

Conscious perception and attention have also been described as actors operating at different time scales. Indeed, the prediction of basic sensory inputs and causal regularities may arise at lower levels in the cortical hierarchy and thus, be tuned at very fast timescales (milliseconds), while more complex regularities are detected at higher levels and thus, emerge at slower timescales (Kiebel, Daunizeau, & Friston, 2008; Mumford, 1992). Other constraints have also evidenced that attention and conscious perception can be implemented independently according to task demands. Indeed, conscious perception is expected to arose in situation in which the input signals are imprecise, hencethe world requires to be represented in a simplified manner. By contrast, attention is expected to arose when the causal relationships between the sensory inputs and their impact are clearly defined with a task goal to improve the accuracy of the predictive model. Hence, according to Hohwy (2012), when the constraints are geared towards the needs to clarify or to improve the "precision" of my knowledge about the world, conscious perception is expected, while when the task goal is to improve "accuracy", attention is required. There is growing evidence that suggests that attention can take place without conscious perception, perception without attention, or attention with conscious perception (Boxtel et al., 2010). Hence, attention and conscious perception could intervene independently in function of accuracy and timing demands. Although this frameworks becoming increasingly influential, it remains highly speculative without tangible data. In the present study, we propose to bring empirical arguments in favor of this theoretical view within the specific context of action planning.

2.1.3 Attention and motor control

Whether conscious perception is seen as the opponent computation of attention the question that holds here is in which situations may attention optimize the motor performance and in which situations attention cannot be used in this way and thus, conscious perception is required to maintain acceptable level of motor performance?

It has been largely accepted since the precursor work of Posner that cues provided in a valid way, i.e., before the appearance of a target, lead to observed facilitation effects in the participants reaction times. Cues can be endogenous or exogenous. In the first case, while the targets are presented in the left or right visual hemifields, the cue is provided at the center of the screen and indicates where the target will potentially appear. In the second case the cues are directly and briefly displayed at the future location of appearance of the target. Both types of cues reveal facilitation effects on the participants' performances through the orientation of attention to the target position that required processing. In a study by Jonides (1981), it was further demonstrated that cues provided at the spatial location of the target (exogenous cues) invariably and automatically attract attention while cues provided centrally (endogenous cues) affect attention depending on the participant's desire to use the cue. Indeed, in this study, participants were asked to search for a letter (L or R) among an array of eight letters arranged in a circle. When the letter was found, their task was to press the corresponding left or right button. Arrowhead cues were used to orient attention in an endogenous way (the central cue was placed at the level of the fixation point); flashed cues placed to the right or to the left close to the target letters were used to attract attention in an exogenous way. Both cues could be valid or invalid. Two groups of participants did the experiment, i.e. the "attend" group, which was asked to focus attention on the cues, and the "ignore" group that was asked to ignore the cues. Distinct effects were reported on reaction times: while in the "attend group", substantial effects of cue validity were reported for both types of cues, in the "ignore group" effects of cue validity was reported for the exogenous cues only. These results suggest that endogenous cues are effective only when participants voluntarily focus attention on the task; exogenous cues that are displayed close to the stimulus capture attention automatically, i.e. even when participants attempt to ignore them. In a later study of Remington, Johnston & Yantis (1992), in four different conditions, the peripheral cues (1) never appeared in the target location (DIF condition), (2) always appeared at the target location, (3) appeared at all locations, (4) did not appear at all. The cues that were used here were a salient array of four crosses surrounding the potential target location. Response times in the DIF condition were always longer than in all other conditions, suggesting that even when the cue was not relevant, attention was automatically attracted with a significant effect of cue existence on the motor responses. Hence, flashed cueing seems to attract attention automatically and invariably in particular when the cues are provided at the spatial location of potential targets and this is true even when the cue is not valid.

The invariable impact of distractors on motor responses have also been reported in oculomotor studies, where a distractor was displayed during the preparation of a saccadic movement. In these sorts of settings, the distractor does not exactly act like a cue because the eyes remain fixated until the production of the saccadic movement. Nevertheless, the mere presence of a distractor within the visual display was shown to capture attention, i.e. to influence the saccade trajectories causing deviations (1) away from the distractor when the target was successfully selected apart from the distractor but (2) deviation towards the distractor in the case of unsuccessful isolation of the target (see Van der Stigchel, 2010 for a review). Trajectories were shown to deviate more away from the straight path as a function of the degree of similarity between the target and the distractor (Al-Aidroos & Pratt, 2010; Ludwig & Gilchrist, 2002, 2003) or as a function of the salience of the distractor (Cardoso-Leite & Gorea, 2009; Van der Stigchel, Mulckhuyse, & Theeuwes, 2009; van Zoest, Van der Stigchel, & Barton, 2008), suggesting that these distractors had a larger impact on motor performances than simply being distractors during motor planning. Deviations towards the distractor, i.e. automatic capture of the distractor, rather appeared when the distractors were presented simultaneously and close to the target location (Walker, McSorley, & Haggard, 2006). Hence, in these paradigms and overall in studies involving the production of a saccadic movements, the automatic capture of attention by distractors cause deviations in the movements that are measurable in the spatial trajectories.

Similar effects have been reported when an arm movement was required to be produced towards a visual target in the presence of nearby distractors (Pratt & Abrams, 1994).When rapid pointing movements were produced towards targets that were accompanied by distractors emitted on the movement path, both the reaction times (RTs) and the movement times (MTs) were affected by the presence of the distractors, i.e. RTs were longer and MTs were slower. The effects were weaker when the distractor was provided beyond the target. This result reflects that a distractor presented near a potential target affords a movement towards its location, while no such selection for competition enters into play when the distractor is presented sufficiently far from the target to reach. In another study, it was shown that when a distractor was presented on the same trajectory path than the target but farther than the location of the target, the movement trajectories were longer and had to achieve higher peak velocities for completion, suggesting that the movements were planned first towards the distractor and then stopped through corrective mechanisms at the location of the target (Welsh & Elliott, 2004). This pattern of results hence confirmed the affording properties of a distractor emitted on the trajectory path. When a cueing technique was combined to a distractor interference paradigm (Welsh & Elliott, 2005), i.e. the target was validly or invalidly precued and appeared simultaneously to the distractor, the movements were unaffected by the presence of the distractor in the valid situations. By contrast, when the distractor was presented during motor planning, interference effects were reported independently of the distance between the target and the distractor. More specifically, the reaction times were significantly increased when the distractor was presented beyond the target, decreased when the distractor was presented closer than the target, and the trajectories of the hand were significantly deviated towards the location of the distractor in all cases. Overall, these findings suggest that a distractor can influence arm trajectories especailly when the distractor is presented during motor preparation. Indeed, at this moment the distractor is a potential competitor for the target and dissociation between target and distractor becomes difficult. In the present study, we will be using this principle to modulate the capture strength of a target during motor preparation in a sequential synchronisation tapping task.

In conclusion, attention is needed to plan an ocular or an arm movement towards a spatial location. Attention seems to be automatically attracted when distractors are flashed during motor preparation. In the case of pointing movements, effects were not forcibly observable when the distractors were emitted sufficiently far from the target. However, in all cases, attention is automatically captured when a distractor was emitted close to the target or at the location of targets to come. Hence, flashing paradigms may be an ideal approach to study the effects of attention on motor preparation and execution, with the use of brief onsets to assess facilitation and distracting effects in sequential movements. In the following section, we will now report some literature results obtained in more complex sequential motor tasks suggesting the need of conscious perception when a general (global) plan is required.

2.1.4 Conscious perception and motor control

Contextual effects in motor task have been documented in the motor control domain, e.g. in hand writing, it was shown that the shape and timing of a letter were dependent on the properties of both the preceding and the following letter to write (van Galen, 1991). Such sorts of effects necessarily require some sort of bound representation or entire action plan about the action pattern to produce, i.e. conscious perception. Similar effects were reported in typewriting (Terzuolo & Viviani, 1980), piano playing (Shaffer, 1976; Winges, Furuya, Faber, & Flanders, 2013), speech (Fowler, 1985), fingerspelling (Jerde, Soechting, & Flanders, 2003)but also in more lab-based situations such as in finger-tapping (Adam et al., 2000). To produce series of embedded actions, there is some evidence that specific motor control strategies are required as compared to the production of isolated actions. For example, in the series of experiments proposed by Adam et al. (2000), a one-tap condition in which a movement was produced from a starting point to a visual target was compared to a two-tap condition in which the two targets were initially arranged according to a straight line. The rapid aim movements to produce were shown to be faster (shorter movement times) in the one-tap condition as compared to the first movement of the two-tap condition. This effect, namely the one-target advantage, was shown to disappear when the visual targets were smaller or/and when the interval of times separating the two actions was long rather than short, which suggests that in these cases, each action was processed in isolation while in the classic case the control parameters required to implement the second action overlapped with the production of the first action. The one-target advantage was suggested to depends upon the complexity of the motor program engaged to produce a series of actions. Indeed, the effect was further shown to disappear when a reversal movement back to the start location was produced rather than an extension movement in the two-tap condition. By contrast, when participants were then asked to produce a reversal movement with the specific constraint geared on the second movement to elevate the second movement at least of 10 cm from the platform, the effect reappeared. The pattern of electromyographic activity was in fact shown to be more complex in the extension condition (triphasic electromyographic pattern), as compared to the reversal condition (biphasic electromyographic pattern), suggesting that the extension condition was more cognitively demanding in terms of motor planning as compared to the reversal condition. This interpretation was confirmed and extended through other studies describing complexity effects for the control of action sequences (Christina, Fischman, & Vercruyssen, 1982; Fischman & Lim, 1991; Henry & Rogers, 1960). It was shown that the time required to initiate a sequence of embedded actions (here, the reaction time) depends upon the complexity of the sequence, e.g. the number of sub-movements involved in the sequence. Within this context, it was suggested that the motor program was fully determined and loaded before the initiation of the movement sequence. Hence, the motor performance could guided through prior knowledge about the overall context within specific situations, i.e. conscious perception when: (1) multiple actions are performed the one after the other with a specific anticipation of forthcoming events required while producing the preparing the current movement, (2) when the motor complexity is sufficiently high, (3) when no constraints are geared towards the needs to produce too accurate movements (small vs. large targets in Adam et al. study, 2000), (3) when the dwell time separating the successive actions is sufficiently short. In these situations, the entire motor program is loaded before motor execution, to make emerging a motor pattern that makes sense in the world, e.g. a word in writing, fingerspelling, a melody, etc.

Overall, we propose that studying how attention intervenes or interferes with the production of isolated vs. embedded sequences of actions will provide a way to reveal the specific role played by attention and conscious perception, respectively. It will be proposed that attention is involved in isolating and optimizing the production of discrete actions; conscious perception may play the role of providing a motor plant for the production of embedded sequences of actions hence, guiding the body on the basis of an internal representation of a global idea..

In the present study, we propose the spatial-tapping task (Dione, Ott, & Delevoye-Turrell, 2013) as an empirical example of the predictive coding hypothesis in humans. In this task, participants are asked to produce a series of tapping actions towards six visual targets arranged along a virtual circle in a repetitive manner. A metronome indicates the tempo to follow. The test begins with a slow pace of 1200 ms, which is increased by periods of 100 ms at each trial (ten trials are performed), until the faster pace of 300 ms. The instruction provided to the participant is to point each target one after the other and to try to be at best synchronized with the metronome. Previous results have shown that in this task, the task goal was oriented towards the needs to maintain the timing accuracy at slow tempi (between periods of 1200 to 900 ms), to inhibit the motor response at intermediate tempi (between periods of 800 to 600 ms) in order to keep maintaining the timing accuracy while the task demands induced a pressure to go faster and thus to anticipate future spatial locations, to produce a smooth circle at slow tempi (between periods of 500 to 300 ms) by reducing a switching cost in space and time at the specific point of transition from extension to flexion movement (top-left target), namely the anchor point. Hence, we propose that in this task, selective attention may be required at slow tempi in order to produce discrete and well-timed tapping actions. With increasing pace, and thus increasing pressure to anticipate the location of future events to go faster, we propose that a transition towards conscious perception, i.e. awareness of the global trajectory path to follow, takes place with the consequence that individual motor elements become embedded within a more global sequence plan.

In the present study, we propose to test this specific hypothesis through the use of abrupt onsets (AOs). We choose to use the word "abrupt onset" rather than "distractor" with the idea that AOs are susceptible to attract, distract or orient attention. AOs were provided as brief disappearances of a visual target just before the expected moment of action execution in order to bias the action preparation, (1) on the current target to point, to favor a focused attention on the ongoing motor goal, (2) on the next target to point, to favor the anticipation of forthcoming events and the use of conscious perception. We predict that timing performances will be enhanced in the "current" condition, while the "next" condition will favor the emergence of a more global action pattern, with more circular/global trajectories to guide tapping sequences.

2.2 Material and Methods

2.2.1 Participants

Twenty three right-handed students between 18 to 25 years of age and recruited from the University of Lille 3 participated voluntarily in the study. All participants received an information letter and provided written informed consent. All participants performed the task with their right hand and reported having normal or corrected-to-normal vision. The protocol received approval from the local institutional ethics committee of the University of Lille 3.

2.2.2 Material and procedure

A picture composed of six black targets was displayed on a touch screen Elo Touch 19" 1915L. The targets (10 mm diameter, 100 mm apart) were placed around a virtual circle of 100 mm radius. The participants were invited to stand in front of the screen that was placed upon a table and oriented parallel to the table (see Figure II.9).

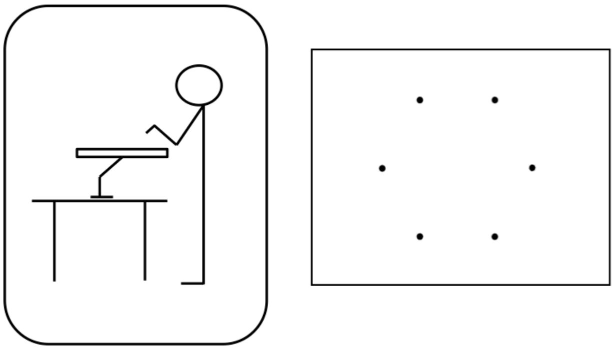


Figure II.9: Schematic representation of the experimental protocol

The subjects' task was to touch each visual target one after the other, starting from the bottom right target, and moving counter-clockwise using the right index finger (fist closed). Participants were instructed to synchronize each pointing action to a series of regular auditory tones (beep duration = 100 ms) that was played through computer speakers. Participants were encouraged to let their left arm hang relaxed along the body side. They were clearly instructed that the goal of the task was to be synchronized with the metronome. Each subject performed a total of nine trials. The initial tempo was an inter-onset interval (IOI) of 1200 ms. The temporal interval was increased by 100 ms after each trial with the fastest tempo having an IOI of 300 ms. Participants were required to produce sixty taps for each trial. The total duration of the session was 10 minutes, approximately. Picture display, auditory tones, and data collection were controlled through Matlab's customed software.

Abrupt onsets (AO) were further used to orient the participants' attention towards specific spatial locations. AOs were provided as brief disappearances (100 ms) of a black visual target just before the expected moment of action execution, i.e. at the 2/3 of each metronome period. Four experimental conditions were proposed: the "neutral", "current", "next" and "random" conditions. The "neutral" condition was the reference situation for which the trial was performed without AO. In the three other conditions, AO were displayed on the current target to point, on the next target to point, in a semi-random fashion (a target could not be flashed twice in a row), respectively. The AOs were manipulated through a custom made real-time controller software under Matlab, which followed the strict constraint of displaying an AO in function of the previous position in space that had been touched by the participant.

2.2.3 Measured response parameters

Dependent variables commonly measured in tapping tasks, i.e. inter-response interval error, asynchronies were used as indicators of the timing performance (see Repp & Su, 2013; Repp, 2005). Other dependent variables more specifically related to the motor and spatial constraints specific to the spatial-tapping task were computed (see Dione et al., 2013), i.e. the contact times that were measured as indicators of motor fluency/inhibition and the spatial error that was computed as ellipses of confidence around the endpoint distributions in space as an indicator of the spatial performance.

2.2.3.1 Interval timing errors

Inter-response intervals (IRIs) were first measured as the time intervals between the onsets of successive taps. The $\mathrm{IRI}_{\mathrm{error}}$ was then computed as the percentage of difference between each IRI and the reference inter-onset interval (IOI, metronome period) of a given trial ($\mathrm{IRI}_{\mathrm{error}}(i) = (\mathrm{IRIi}\text{-}\mathrm{IOI})/\mathrm{IOI}*100$). The $\mathrm{IRI}_{\mathrm{error}}$s were then averaged for each position, IOI and participant. This measure served as an indicator of the timing error.

2.2.3.2 Asynchronies

Asynchronies were calculated as the difference in time between the onset of a tap and the start of the nearest auditory tone. Asynchronies were averaged for each position, IOI and served as an indicator of the participants' capacity to synchronize their pointing action with the external metronome.

2.2.3.3 Contact times

The Contact time (CT) was defined as the time of finger contact with the touch screen. This measure (in ms) was used to assess the level of control of the motor response output, with shorter CTs being related to a more fluent gesture (see Figure II.10 for a schematic representation of the timing variables).

2.2.3.4 Spatial error

The endpoint distributions of the tapping actions were plotted for each target position (Figure II.11). Using principal component analysis, spatial ellipses were then fitted to the movement endpoint distributions (Figure II.11c, for details on the calculations, see Gordon, Ghilardi, & Ghez, 1994). The confidence intervals were set to 95% on axis length. The area of spatial ellipses was then computed and used as an indicator of the spatial error.

2.2.4 Analyses to reveal time keeping mechanisms

Autocorrelation values (AC) were computed from the IRIs and asynchronies. The series of events were staggered of one off position and correlation measures were conducted. These dependent variables are usually used in the timing domain to identify the planning strategies that guide action sequences through time (Wing & Kristofferson, 1973a). When the timing is event-based or discrete, a representation of the referential timing interval is needed, and is updated in working memory to match at best the referential interval of time (Treisman, 1963). In this case, the AC values of IRIs are typically strong and negative at lag-1 (AC-1). When the timing is corrected a posteriori, i.e. through an emergent representation of the trajectory path, AC-1 values of asynchronies are

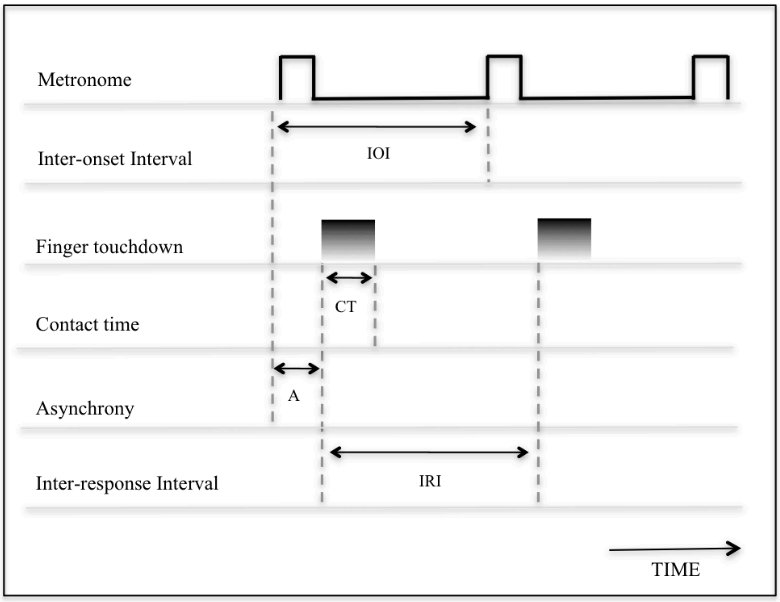


Figure II.10: Illustration of the timing variables that were measured in the spatial-tapping task: the metronome consisted in a sequence of regular auditory tones. Inter-onset intervals (IOI) were considered as the time intervals between the start of two successive auditory tones. Contact times (CTs) were measured as the duration of finger tactile contact with the screen. Inter-response Intervals (IRI) were measured as the time intervals between the start of two successive touchdowns. Asynchronies (A) were measured as the difference in time between the onset of the tap and the start of the nearest auditory tone

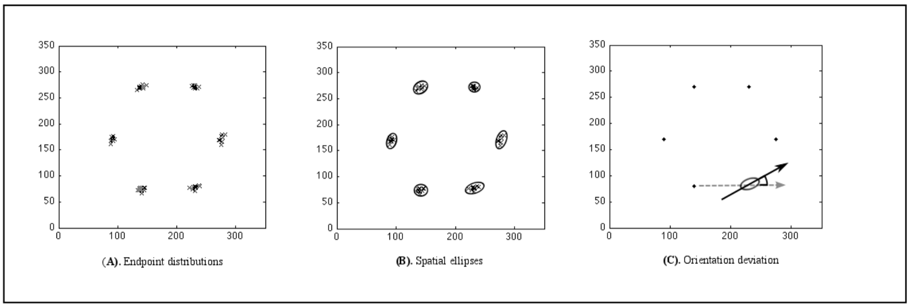


Figure II.11: Visual illustration of the three methodological steps that were implemented to calculate the orientation deviation (OD) of the endpoint scatterplots positive. In the present study, and after omitting the first six IRIs and asynchronies of each trial, autocorrelation values were calculated up to six lags. The values observed at lag-1 and lag-6 for the IRIs and at lag-1 for the asynchronies were considered for statistical analysis. These measures served as an indicator of the presence or absence of action control through timekeeping mechanisms.

2.2.5 Analyses to reveal trajectory formation

In order to assess whether the spatial trajectories became more circular or whether future targets were anticipated to plan the current actions, the main orientation of each spatial ellipse was computed. Then, angular deviations from expected trajectories (e.g. tangent to the circle) were measured. This method has been used in a number of studies to infer whether the planning trajectories are oriented or not in function of the context (Desmurget, Jordan, Prablanc, & Jeannerod, 1997; Desmurget, Pélisson, Rossetti, & Prablanc, 1998; Rossetti & Régnier, 1995; Van Beers, Haggard, & Wolpert, 2004). In the present study, an aspect ratio was first measured for each ellipse as the square root of the ratio of the two axis lengths (the larger divided by the smaller) and was used as an indicator of the shape of the ellipses with an aspect ratio superior to 1 suggesting an elongated ellipse(see Van Beers et al., 2004). Second, the orientations of the main axis of each ellipse were computed. Finally, an orientation deviation (OD) was calculated as the angular difference between the orientation of the main axis of each ellipse and two referential orientations computed as the orientation of (1) the line linking the current target (n) to the next (n+1), and (2) the tangent to the virtual circle computed for each target position (see Figure II.11). These measures were used as indicators of the spatial planning strategies used to control hand trajectory.

Analyses of variance analyses (ANOVAs) were performed on each variable, with CONDITION and IOI as repeated measures. There was the additional MODELS factor for the orientation deviation measures. All statistical analyses were performed using Statistica Software. Fisher LSD post hoc tests were used when required. The alpha level was set to 0.05.The TP and IP position are presented in Figure II.12.

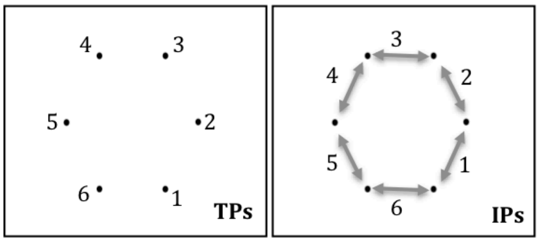


Figure II.12: Schematic description of the target positions (left) and the interval positions (right)

2.3 Results

2.3.1 Performance measures in space and time

2.3.1.1 $\mathbf{IRI_{error}}$

A significant effect of IOI was revealed (F(9, 198)=6.573, p<0.001). Post hoc tests revealed that the IRI_{error} was the smaller and close to zero between 1200 to 600 ms of IOI and was significantly larger between 500 to 300 ms of IOI. No main effect of CONDITION was revealed (F(3, 66)=2.166, ns.). A significant effect of IP was revealed (F(5, 110)= 53.982, p<0.001). In average, the IRI_{error} was negative and close to -2% at IP-1, IP-3 and IP-4, positive and close to 2% at IP-2 and IP-5 and finally close to zero at TP-6. Concerning the interaction effects, a significant IOI*IP effect was revealed (F(27, 594)=2.660, p<0.001). The IRI_{error} was in fact revealed to be close to zero at IP-3 between 1200 to 900 ms of IOI and became significantly larger and negative at faster tempi (see Figure II.13A). This result suggest the timing corrections were applied at the transition point between extension to flexion movements, i.e. at IP-3, our timing anchor point only from 800 ms of IOI and faster (see Figure II.13A).

A significant IOI*CONDITION effect was reported, with post hoc tests revealing that the IRI_{error} was significantly smaller (less positive) at 300 ms of IOI for all three conditions as compared to the neutral condition. A significant CONDITION*IP effect was revealed (F(15, 330)=1.840, p<0.05). The $IRI_{error}$was significantly more negative at IP-2, IP-3 and IP-5 in the "current" condition, suggesting a reduction in the IRI_{error} at IP-2 and IP-5 and an increase in the $\text{IRI}_{\text{error}}$ at IP-3 as compared to their base levels. The $\text{IRI}_{\text{error}}$ was also significantly more negative at IP-3 in the next condition (see Figure II.13B-C-D). No significant three order interaction effects were observed (statistics are not presented for readability purposes). These results suggest that the timing was better maintained at slower tempi as compared to faster tempi. Accurate timing was further encouraged timing in the current condition as compared to other conditions especially for those interval positions showing a positive error at their base level (IP-2 and IP-5). Furthermore, both the next and the current conditions make emerging a larger correction at the level of the anchor point, i.e. just before TP-4.

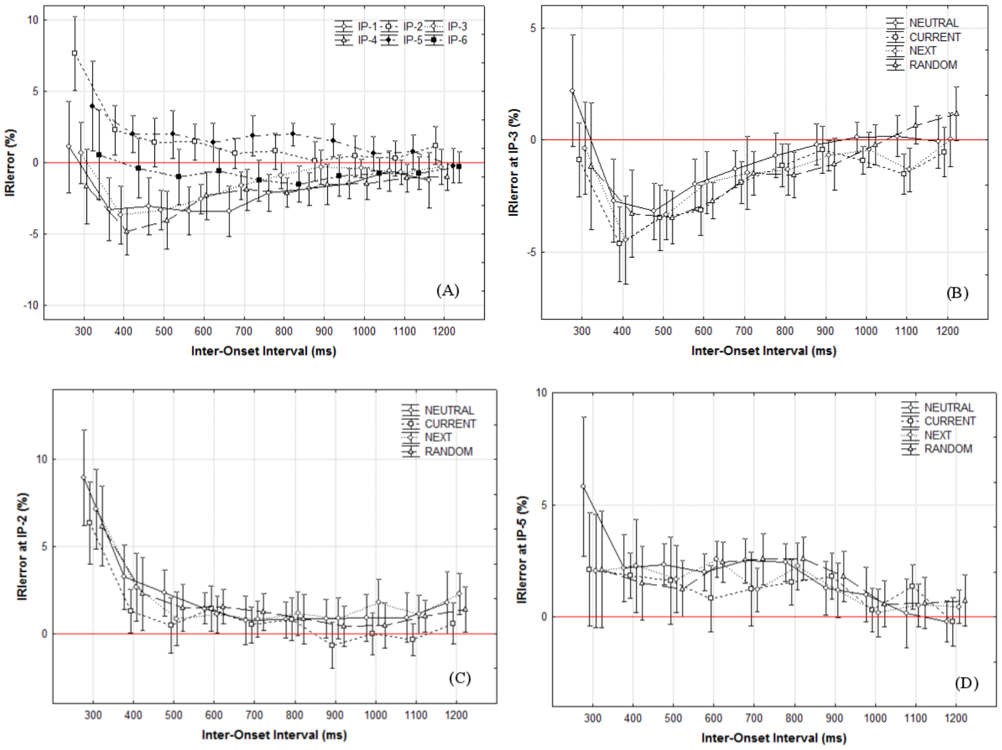


Figure II.13: Temporal errors (inter response interval error – $\text{IRI}_{\text{error}}$) are presented as a function of the tempo (inter onset interval – IOI) imposed by an external metronome

2.3.1.2 Asynchronies

A significant effect of IOI was revealed (F(9, 198)=33.771, $p<0.001$). Post hoc tests showed that asynchronies were on average large and negative between 1200 to 600 ms of IOI and significantly smaller between 500 to 600 ms of IOI. A significant effect of CONDITION was revealed (F(3,66)=12.841, $p<0.001$), indicating that asynchronies were on average negative in all conditions but were significantly closer to zero in the neutral and random conditions as compared to the two other conditions. A significant effect of TP was revealed (F(5, 110)=21.543, $p<0.001$). Post hoc tests suggested that asynchronies were more negative at TP-2 and TP-5 especially as compared to other TPs. Concerning the interaction effect, there was a significant effect of CONDITION*IOI (F(27, 594)=4.675, $p<0.001$). The error of synchrony was in fact significantly more negative for all three flash conditions as compared to the “neutral” condition at the slowest tempo of 1200 ms, and between 800 to 600 ms of IOI. The error was further more negative for the “current” and the “next” conditions between 500 to 400 ms of IOI as compared to the two other conditions (see Figure II.14A).

A significant effect of COND*TP (F(15, 330)=2.483, $p<0.01$) was also revealed. Post hoc tests confirmed that the asynchronies were larger at TP-2 in the “next” condition as compared to the “current” condition. To note however that according to Figure II.14B, the error of synchrony was in fact the largest (more negative) in the next condition at slow tempi (between preriods of 1200 to 900 ms), and in the current condition at fast tempi (between periods of 600 to 300 ms). The three level interaction was not significant. These results suggest that the abrupt onsets overall lead participants to produce a more negative error as compared to the neutral condition. However, the amplitude of the effect was dependent on the flash condition and the tempi.

2.3.1.3 Contact times

A significant effect of IOI was reported here (F(9, 198)=17.812, $p<0.001$). Contact times were on average longer at slow tempi and shorter at fast tempi, without however significant differences observed between 1200 to 900 ms of IOI and without significant differences reported between neighboring periods at faster tempi. No significant effects of CONDITION were reported (F(3, 66)=0.236, ns.). A significant effect of TP was found (F(5, 110)=28.177, $p<0.001$).The contact times were on average shorter at TP-5 and TP-6, i.e. when tapping in the

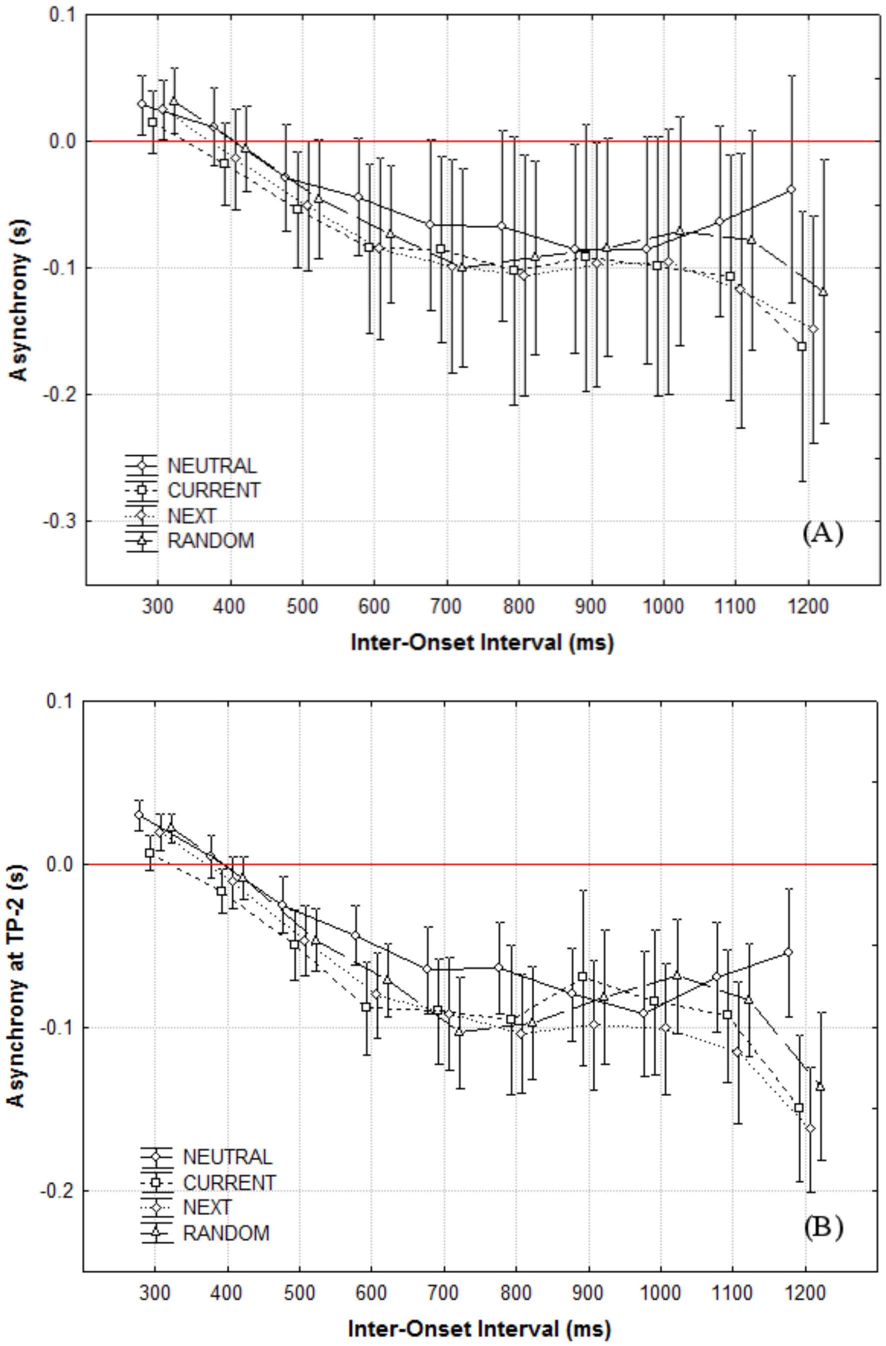


Figure II.14: Synchrony errors (asynchronies) are presented as a function of the tempo (inter onset interval – IOI) imposed by an external metronome left hemisphere. Concerning the interaction effect, a significant IOI*TP effect was revealed (F(45, 990)=4.376, p<0.001). Post hoc tests confirmed that on average contact times were shorter with changing tempi (longer at TP-1 and shorter at TP-6) especially between 500 to 300 ms of IOI, with however shorter contact times observed at TP-1 as compared to TP-2 and TP-3 between 1200 to 600 ms of IOI (see Figure II.15).

The CONDITION*IOI effect was not significant (F(27, 594)=.36674, p=.998) but the CONDITION*TP effect was (F(15, 330)=2.2038, p=.006). Post hoc tests indicated that the contact times were significantly shorter in the "current" condition for all TPs as compared to the "neutral" condition. In the "next" and in the "random" conditions, the contact times were significantly shorter than in the neutral condition at TP-5 and TP-6 only.

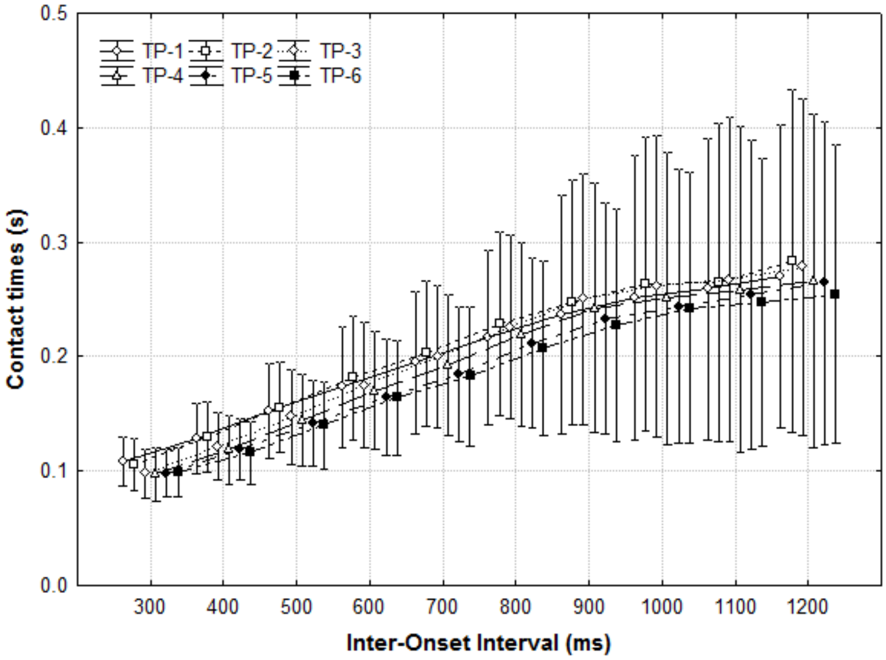


Figure II.15: Contact times are presented as a function of the tempo (inter onset interval – IOI) imposed by an external metronome

2.3.1.4 Spatial error

A significant effect of IOI was revealed (F(9, 198)=136.87, p<0.001). The area was the smaller at slower tempi, i.e. between 1200 to 900 ms of IOI. A significant but slight increase in the spatial error was observed from 800 ms of IOI and faster; it was maintained constant until 600 ms of IOI. The spatial error was finally the largest between 500 to 300 ms of IOI. A significant effect of CONDITION was revealed (F(3, 66)=6.339, p<0.001). Post hoc tests indicated that the area of spatial ellipses was larger in the "next" condition as compared to all other conditions.

A significant effect of TP was revealed (F(5, 110)=27.427, p<0.001). Post hoc tests indicated that the error was on average smaller at TP-2, TP-3 and TP-4, was intermediate at TP-5 and was finally the largest at TP-6 and TP-1. Concerning the interaction effects, a significant effect of IOI*TP was revealed (F(45, 990)=10.006, p<0.001). Post hoc test indicated an absence of differences in the spatial error in function of TP between 1200 to 900 ms of IOI. Between 800 to 500 ms of IOI, the spatial error became significantly larger at TP-5, TP-6, TP-1 as compare the three other TPs. Finally, between 400 to 300 ms of IOI, the spatial error was the smaller at TP-3 and TP-4 as compared to other TPs. This results suggest that a specific structuring if the errors appeared when the speed of the task was faster than 800 ms of IOI, with the spatial error being the smaller on the extension part of the movement and the larger in the flexion part of the movement, namely the anchoring phenomenon (see Figure II.16A). The CONDITION*TP effect was not significant (F(15, 330)=1.080, ns.). However, the CONDITION*IOI effect was (F(27, 594)= 3.546, p<0.001). Post hoc tests indicated that the spatial error was in fact the largest in the next condition as compared to the neutral condition especially between 600 to 300 ms of IOI (see Figure II.16B). No additional three level interaction effects were revealed.

2.3.2 Planning through time

AC-1 values of IRIs. A significant effect of IOI was revealed (F(9, 198)=11.736, p<0.001). On average, the AC-1 values of IRIs were negative across all tempi, and were the smallest between 1200 to 900 ms of IOI, they were slightly but significantly less negative between 900 to 600 ms of IOI, and they reached their smallest values between 500 to 300 ms of IOI (see Figure II.16A). No effects of CONDITION (F(3, 66)=1.114, ns.) or interaction effect CONDITION*IOI were

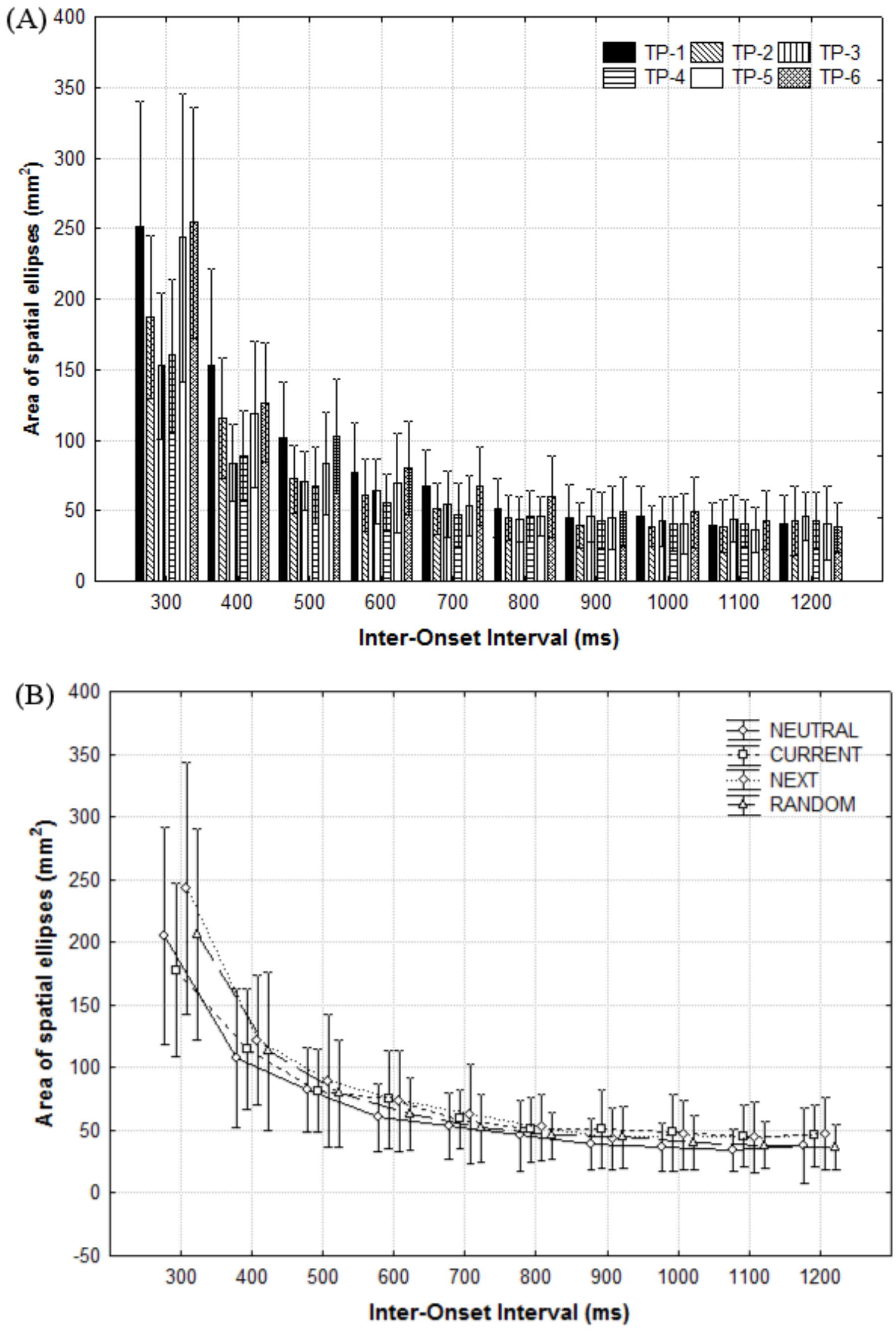


Figure II.16: Spatial errors (area of the endpoint scatterplots) are presented as a function of the tempo (inter onset interval – IOI) imposed by an external metronome observed here (F(27, 594)=1.284, ns.). These results suggest that the actions were primarily under the control event-based timekeeping strategies between 1200 to 900 ms of IOI.

AC-6 values of IRIs. A significant effect of IOI was revealed (F(9, 198)=13.040, p<0.001). Post hoc tests revealed that the AC-6 values of IRIs were positive and were the smallest between 1200 to 700 ms of IOI and were significantly larger between 600 to 300 ms of IOI (see Figure II.16B). No significant effects of CONDITION (F(3, 66)=0.189, ns.) or interaction effect CONDITION*IOI (F(27, 594)=0.661, ns.) were observed. These results suggest that more dependencies between successive cycles entered into play for the fast tempi between 600 ms and 300 ms of IOI.

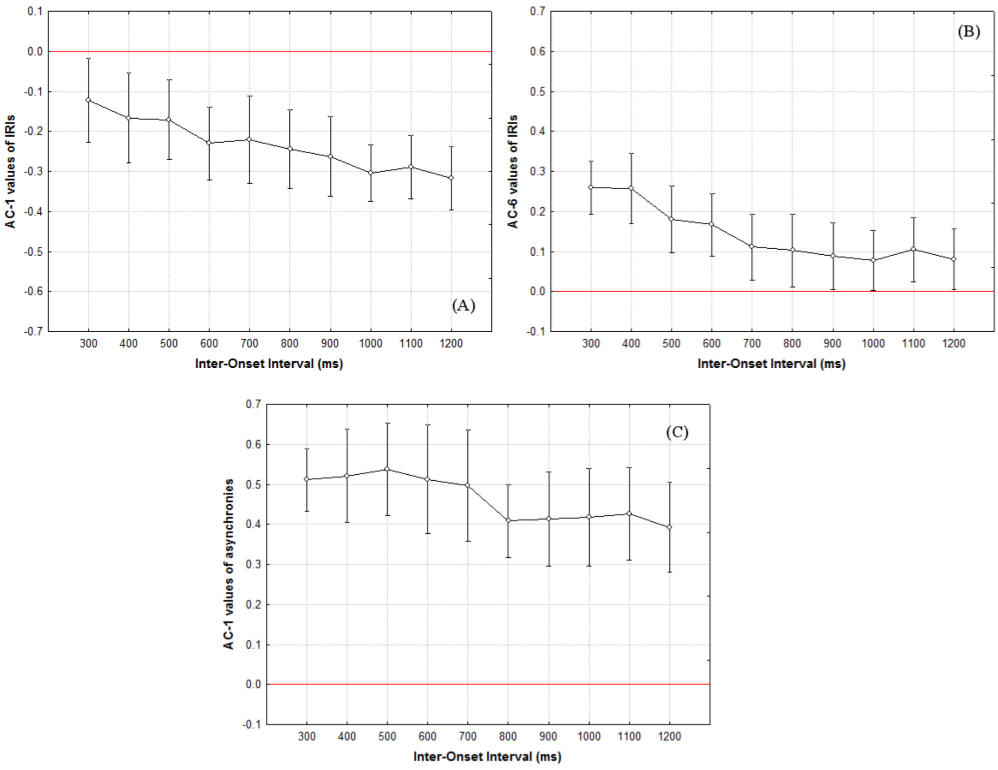


Figure II.17: Autocorrelation functions of the asynchronies and of the inter-response intervals (IRI) are presented as a function of the tempo (inter onset interval – IOI) imposed by an external metronome. The legends specify for each figure the considered time lags

2.3.3 Planning through space

2.3.3.1 Aspect ratio

No significant differences were revealed according to conditions. The ellipses were on average elongated (M= 1.40) in all conditions.

2.3.3.2 Planning models

Here, the statistical effects that constitute an average of the two planning models measured are not considered for interpretation. The CONDITION*MODELS effect did not reach significance (F(3, 66)=0.353, ns.). A significant MODELS*IOI interaction effect was observed (F(9, 198)=23.280, $p<0.001$). Post hoc tests revealed that on average the ellipses were slightly more oriented towards the next target at slow tempi as compared to the faster ones. In addition, the ellipses were significantly more oriented in function of the tangent to the circle for tempi faster than 600 ms (see Figure II.18A). The CONDITION*MODELS*TP effect was significant (F(15, 330)=2.311, $p<0.01$). Post hoc tests indicated that that the "next" condition had specific effects on TP-1, TP-4, TP-5 and TP-6. This condition favored an orientation towards the next target at TP-1 and had the reversed effect at TP-6. In this next condition, the spatial ellipses were significantly more oriented according to the tangent to the circle at TP-4 and TP-5. Hence, the "next" condition favored trajectories based on the circle and required especially anticipatory mechanisms for the first sub-component of the movement (between TP-1 and TP-2).

The "current" condition showed specific effects at TP-2 and TP-3 by rendering the movements less oriented in function of the tangent to the circle at TP-2, and more oriented according to this model at TP-3. The movements were further less oriented in function of the tangent to the circle at TP-4 and TP-5, without showing significant differences with the "random" condition. Hence, the current condition and the random conditions rendered the movements less circular for most of the TPs. The "random" condition further disfavored an orientation towards the next target at TP-1 (see Figure II.18C).

Unspecific effects of conditions were also reported at TP-3 and TP-4. The ellipses were significantly more oriented in function of the next target at TP-4 in the three AO condition as compared to the neutral condition, while the reversed effect was observed at TP-3, suggesting that specific planning strategies were available in the neutral condition and were not modulated with the AO

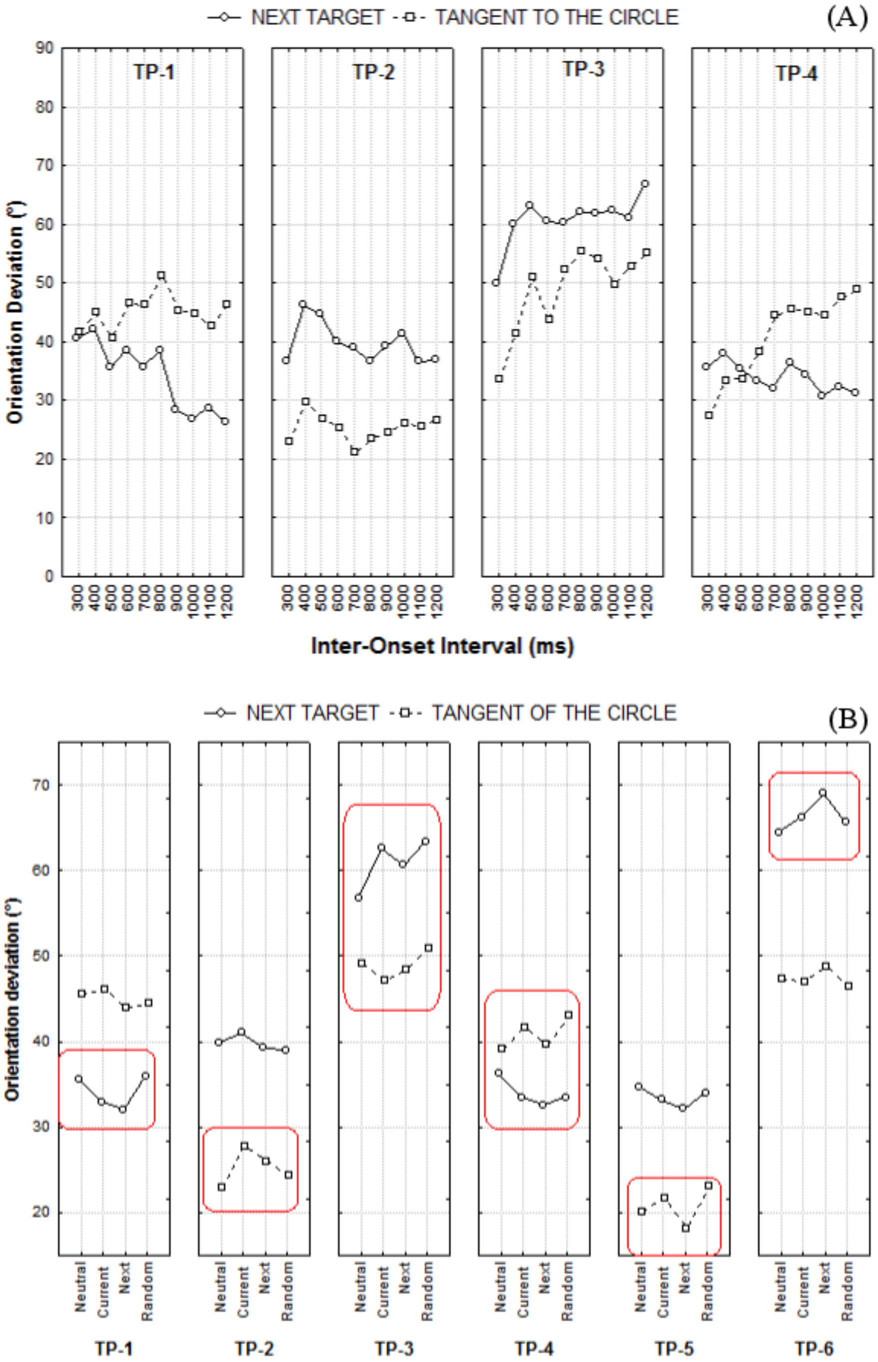


Figure II.18: Orientation deviations of the endpoint scatterplots are presented as a function of the tempo (inter onset interval – IOI) imposed by an external metronome for each target position (TP). The legends specify the three selected models that are considered: fit to the tangent to the circle (squares); fit to the next target (diamonds) manipulation.

2.4 Discussion

Conscious perception and selective attention have been recently considered within the predictive coding hypothesis as two opponent mental computations that activate same brain functions of representing and simplifying the multiple information presented to us at anytime to allow the production of adapted behaviors (Hohwy, 2012). While conscious perception is described as a “synthethiser” that binds together the information available within the internal and/or external context in order to act meaningfully on the world, selective attention is defined as an “analyzer” which focuses cognitive resources on specific perception-action links targets to optimize the accuracy of discrete behaviors (Boxtel et al., 2010). Although the predictive coding hypothesis represents an attractive framework to consider the roles played by conscious perception and selective attention in human cognition, it remains speculative, i.e. no empirical examples have been proposed in humans to support the model.

The objective of the present study was to propose the spatial-tapping task (Dione et al., 2013) as an empirical example to support the predictive coding hypothesis. In this task, a transition is induced from the production of discrete tapping actions at slow tempi to the production of more continuous movements at fast tempi. Because the production of more continuous movements at very fast pace ($\leq$ 500 ms) involves global representation of the overall pattern of action to produce, we proposed that in this case, the synthetising function of conscious perception may be required. In contrast, at slower tempi, we proposed that selective attention is needed for the production of discrete actions that require to maintain high levels of timing and spatial accuracy in regards to a set referential.

In the present study, we used abrupt onsets (AOs), which were defined as brief disappearances of the visual target in order to test the effects of selective attention in function of when the flash occurred in relationship to motor planning. Furthermore, we set the hypothesis that if conscious perception is the opponent computation of attention, conscious perception should emerge when no attention can be focused on discrete events. To produce a more focused attention on each discrete attention AOs were provided during motor preparation on the spatial target to reach (current condition). To disengage attention from the current action, and hence orient cognitive resources towards the forthcoming events, AOs of the next spatial target to reach was set, e.g. TP-2 was flashed when the participant had to produce an action towards TP-1. As a control condition for attention capture, AOs were in a third condition displayed in a semi-random manner on each spatial target. Our results confirmed our hypotheses, indeed, the “current” condition especially improved the timing accuracy ($\mathrm{IRI}_{\mathrm{error}}$) and rendered the actions more discrete (shorter contact times) and less continuous (orientation deviation), while the “next” condition increased the spatial variability and rendered the movements significantly more continuous and global. These results are detailed and discussed in the next sections.

2.4.1 Impact of the AO conditions on performance in the spatial-tapping task

2.4.1.1 Abrupt onsets did not impact the transition from discrete to continuous actions in the spatial-tapping task

The autocorrelation values of IRIs and the asynchronies are variables that are usually used in the timing literature to identify whether series of tapping actions are produced (1) in a discrete way, hence involving event-based timing strategies or (2) in a more continuous way, hence through the support of emergent timing strategies (Repp & Steinman, 2010; Studenka & Zelaznik, 2008; Wing & Kristofferson, 1973a; Zelaznik, Spencer, & Doffin, 2000; Zelaznik, Spencer, & Ivry, 2002). It is to note that emergent timing strategies are spatial in nature: the task goal is focused on the production of a given spatial trajectory, drawing a circle or a straight line. Here, the timing is inferred from the time needed to produce such action pattern and corrected a posteriori, i.e. on the subsequent cycles (Delignières, Lemoine, & Torre, 2004; Delignières, Torre, & Lemoine, 2008; Robertson et al., 1999; Torre & Delignières, 2008a, 2008b).

In timing studies, finger tapping and circle drawing tasks are the paradigms commonly used to reveal respectively event-based and emergent timing. While autocorrelation values of IRIs measured at lag-1 (AC-1) are commonly strong and negative in finger tapping task, they are generally close to zero or positive in circle drawing tasks. In a preceding study, we reported how the spatial-tapping task was designed as a hybrid of these tasks. Results showed that through the modification of the rhythmic pace, the timing transitioned from an event-based to an emergent mode of control in function with increasing tempi, with a switch in AC-1 values of IRIs observed around periods of 700 ms (Dione et al., 2013). To introduce the spatial-tapping task, AC values were measured up to six lags. Significant changes in AC-6 values were also reported in the spatial tapping task. These values were positive at slow tempi and significantly larger with increasing tempi, hence supporting the idea that more correlations between entire cycles (composed of six taps) were observable with increasing tempi. These results were replicated in the present study, while no effects of conditions were reported. Indeed, the AC-1 values of IRIs were the largest at slow tempi and increased with increasing tempi. The AC-1 values of asynchronies were positive and significantly larger for tempi faster than 700 ms of IOI. The AC-6 values of IRIs were positive and were significantly larger for tempi faster than 600 ms of IOI. Overall, these results suggest that participants used a more event-based timing mode at slow tempi and a more emergent mode at faster tempi, as revealed through augmented positive dependencies of the series for tempi faster than 700 ms of IOI.

The experimental manipulation of attention that we proposed here using abrupt onset (AO) did not impact the nature of the results suggesting that participants used similar cognitive strategies when planning rhythmic pointing movements in all AO conditions. However, as reported in the next sections, the motor performance in space and time was significantly impacted by the AO manipulations.

2.4.1.2 Abrupt onset helped maintain the predictive timing strategies across tempi

The instructions provided to our participants was to be as best synchronized as possible with the external metronome at all tempi. Analyses of the error in synchrony (asynchronies) revealed that our participants successfully followed the instructions with errors comprised between -100 ms to +50 ms on average across tempi. Note that expert musicians typically show a mean negative asynchrony of -50 ms approximately (Repp, 2005). In the present study, the asynchronies were on average negative between periods of 1200 to 600 ms and were close to zero or positive at faster tempi, suggesting that more prediction in time was required at slow and intermediate tempi as compared to faster ones. Significant differences were reported in function of the AO conditions. The error of synchrony was significantly more negative in the “random” condition as compared to the neutral condition between 800 to 600 ms of IOI, i.e. especially in the intermediate phase of the task, and was significantly more negative across all tempi in the “current” and “next” conditions as compared to the two other conditions. Overall, the flashes helped to involved predictive timing mechanisms. This result could be explained by the fact that whatever the spatial location that was flashed, the AOs always provided a discrete, regular timing information about when to tap, and hence could be used for the temporal control of the task.

We have defined the intermediate phase of the spatial-tapping task as the moment at which a transition from discrete to more continuous movements arises (as revealed through AC values, see Dione et al. 2013). Hence, these results suggest that all AO conditions revealed a faster transition towards emergent timing mechanisms, and maintained the strategies oriented towards predictive timing especially in the intermediate phase.

Some effects of conditions were also reported according to specific spatial locations, in particular at TP-2 and allow interpreting the nature of the effect. The error of synchrony was in fact the largest (and negative) in the “next” condition at slow tempi only (between periods of 1200 to 900 ms), and in the “current” condition at fast tempi only (between periods of 600 to 300 ms). These results suggest a congruency/incongruency effect in the task. Indeed, at slow tempi, the task constraints were geared towards the production of discrete actions. When attention was capture on the next target, the error was increased: the AOs lead attention to be oriented towards the next spatial location whereas the best strategy is to maintain selective attention focussed on the current target. In contrast, at faster tempi, the task constraints lead participants to produce more circular actions (globalising the targets). In this case, the participants needed to orient attention in a predictive matter, towards the next target in order to be able to perform the fast sequential pointing. Compared to the neutral condition, the error was here more negative in the current condition, when attention was attracted towards each current location and thus, rendering the predictive control of eye movements more difficult. Overall, these results suggest that the participants were right on time across tempi and that the AO conditions successfully attracted attention. AOs further helped maintain acceptable levels of accuracy in time when the spatial information provided by the flash was congruent with the strategy to adopt in function of the task constraints.

2.4.2 The role of selective attention for sequential motor planning under timing constraints

2.4.2.1 Attention focused on each discrete action improved the timing accuracy across all tempi

The analysis of the percentage of $\mathrm{IRI}_{\mathrm{error}}$, variable that was used as an indicator of the timing accuracy revealed that the $\mathrm{IRI}_{\mathrm{error}}$ was the smallest between periods of 1200 to 900 ms and the largest for tempi that were faster than 800 ms of IOI, with the emergence of an anchor point in the spatial trajectory, i.e. more negative error at IP-3, at this same tempo. This first result confirms that the timing of intervals was harder to maintain when the tempi were faster than 800 ms of IOI. The $\mathrm{IRI}_{\mathrm{error}}$ also reflected an alternation of short/long intervals at slow tempi, for all positions except IP-3 and IP-6 for which the error was close to zero. This result supports the idea that event-based timing was used at these tempi to guide the action sequences. Indeed, AC-1 values of IRIs reflect the existence of negative correlations between the current and the next intervals of time (Wing & Kristofferson, 1973a). Significant differences were also reported in function of the AO conditions. The $\mathrm{IRI}_{\mathrm{error}}$ was significantly more negative at IP-2 and IP-5 in the current condition, i.e. at the specific IPs showing a positive error at their base levels, as compared to all other conditions. This result suggest that focusing attention on each discrete action (current condition) helped maintain higher levels of timing accuracy as compared to the other conditions. Furthermore, the $\mathrm{IRI}_{\mathrm{error}}$ was significantly more negative at IP-3, i.e. just before the location of the anchor point (TP-4), in the current and in the next condition as compared to the two other conditions. This suggests that the AO conditions allowed to produce larger corrections to reduce the cost of transition from flexion to extension movements for the production of a smooth action patterns (Beek, Turvey, & Schmidt, 1992; Roerdink et al., 2008). It is probable by this effect was only due to the fact that the actions were more discrete in the “current” condition favoring overall the use of predictive mechanisms in time, whereas this effect was probably rather due to the possibility to anticipate in space the spatial location of the anchor point in the “next” condition.

2.4.2.2 More inhibition of the motor response was required in the ”next” and ”random” conditions as revealed by the dwell or contact times

The contact times, also referred as dwell times in the study of Adam et al. (2000) were measured in the present study. Results revealed that they were significantly longer at slow tempi as compared to faster ones. In the study by Adam et al. (2000), longer dwell times were shown to allow the production of more discrete actions as compared to shorter ones. Hence, following this interpretation, our results suggest that the actions sequences were more discrete at slower tempi and more fluent at faster tempi. In the study by Dione et al. (2013), the contact times were correlated with the scores obtained in the a classic inhibition tasks used in neuropsychology, i.e. a go-no-go task, especially in the intermediate phase of the spatial-tapping task, i.e. between periods of 800 to 600 ms. These results were interpreted as reflecting a voluntary will to inhibit the motor urge to go on tapping quickly the next target without respecting the set timing interval, i.e., the urge to anticipate too fast the locations of future targets. Hence, longer contact times may be interpreted here as a constraint that is imposed to the ongoing movement to inhibit going on to the next target too fast. In the present study, our analyses further revealed that the contact times were overall longer at TP-2 and TP-3 as compared to other TPs, which suggests that more cognitive control was required to produce the extension part of the movement as compared to the flexion part.

Finally, results revealed that the contact times were significantly shorter in the “current” condition as compared to the three other conditions. Hence, when the AOs favored a focused attention (current condition), participants may have felt that there was no need to inhibit the motor response and “let go” in order to quickly transition towards future targets allowing a control of the motor sequence through an emergent timing process. On the contrary, when attention was attracted towards future events (next condition) or in a random fashion while the action was to be produced on the current event, contact times were significantly longer, suggesting that in these conditions, the AOs afforded a movement towards their corresponding locations, which was inhibited to meet the current task goal.

2.4.2.3 The spatial error and variability increased when attention was captured on next targets

In the present study, the spatial error was computed as the area of spatial ellipses drawn around the spatial location of the taps endpoints surrounding each spatial target. The spatial error was the smallest between periods of 1200 to 900 ms, slightly increased between periods of 800 to 600 ms and was finally the largest between periods 500 to 300 ms of IOI. An anchor point was further revealed in the spatial-trajectory, i.e. a specific reduction in the spatial error at TP-4, from periods of 700 ms of IOI and faster. This pattern of results support the idea that the emergence of more continuous movement arose conjointly with an increase in the spatial variability. It is possible that at fast tempi, the task goal was not geared towards the needs to maintain accuracy in space and time but towards the needs to produce a circle, i.e. to favor a smooth transition from the extension and flexion sub-components of the movements.

An effect of condition was also reported: the spatial error was significantly larger in the "next" conditions between periods 600 to 300 ms especially. Hence, while the spatial variability was already high at these fast tempi, the AOs occurring at the next positions further increased it. This result could suggest that this specific condition optimized the production of more global actions.

In order to assess how the spatial trajectories were planned in space in function of the task constraints and conditions, we measured the deviations of the main axis of the spatial ellipses (1) from the tangent to the circle, in order to test whether the actions became more circular, and (2) in function of an imaginary line drawn between the current and the next target, to assess whether anticipatory of future events took place to plan the action sequences. For the second measure, it was expected that more anticipation will be required especially at the point of transition from emergent to predictive timing modes. The results reported here revealed that on average movements were significantly more oriented in function of the tangent to the circle for IOIs of 500 ms and faster. At slower tempi, the movements were significantly more oriented in function of the imaginary line, especially at TP-1 and TP-4, targets that were used to initiate the extension and flexion movements of the sequence.

Differences were also reported according to conditions. Results revealed that the "next" condition favored ellipses oriented towards the tangent to the circle suggesting that the tapping sequence was guided through an internal representation of the global circle. This was true especially on the flexion part of the movement (i.e. at TP-4 and TP-5) and at all tempi. Nevertheless, ellipses were significantly more oriented towards the next target at TP-1. This observation supports the idea that anticipatory mechanisms were required especially to initiate the action sequence, probably in order to reduce the cost due to the requirement of loading the entire motor program before the initiation of an embedded sequence of movements (Adam et al., 2000; Ivry, 1986). Hence, our results suggest that orienting attention towards the forthcoming event rendered the actions more circular with specific constraints geared on the first sub-component of the action sequence. The "current" and the "random" conditions had the reversed effects on the orientation deviations of the ellipses. In both conditions, the ellipses were significantly less oriented in function of the tangent to the circle on the flexion part of the movement especially (i.e. at TP-4 and TP-5). In the "current" condition, the ellipses were further less oriented in function of the tangent to the circle at TP-2. By contrast, they were more oriented in function of this model at TP-3, which reveals that even when attention was focused on each discrete action, there was a need to anticipate the transition from flexion to extension movements. Moreover, in the "random" condition, the ellipses were significantly less oriented towards the next target at TP-1, suggesting that the actions produced in this condition were not embedded within a specific context involving a complex motor program. Hence, both the "random" and the "current" conditions rendered the actions less circular with however an effect affecting more spatial locations when attention was focused on each discrete action, i.e. in the "current" condition.

Effects common to the three flashing conditions were also observed: the ellipses were significantly less oriented towards the next target at TP-3, and significantly more oriented towards the next target at TP-4 in the AO conditions as compared to the neutral condition. This result can be interpreted as a by-product of using AO, i.e. that provide a quite regular information about the moment at which to tap and then favoured the production of more discrete actions overall, i.e. with less constraints to anticipate especially the location of the anchor point and more comfort to dissociate rather than embed the flexion and extension parts of the movements involved in the sequence.

2.4.3 Conclusions

Overall, our results suggest that focusing attention on each discrete action improved the accuracy to produce event-based intervals of time across all tempi. Orienting attention towards the forthcoming events while tapping on the current spatial location, rendered the actions more circular with a special focus on the response initiation to avoid a cost due to the needs to prepare in advance the entire motor plan. In this condition, but also when attention was simply captured (random condition), more control of the motor response, i.e. motor inhibition was required, certainly to deal with the task instructions that were initially geared towards the needs to maintain synchrony across all tempi. It is probable that this effect would disappear if participants were asked to produce the action sequence in a spontaneous way, i.e. without the constraint to synchronize with an external metronome. In this case, the actions would be circular with short contact times to enhance the fluency of the gesture. Independently of the spatial locations at which AOs were flashed, they encouraged the use of event-based timing processes. This effect was especially reflected in the asynchronies and in the measures of the deviation from the trajectory planning models and was certainly due to the fact the abrupt onsets provided an imprecise but regular information about the moment at which the tap was expected to be produced. Hence, it could be interesting in future studies to emit the AOs in a more random manner in time to control whether in this condition the effects reported on asynchronies and orientation deviations would disappear.

2.4.3.1 Food for thought: inhibition within the predictive coding hypothesis

In the present study, we bring arguments in favor of the view that attention and conscious perception are two distinct mental processes working through opponent computations and according to distinct task demands to optimize the conditions by which prediction errors can be minimized to allow the production of adapted behaviors in the world. Indeed, while selective attention was shown to optimize the accuracy to produce precise intervals of time, conscious perception allowed increasing the spatial variability of the motor actions to allow the production of a more circular pattern of embedded actions. Hence, the roles played by selective attention and conscious perception matched the hypotheses proposed by Hohwy (2012) at a theoretical level. Indeed, selective attention was expected to work in an updating fashion, i.e. that selectively sample the world by changing the input on the basis of a precise prediction and with the aim to reduce the variability of the response. The same sorts of updating mechanisms would be expected in regards to clock models of timing (Treisman, 1963; Wing & Kristofferson, 1973a, 1973b). Indeed, these models assume the existence of a referential memory, in which the referential interval of time to follow is loaded, and of a working memory in which a representation of the produced interval of time is maintained. The referential interval and the produced intervals would then be compared and a judgement could be provided (e.g. the interval produced was longer that the referential). If the deviation from the referential interval is judged as important, a correction could be implemented through successive adjustments at later points in the series. Note that these adjustments are not expected to be produced at each taps in an effortful manner, a precise interval of time being defined as an interval that is close to the mean according to a acceptable level of standard deviation.

Conscious perception was expected to work as a sort of binding process (Treisman & Gelade, 1980) and through changing the initial predictive model to improve overall the context in which to act (Hohwy, 2012). Such sort of mechanism was reported in the spatial-tapping task. Indeed, the spatial variability was significantly higher across almost of the tempi (even if significant differences were almost reported in the faster tempi) when attention was oriented towards forthcoming events. In this specific context, the actions became significantly more circular as compared to the two other conditions. Hence, in regards to the arguments reported here, we suggest that the spatial-tapping task could be an empirical example to support the framework by which attention and conscious perception act as opponent computations to allow predictive error minimization, with the one or the other mechanism being required in function of the task demands, i.e. conscious perception when multiple information needed to be summarized, selective attention when a focus on specific perception-action links is required.

The findings reported in the present study also highlight the importance of inhibitory mechanisms and we propose that this specific brain computation should be integrated in some fashion within the predictive model hypothesis. In the present study, inhibitory mechanisms were used in order to favour or disfavour a transition from attention to conscious perception, with longer contact times introducing a cognitive bias to dissociate the current action from the next one. These mechanisms were especially measurable when attention was attracted in a random fashion on the visual targets, and when attention was attracted towards the forthcoming events i.e., when attention was not successfully biased on the current event through prior expectations. The fact that the role of inhibition is at the foundation of most of the research work studying the role of selective attention for action planning (e.g. Van der Stigchel, 2010; Welsh & Elliott, 2005) is another argument to support the view that inhibition mechanisms play an important role in the dynamics of human cognition and hence should certainly be integrated within the predictive coding model. This enterprise would lead to define a three component model with updating, inhibition and binding as the principle mechanisms of human cognition, and with attention and conscious perception constituing optimizers for the predictive models.

2.4.3.2 Food for thought: circle-tapping as a clinical test for Executive Functions

Note that such sorts of three-component model matches with current views about the high-level executive functions of actions planning (Miyake & Friedman, 2012). Indeed, from the historical findings about frontal diseases observed in patients in the neuropsychological domain, three main executive functions have been described, namely the updating, inhibiting and switching functions. In clinical neuropsychology, batteries of multiple tasks are often used to target each of the functions separately. However, the classical tasks are known to suffer a number of validity issues (Burgess, 1997; Miyake et al., 2000; Phillips, 1997; Rabbitt, 1997). Due in part to the fact that they are too complex, these tasks often resemble logical reasoning games, e.g. the tower of Hano (Goel & Grafman, 1995; Shallice, 1982). Recently, we proposed to use the spatial-tapping task rather than complex battery of neuropsychological in order to assess the executive functions of planning (Dione et al., 2013). Each dependent variable ($\text{IRI}_{\text{error}}$, contact times, area of ellipses) was averaged in function of the three behavioural phase of action control observed in the task to obtain a unique score by variable to assess each function. Multiple regression analyses revealed, (1) a correlation between the scores obtained in the updating task (n-back) and the $\text{IRI}_{\text{error}}$ in the slow phase of the task, (2) between the scores obtained in the inhibiting task (go-no-go) and the contact times in the intermediate phase of the task, (3) between the scores obtained in the switching task (letter-number) and the area in the fast phase of the task. These results support the view that three distinct cognitive mechanisms are involved in the planning and control of action sequences and are completed today by the view that conscious perception and attention could play optimizer roles to improve in a direct way the causality of stimulus-response relationships. They could also play an important role as context stabilizers and/or optimizers to favour the emergence of more complex behaviours. Future research is now required using the spatial-tapping task or similar non-verbal motor tasks to gain better understanding and definitions about the brain networks implementing the three executive functions of updating, inhibiting and switching.

Study 3

Planning ahead through space and time: from neuropsychology to motor control

Abstract

The executive functions have been studied separately in the fields of neuropsychology and of motor control. However, it is not clear whether across fields one is referring to similar cognitive functions. In the present study, we compared the performance scores obtained in a motor spatial-tapping task with those scores obtained in a battery of three neuropsychological tasks which assess respectively the executive functions of updating (N-back task), inhibiting (Go-noGo task) and switching (Letter-number task). Multiple regression analyses revealed significant and specific effects between the motor task and the classical neuropsychological tasks: the timing error measured at slow tempi in the tapping task predicted the scores observed in the updating task only; the spatial error at faster tempi predicted the scores obtained in the switching task only; the contact times at intermediate tempi predicted the scores obtained in the inhibiting task only. Hence, we introduce this easy-to-use non-verbal task as a novel paradigm to assess executive functioning.

3.1 Introduction

3.1.1 Neuropsychological approach of Planning

Research on the executive functions has historical roots in the study of patients with frontal lobe damage. These patients were the first to demonstrate disruptions to control and organize daily activities independent of any language or memory disorders (Damasio, 1994; Harlow, 1868). The so-called “frontal” or “executive” tasks were specifically developed to assess how the main functional deficit encountered by frontal patients, i.e. the planning of daily activities, was affected following brain injury. For example, the Tower of London (Shallice, 1982), a task inspired by a logical reasoning game (the Tower of Hanoi) was proposed to evaluate the ability to inhibit a routine schema that consisted in producing each move in an isolated and impulsive fashion in response to the true visual configuration of the Tower in order to define and adopt a cognitive plan to achieve the puzzle in fewer moves (see the model of SAS/GOC, Shallice, 1988). The Wisconsin Card Sorting Test (WCST, Grant & Berg, 1948), on the other hand, was proposed to target individuals’ inability to switch efficiently from an ongoing plan to a novel one. In this task, perseverating errors were measured and used as indicators of cognitive flexibility (Milner, 1963). Finally, working memory tasks, e.g., the n-back task, were developed to target a person’s ability to maintain a cognitive plan active and to update between relevant parts of the plan in function of a given situation. Hence, the executive functions are here directly related to the abilities to inhibit a routine schema in order to adopt and adapt a novel more cognitive plan, to maintain and update parts of a given plan across time and/or to switch flexibly from one plan to another. In the last decade, these cognitive abilities have been referred to in the literature as the inhibiting, the updating, and the switching executive functions (Miyake & Friedman, 2012; Miyake et al., 2000) and it is common today to use a multiple-test battery to assess the well functioning of the executive functions related to planning abilities.

However, it is the case that the neuropsychological tasks that are classically used to assess the executive functions suffer from a number of validity problems that limits severely the possibility to compare the functions between them. Indeed, the tasks are known to have impurity issues because of the presence of non-executive demands specifically related to the various contents that are used in the tasks (e.g., language, limb displacements, object identification, etc., Burgess, 1997; Phillips, 1997). Second, they present a lack of test-retest reliability, i.e. people can adopt different executive strategies to perform the same task across sessions (Rabbitt, 1997). For example, although the WCST has been designed to reveal a lack of cognitive flexibility, subjects may perform the task by inhibiting certain responses that are no longer appropriate (Miyake et al., 2000). Thus, scores in different sessions may reflect different cognitive strategies, with participants who are sometimes switching between rules and at other times using inhibition to solve the task. The difficulty to characterize the possible relationships between the executive functions is in itself a motivator to consider today a different approach to the evaluation of executive functioning.

3.1.2 Planning in the Motor Control domain

A major interest in the field of motor control is to understand how actions are coordinated to enable the execution of complex sequential motor activities, e.g. playing a musical instrument or dancing in rhythm. This question has been particularly studied in the context of sensorimotor synchronization (for a review on SMS, see Repp, 2005). Even if synchronized behaviors require motor coordination both through space and time, research has focused historically on the timing aspects of motor planning and experimental findings have led to the acceptance today of the existence of two distinct timing modes related to the control and execution of rhythmical action sequences (Robertson et al., 1999; Zelaznik, Spencer, & Ivry, 2002). The event-based timing mode is primarily involved in tasks that have a clear temporal goal, e.g. trying to keep the beat of a metronome, and is assumed to require an explicit internal representation or memory of the referential temporal interval to produce (Wing & Kristofferson, 1973). By contrast, emergent timing is assumed to arise implicitly, i.e. from the extraction of temporal regularities emerging naturally from the dynamics of movement control when actions are repeated in smooth oscillatory cycles (Ivry, Spencer, Zelaznik, & Diedrichsen, 2002; Turvey, 1977). For example I can infer that “I will be late given the speed of my successive footsteps”. While finger tapping is the prevailing paradigm to reveal event-based timing, circle drawing has been proposed as the exemplar task to reveal emergent timing (Zelaznik et al., 2002). In terms of statistics, negative lag-1 autocorrelation values are typically observed in finger-tapping tasks suggesting that motor responses are controlled through an internal timekeeper (Vorberg & Wing, 1996;

Wing & Kristofferson, 1973). In contrast, positive or near-to-zero AC-1 values are classically reported in circle drawing tasks suggesting that other mechanisms of control enter into play and enable the implicit emergence of a certain sense of rhythmicity (Lemoine & Delignières, 2009; Torre & Delignières, 2008; Zelaznik et al., 2002). Anchoring has been described as a possible mechanism that could explain how timing emerges when movements are continuous rather than discrete. This phenomenon, commonly observed in cyclical movements, consists in a local reduction in spatial and/or temporal errors at a specific location along the trajectory path and is often observed around reversal points, i.e. at points of transition between flexion/extension movements (Beek, Turvey, & Schmidt, 1992; Roerdink, Ophoff, Peper, & Beek, 2008). This specific point of transition could be used as a referential to infer timing regularities in the case of continuous movements (Repp & Steinman, 2010).

In a recent study (Dione & Delevoye-Turrell, unpublished) the use of a unique task designed as a hybrid of finger tapping and circle drawing was suggested to reveal, assess and compare the two modes of timing between them. In this “spatial-tapping” task, a picture composed of six discrete visual targets (disposed around a virtual circle) was displayed on a tactile screen. Participants were asked to produce discrete taps on each target, one after the other and to follow the circular trajectory with the arm at the regular pace of a metronome (from 1100 to 300 ms of inter-tone intervals, ITI). The motor actions were assumed to be discrete at slower tempi with the need of cognitive control to maintain long timing intervals through timekeeping at slow tempi; motor actions were proposed to be continuous at faster tempi through the capacity to anticipate only the point of transition between flexion/extension movements when the tempi were too fast. Autocorrelation values were measured up to ten lags to reveal event-based timing at slow tempi (negative AC-1) and emergent timing at faster tempi (positive AC-6). Furthermore, a detailed spatial analysis was conducted on the spatial endpoint distributions to assess whether the cognitive strategy was turned towards the need to anticipate the point of transition between flexion and extension movement at faster tempi. Spatial ellipses were first measured for each target. The mean area and the angular orientation of each ellipse were then computed. An orientation error was finally calculated as the angular difference between the orientation of the ellipse and the tangent to the circle measured at each target. Performance results revealed first that both the timing (% of $\mathrm{IRI}_{\mathrm{error}}$) and the spatial accuracy (mean spatial area) were perfectly maintained at slowest tempi (from 1100 to 900 ms). A first small but significant decrease in the performance arose at 800 ms and was maintained until 600 ms. For tempi that were faster than 500 ms the performance was the worst with rather large spatial and timing errors. As predicted for the timing strategies, significant negative autocorrelation values emerged at lag-1 at slow tempi only (from 1100 to 700 ms) and significant positive AC emerged at lag-6 at faster tempi only (from 500 to 300 ms). In order to assess whether the actions were controlled or not through an internal timekeeper (event-based timing), the motor delays were measured for each tempo and both lags according to the W-K model. Results revealed that the motor delays increased in function of tempi at lag-1 only, suggesting that the timing was event-based at slow tempi only in this spatial-tapping task and that other mechanisms entered into play to explain the correlation factors observed at lag-6. Finally, the spatial analysis confirmed that the endpoint distributions were more oriented in relation to the tangent to the circle at faster tempi, with the emergence of an anchor point at the point of maximal extension in the fastest tempi only.

Overall, these results suggested that in the spatial-tapping task, the timing mode was changed from event-based timing at slow tempi towards emergent timing at faster tempi. Consequently, it is possible to presume that in this motor task the cognitive demands depended on different behavioral strategies in function of the cognitive needs to actively maintain a referential timing interval in working memory (from 1100 to 900 ms), and to anticipate the spatial point of transition between the two movements of flexion vs. extension involved in the sequence (from 500 to 300 ms). An intermediate phase was here observed for those tempi between 800 to 600 ms in which the performance was decreased in space and time but in which at the same time the event-based timing strategy was efficiently maintained for 2/3 of the trials. It is thus possible that in this phase motor inhibition was used in order to avoid a too fast transition from discrete to continuous movement by making an effort to maintain attention on each discrete action in spite of the increase in temporal pressure.

3.1.3 From neuropsychology to motor control

In the present study, we suggest that the spatial-tapping task, a task in which several motor actions need to be planned and executed both in space and time could be an interesting method to assess the so-called executive functions. Indeed, the spatial-tapping task requires: (1) working-memory at slow tempi in order to produce discrete tapping actions in reference to memorized timing intervals, (2) the active reduction of a switching cost related to the motor switching between the two biomecanically distinct movements of flexion and extension that compose the movement sequence with the idea that bad switching will lead to poor spatial control of movement trajectory, (3) and finally inhibition of a too fast transition from discrete to continuous actions at intermediate tempi, with finger contact times that are too short to maintain high timing levels of performance.

In order to test this hypothesis performance scores were measured both in a spatial-tapping task and in a battery of neuropsychological tests assessing the three main executive functions. Multiple regression analyses were then computed to explore and reveal specific relationships between the functions.

3.2 Methods

3.2.1 Participants

Twenty-six right-handed students between 18 to 21 years of age and recruited from the University of Lille 3 participated voluntarily in the study. All participants received an information letter and provided written informed consent. All participants performed the task with their right hand and reported having normal or corrected-to-normal vision. The protocol received approval of the ethics committee in human sciences of the University of Lille 3.

3.2.2 The spatial-tapping task

3.2.2.1 Material & Stimuli

A picture composed of 6 black targets was displayed on a touch screen Elo Touch 19" 1915L. The targets (10 mm of diameter, distanced of 100 mm) were placed around a virtual circle of 100 mm of radius. The participants were invited to stand in front of the screen that was placed upon a table and titled at 90 degrees of angle.

3.2.2.2 Procedure

The subjects' task was to touch each visual target one after the other, starting from the bottom right target, and moving counter-clockwise using the right index finger (fist closed). Participants were instructed to synchronize each pointing action to a series of regular auditory tones (beep duration = 100 ms) that was played through classic computer speakers. Participants were encouraged to maintain their left arm relaxed along the body side. They were clearly instructed of the goal of the task that was to be at best synchronized with the metronome. Each subject performed a total of ten trials. The initial tempo was an inter-tone interval (ITI) of 1200 ms. The temporal interval was increased by 100 ms between each trial with the fastest one being at an ITI of 300 ms. Participants were required to produce sixty taps for each trial. The total duration of the session was 10 minutes, approximately.

3.2.2.3 Performance measures

Timing performance. Inter-response intervals (IRIs) were measured as the time interval between the start of two successive taps. Long intervals (> 2*ITI) were omitted from all calculations. The $\mathrm{IRI}_{\mathrm{error}}$ was then computed as the percentage of absolute difference between each IRI and the reference ITI of a given trial. This measure served as an indicator of the magnitude of the timing error.

Spatial performance. The endpoint distributions of the pointing actions were plotted in function of each visual target position. All taps were used (ten data points per ellipse). Through vector calculations, spatial ellipses were then calculated. The mean area of the spatial ellipses was finally measured in mm2 as an indicator of the magnitude of the spatial error (SE).

Motor Fluency. The Contact time (CT) was defined as the time of finger contact with the touch screen. This measure (in ms) was used to assess the level of control of the motor response output, with shorter CTs being related to a more fluent gesture.

Planning indicators: Event-based vs. emergent timing. After having suppressed the first six IRIs of each trial, autocorrelation (AC) values were calculated at lag-1 and lag-6 (for details, see Vorberg & Wing, 1996). These measures served as an indicator of the timing mode that was used to guide the pointing actions with event-based timing being revealed through negative AC-1 values, and emergent timing through positive AC-6 values.

3.2.2.4 Statistical Analyses

Performance measures and planning indicators were first calculated for individual trials and then averaged across participants. Second, analyses of variances (ANOVA) were conducted with ITI as a repeated measure on measures and indicators. Fisher LSD post hoc tests were used when required and the alpha level was set to 0.05. The performance measures were then averaged within three phases for each subject according to the moment of change in planning strategy: slow or updating phase, intermediate or inhibiting phase, fast or switching phase.

3.2.3 Neuropsychological tasks

3.2.3.1 Material & Stimuli

The tasks were all selected from a French version of the TAP computerized battery of tests (Zimmermann & Fimm, 1994). Participants were seated in front of the computer. The experimenter provided instructions orally. The same instructions were then displayed on the screen. A familiarization trial was performed before each task. One or two response keys were used, in function of task requirements. When only one response key was presented, subjects were asked to respond with their right hand only. When two response keys were required, participants were asked to respond with their right hand on the right key, and their left hand on the left key. For each task, participants were asked to respond as rapidly as possible while maintaining a low error-rate.

3.2.3.2 Tasks procedures

Updating & N-back task. A series of one-digit numbers were presented one after the other, in the centre of the screen (100 items that 15 target items). The subjects' task was to press the response key as fast as possible when the item on the screen was the same as the item presented two times before. Subjects were scored according to the median of their reaction times (RT).

Inhibiting & Go-noGo task. A straight or a diagonal cross ('+' or 'x') appeared briefly in the centre of the screen, for a total sequence length of 40 items. The participant's task was to press a response key as fast as possible for the diagonal cross ('x') only. The target item was present 50% of the time. Participants were scored according to the number of false responses.

Switching & The Letter-number task. A letter and a number were simultaneously presented on the computer screen, for a total sequence of 100 items. Two control conditions and one alternation condition were performed. Two response-keys were used. In the first control or pure block condition, the participants' task was to press the response key that was in the same hemi-field than the letter (for example, if the letter was presented on the left side of the screen, subjects had to press the left response key). In the second control condition, participants had to press the response key that was in the same hemi-field than the number. In the alternation condition, the participants were instructed to alternate a response to a letter, and a response to a number, from trial-to-trial, by pressing the response key that was located in the corresponding hemi-field. Participants were scored according to a switching cost that was measured as the difference in reaction time between the pure blocks (that were pooled together) and the alternation condition.

3.2.3.3 Statistical Analyses

Performance scores were calculated for each individual in each task and then averaged across participants. Descriptive results (mean, standard, deviation, min & max values) were then computed. χ^2 tests were then performed to ensure that performance scores were normally distributed across tasks.

3.2.4 Multiple regression analyses: ST vs. classical tasks

Standard multiple regression analyses were conducted to evaluate how well each performance scores ($\mathrm{IRI_{error}}$, CTs, area) obtained in each phase of the spatial-tapping task (regressors) could predict the scores obtained in each of the neuropsychological tasks (dependent variables). The alpha value was set at 0.05. Following our hypotheses, (1) the timing accuracy in the slow phase of the spatial-tapping task ($\mathrm{IRI_{error}}$) should require WM abilities (n-back task); (2)

control of the motor response (CTs) as required in the intermediate phase of the spatial-tapping task should be an indicator of inhibition abilities (go-no-go); (3) decrease in the spatial error in the faster phase of the spatial-tapping task (area) should be an indicator of the switching abilities (letter-number task).

3.3 Results

3.3.1 The Spatial Tapping task

3.3.1.1 Performance results

Timing performances. Results revealed that all participants closely followed the tempo even at fast tempi, with a maximum mean error of 8% across the ITI spectrum. As an example, the greatest errors were observed in the fastest tempo of ITI=300 ms, with IRIs contained between 276 and 324 ms. ANOVA on the $\mathrm{IRI}_{\mathrm{error}}$ revealed nevertheless that the timing errors were significantly different in function of ITI ($F(9;225) = 7.685$; $p<0.001$). Post hoc tests revealed that timing errors were larger at faster tempi, i.e. for ITI=400 to 300 ms (Mean = 7.6%; SD = 2.8%) and these values were significantly different from that measured at slower tempi (Mean = 5.9%; SD = 1.7%).

Spatial performance. ANOVA conducted on the spatial area revealed an increase in the spatial errors at faster tempi ($F(9; 225) = 83.678$; $p<0.001$). More specifically, the mean area of the endpoint ellipses were the smallest at slower tempi, i.e., at ITI=1100 to 800 ms (Mean = 42.9 mm^2; SD = 23.7 mm^2), with all other tempi being characterized by significantly larger errors. Spatial areas were the largest at faster tempi (from ITI=500 to 300 ms) and these results were significantly different from all other ITIs (Mean = 126.8 mm^2; SD = 73.96 mm^2).

Motor fluency. ANOVA conducted on the mean contact times revealed that the CTs were shorter with increasing tempi ($F(9; 225) = 31.14$; $p < 0.001$). Post Hoc tests revealed that the decrease in CT was linear with increasing tempi, with significant differences between the nth trial and the trial (n+2). Nevertheless, no differences between neighboring ITIs emerged at the slower tempi, i.e. between ITIs=1200 to 1000 ms for which the largest contact times were measured.

Overall, motor actions were precise in space and time at the slowest tempi

(800 ms), less accurate in space but more fluent at intermediate tempi (at 700 and 600 ms of ITI), less precise in both space and time but much more fluent at faster tempi (from 500 to 300 ms of ITI).

3.3.1.2 Planning indicators

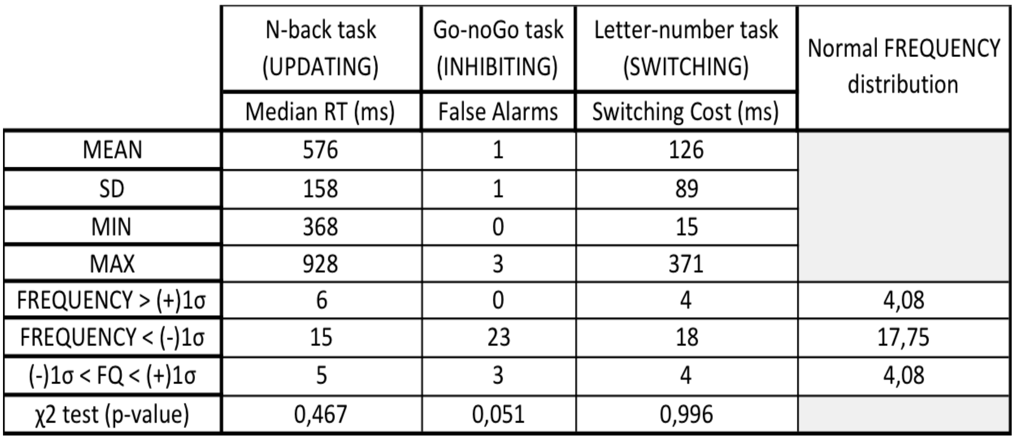
Event-based timing. To note first is the fact that all AC-1 values were negative. Repeated ANOVAs on the AC-1 values showed that these values were significantly different in function of ITI (F(9; 225) = 5.933; p<0.001). Post Hoc tests confirmed that the AC-1 values were the largest at slower tempi, i.e. for ITI=1100 to 900 ms of ITI (Mean = -0.28; SD = 0.15) and significantly smaller with increasing tempi, i.e. from ITI=800 to 400 ms (Mean = -0.17, SD = 0.18). The AC-1 value was finally the smallest at the fastest ITI of 300 ms (Mean = -0.02, SD = 0.21). These results suggest that the timing mode was event-based for slow tempi (1200 to 900 ms) in this task.

Emergent timing. To note first that all AC-6 values were positive. Repeated ANOVAs on the AC-6 values revealed that these values were significantly different in functions of ITI (F(9,225) = 8.524; p<0.001). Post Hoc tests revealed that the AC-6 values were the smallest at slower tempi, i.e. for ITI=1200 to 900 ms (Mean = 0.08; SD = 0.15). At faster tempi (ITI=500 ms to 300 ms), the positive AC-6 values were the largest (Mean = 0.31, SD = 0.20) and not significantly different between each other. At intermediate tempi (from 800 to 600 ms), the AC-6 values were all significantly smaller than at least one of the faster ITIs and larger than at least one of the slower ITI. These results indicate that the timing mode became emergent at fast tempi of 500 to 300 ms of ITI.

Overall, these results suggests that the timing was event-based at slowest tempi (from 1200 to 900 ms), emergent at fastest tempi (500 to 300 ms) and in a transition phase at intermediate tempi (from 800 to 600 ms).

3.3.2 Neuropsychological tasks

Performance scores observed in the neuropsychological tasks are presented in table II.1. χ^2 tests revealed that performance scores were normally distributed across tasks.

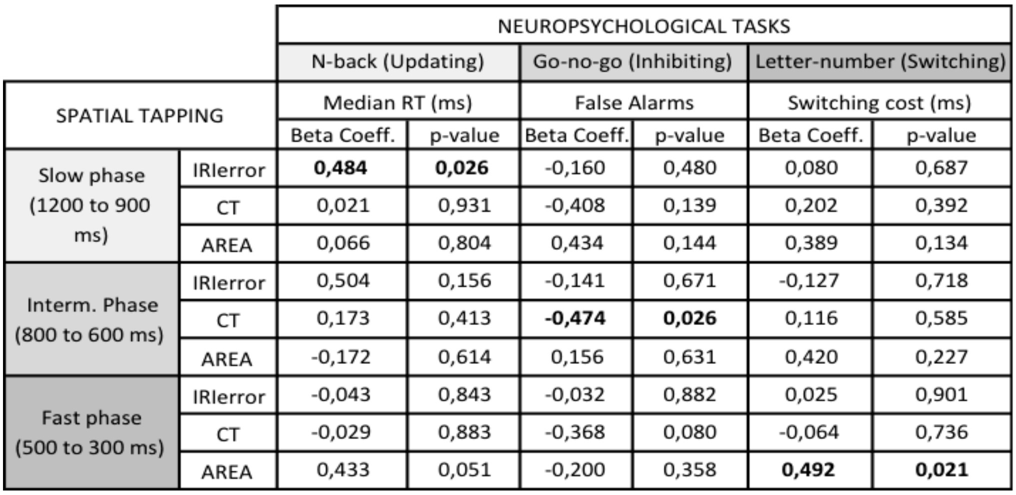


	N-back task (UPDATING)	Go-noGo task (INHIBITING)	Letter-number task (SWITCHING)	Normal FREQUENCY distribution
	Median RT (ms)	False Alarms	Switching Cost (ms)	
MEAN	576	1	126	
SD	158	1	89	
MIN	368	0	15	
MAX	928	3	371	
FREQUENCY > (+)1σ	6	0	4	4,08
FREQUENCY < (-)1σ	15	23	18	17,75
(-)1σ < FQ < (+)1σ	5	3	4	4,08
χ2 test (p-value)	0,467	0,051	0,996	

Table II.1: Performance scores in the classic executive tasks

3.3.3 Multiple Regression Analyses: ST vs. classical tasks

Beta coefficients and corresponding p-values are presented in table II.2 for each regressor in function of each dependent variable. Results confirm our hypotheses: (1) small timing errors in the slow phase of the ST task predict short reaction times in the WM task, (2) short contact times in the intermediate phase of the ST-task predict larger number of inhibition error in the go-no-go task, (3) smaller area in the fast phase of the ST-task predict smaller switching cost in the letter-number task.



		NEUROPSYCHOLOGICAL TASKS					
		N-back (Updating)		Go-no-go (Inhibiting)		Letter-number (Switching)	
SPATIAL TAPPING		Median RT (ms)		False Alarms		Switching cost (ms)	
		Beta Coeff.	p-value	Beta Coeff.	p-value	Beta Coeff.	p-value
Slow phase (1200 to 900 ms)	IRIerror	**0,484**	**0,026**	-0,160	0,480	0,080	0,687
	CT	0,021	0,931	-0,408	0,139	0,202	0,392
	AREA	0,066	0,804	0,434	0,144	0,389	0,134
Interm. Phase (800 to 600 ms)	IRIerror	0,504	0,156	-0,141	0,671	-0,127	0,718
	CT	0,173	0,413	**-0,474**	**0,026**	0,116	0,585
	AREA	-0,172	0,614	0,156	0,631	0,420	0,227
Fast phase (500 to 300 ms)	IRIerror	-0,043	0,843	-0,032	0,882	0,025	0,901
	CT	-0,029	0,883	-0,368	0,080	-0,064	0,736
	AREA	0,433	0,051	-0,200	0,358	**0,492**	**0,021**

Table II.2: Performance scores in the classic executive tasks

3.4 Discussion

In this study, we asked whether a simple motor sequencing task could be used to assess the executive functions of planning described in the neuropsychological literature. This motor task was assumed to involve updating in working memory at slowest tempi, inhibiting at intermediate tempi, and switching at faster tempi. This hypothesis was tested by comparing performance scores in the spatial-tapping task to those scores obtained in three neuropsychological tasks selected to target each specific executive function. The findings reported here confirmed our working hypothesis. Indeed, in the slow phase of the spatial tapping task, results suggested that the motor actions were triggered through an internal representation of time intervals, with larger negative auto-correlations at slow tempi (from 900 to 1200 ms). To perform the task adequately, subjects were required to maintain actively in working memory the target time interval to produce, across the entire duration of the trial.

Regression analyses confirmed furthermore the existence of a relationship between these motor results and those performances obtained in a cognitive WM task, suggesting similar WM functions in the cognitive and in the motor domains. In the faster phase of the spatial-tapping task (from 500 to 300 ms), with actions becoming more circular, it was suggested that the action sequence was divided in two biomecanically distinct movements that compose the sequence, i.e., flexion vs. extension movement patterns. The cognitive goal in this case was then geared towards the need to coordinate smoothly the distinct movements composing the sequence towards a more global trajectory pattern that binds them together, here a circle. In circle drawing, this phenomena is actually measurable through the emergence of an anchor point that is a kinematic reduction in the timing and/or spatial variability at the point of transition between flexion/extension movements (Beek et al., 1992). It has been shown that the anchor point is effectively reduced through explicit anticipatory processes. Indeed, orienting the gaze in advance towards the anchor point significantly reduces the spatial variability observed at this point. In the same vain, flexing and extending the wrist in an anticipatory rhythmic fashion significantly reduces both the spatial and temporal errors respectively at the points of maximum flexion vs. extension related to the movement pathway (Roerdink et al., 2008). In the present results, we observed an anchor point within our circular trajectory at the point of maximal extension (upper left target); point in space at which smaller spatial variability was measured but only in the faster phase of the task, which confirms the role of emergent timing at fast tempi. In reference to the cognitive tests, our results revealed furthermore that the performances at fast tempi in the spatial tapping task were effectively related to smaller switching cost in a classical switching task, suggesting that switching between two biomechanical movements may be in fact controlled by those similar functions used for cognitive switching. Finally, in the intermediate phase of the spatial-tapping task, it was suggested that motor inhibition of a too fast transition from discrete to continuous actions entered into play to maintain high levels of spatial and timing accuracy in spite of the increase in temporal pressure. This hypothesis was confirmed here with longer contact times in the intermediate phase of the spatial-tapping task being significantly related with the ability to inhibit impulsive response in a classical go-no-go task.

In conclusion, we propose the spatial-tapping as a novel paradigm (1) to assess the executive functions in an easy and non-verbal context, (2) to gain a better understanding of the relationships between the distinct executive functions. This approach may be a promising way to reconsider cognitive strategy in broader context and offers a starting point for the study of the functional relationships between motor and cognitive control.

Chapter III

Applications to normal ageing and pathology

Chapter's overview

In the present chapter, we used the spatial tapping task to assess the executive functions in two distinct populations: in an ageing population (**Study 1**), and in an adult population of patients suffering of schizophrenia (**Study 2**).

The spatial-tapping task revealed a specific deficit of inhibition with normal ageing, and updating difficulties associated with a tendency to over-switch at slow tempi in schizophrenia.

S1: Dione, M., Phulpin, X., Delevoye-Turrell, Y. (in prep). Executive functions assessed by the spatial-tapping task with normal ageing: motor and cognitive inhibition mechanisms are impaired while the updating and switching functions are preserved
S2: Dione, M., Giersch, A., Delevoye-Turrell, Y. (in prep). Executive functioning in schizophrenia.

Study 1

Executive functioning in normal ageing: a specific deficit of inhibition

Abstract

Inhibitory mechanisms have been historically described as the main cognitive mechanisms impaired with normal ageing. This hypothesis has been then challenged following the assumption that other functions subserved by the frontal lobes might also be impaired with ageing. This second hypothesis was supported by a number of studies using classical neuropsychological batteries of tests. However, these clinical tools are known to lack of specificity and to suffer impurity and validity issues. In the present study, young, mature and elderly participants (n=54) performed a task recently introduced in the literature to assess the executive functions in a more specific way than does classical tests, namely the spatial-tapping task. Our results revealed preserved updating and switching mechanisms with ageing and the presence of specific impairments related to the inhibition function.

1.1 Introduction

Normal ageing is characterized by a decline in a number of cognitive functions, which mainly depend upon the integrity of the frontal lobes at the brain level (Dempster, 1992; Raz, 2000; West, 1996). Historically, inhibitory mechanisms, i.e. the abilities to retain a dominant or prepotent response, have been described as the core cognitive functions disrupted with ageing, with similarities reported in the performance of elderly subjects and frontal lobe patients in a range of neuropsychological tasks assessing inhibiting capacities (Dempster, 1992). However, it has been recently proposed that other functions depending upon the frontal lobes, such as memory could also be impaired in the course of normal ageing (West, 1996), suggesting a general rather than specific deficit in the executive functions.

In cognitive psychology, the executive functions are described as the high-level cognitive mechanisms that allow organizing, planning, coordinating and executing of daily activities and behaviors. They have been historically described in neuropsychology (Harlow, 1868) after having observed in frontal patients, executive deficits independent of any difficulties in language, memory or general intelligence (Damasio, 1994; Shallice & Burgess, 1991). After brain damage, frontal patients were more impulsive in their choices and daily behaviours and showed difficulties to manage and reach short-terms and long-terms goals. In order to assess the proper functioning of the executive functions, a wide range of neuropsychological tasks assessing the diverse cognitive functions that are thought to be involved in the planning and execution of daily activities, e.g. logical reasoning, memory, cognitive flexibility, inhibition, anticipation, attention, etc., have been developed through the years. For example, the WSCT was created to assess cognitive flexibility (Grant & Berg, 1948), while the Tower of London to assess the inhibition functions (Shallice, 1982). These tasks were considered as valid and the corresponding functions were considered to pertain to the range of the executive functions as soon as frontal patients failed to perform them.

The hypothesis of a general decline in the executive functions with normal ageing is supported today by a number of studies that mainly have used classical neuropsychological tasks in elderly subjects (see Bherer, Belleville, & Hudon, 2004 for a review). However, the reliability and validity of these tasks is questioned today, and hence, the hypothesis of a general decline in the executive functions with ageing remains unclear. Indeed, the functions that are commonly considered as executive often overlap, e.g. logical reasoning may require both attention and cognitive flexibility abilities. As a consequence, the classical executive tasks often lack of specificity, i.e. the same task may require several executive processes at the same time (Miyake et al., 2000). Moreover, they often present impurity issues in the sense that non-executive processes and irrelevant contents are frequently seen in these tasks (Phillips, 1997; Rabbitt, 1997). Hence, the field lacks of a compelling model that would define some elementary executive functions, their relationships to each other, and their potential interactions to support the performance of complex tasks. The absence of such model and the defaults reported with the classical tasks constitute barriers today in the understanding of the role played by the executive functions in human cognition, and in addition, render the interpretation of research results difficult (e.g. Charlot & Feyereisen, 2005; Clarys, Bugaiska, Tapia, & Baudouin, 2009).

It is to note that some older adults seem to perform as well as young adults in a range of cognitive tasks. For example, high-performing older adults were shown to compensate age-related deficits by recruiting a larger number of brain regions to perform cognitive tasks at same levels of performance than young adults (Cabeza, Anderson, Locantore, & McIntosh, 2002). Hence, one could argue that the deficits encountered with ageing are due to a general diminution in cognitive resources associated to a lack of brain plasticity rather than to a specific deficit in executive functioning. In addition, deficits that are not executive in nature have also been found with ageing and could impact the performance scores reported in executive tasks as a consequence. For example, behavioural slowing was seen in elderly participants that performed sensorimotor tasks and was found to increase with task complexity (Salthouse, 2000; Yordanova, Kolev, Hohnsbein, & Falkenstein, 2004). In the study by Yordanova et al. (2004), using event-related potentials, simple and choice reaction tasks were presented both in auditory and visual modalities. Slowing was reported in the choice reaction time only and was shown to not originate from the early stages of stimulus processing and response selection. Slower patterns of activation were in fact found in the motor cortex underlying response generation. Hence, behavioral slowing may engage difficulties to generate motor responses that are independent from the early cognitive mechanisms required to solve a given complex task but that will affect reaction times as a consequence.

Overall, there is a need today in the executive field to better define the executive functions and to propose cognitive models supporting their specific roles and potential interactions. A first attempt in this direction has been proposed by Miyake (2000, 2012), who through the analysis of the latent variables shared across a number of more or less complex executive tasks has proposed a first model for the executive functioning (Miyake & Friedman, 2012; Miyake et al., 2000). This model suggests the existence of three main executive functions: the updating, inhibition and switching functions, which are sometimes combined to deal with more complex situations. Updating refers to the ability to hold relevant information in working memory and to update efficiently this information according to task demands. Inhibition refers to the ability to retain a prepotent or dominant motor response. Switching abilities are involved to disengage attention from a set of task rules and to reengage attention on a novel task-set that is more relevant according to the situation. These three functions were shown to share some commonalities while being independent in nature (Miyake et al., 2000). There is also a necessity today to propose more simple tasks than traditional neuropsychological tasks to assess these three main executive functions in a specific way. An attempt in this direction have also been recently proposed in the literature (Dione, Ott, & Delevoye-Turrell, 2013a, 2013b). Indeed, we recently developed the spatial-tapping task as a novel visuo-motor task to assess the executive functioning. In this task, participants were asked to produce discrete tapping movements of the finger towards six visual targets arranged as a circle across distinct tempi (from periods of 1200 ms to 300 ms between taps). This task was designed as a hybrid of finger tapping and circle drawing tasks, two simple motor tasks that require respectively updating-like and switching-like abilities. Indeed, in finger tapping tasks, finger taps are produced on a platform at the rhythm of a metronome. In order to keep the beat, a referential interval of time is maintained in working memory and the motor response is updated as a function of the previously produced errors (Treisman & Gelade, 1980; Wing & Kristofferson, 1973a, 1973b). In circle drawing tasks, simple circles are repetitively drawn on a platform with the arm (e.g. Zelaznik, Spencer, & Doffin, 2000). However, the production of a circular movement is not so simple in the sense that it requires the production of two motor sub-components: an extension movement of the arm followed by a flexion movement of the arm (if the movement is produced counter-clockwise). Then, to produce a smooth and graceful circle, a cost of transition (or switching cost) from extension to flexion movements must be reduced both in space and time. These reduction in the spatial and temporal errors are referred to "anchor points" in the literature (Beek, Turvey, & Schmidt, 1992; Hogan & Sternad, 2007; Hogan, 1987; Roerdink, Ophoff, Peper, & Beek, 2008). In the spatial-tapping task, the task resembles finger tapping at slow tempi and circle drawing at faster tempi. Indeed, autocorrelation functions of IRIs measured at lag-1 are generally negative in finger tapping and became more positive in circle drawing (Dione et al., 2013b). Furthermore, in the spatial-tapping task, a transition phase from one task to another was reported at intermediate tempi (between periods 800 to 600 ms). In this "inhibition phase" participants were shown to try to maintain timing accuracy in spite of an increasing task pressure to anticipate forthcoming events. In the present study, we propose to compare the performances of young, mature and elderly participants in the spatial-tapping task with the specific hypothesis that performance patterns for inhibition should be affected by normal ageing.

1.2 Methods

1.2.1 Participants

Fifty-four right-handed individuals between 18 to 92 years of age participated voluntarily in the study. Participants were divided in three groups of 18 participants, i.e. the "young" group (5 males, 13 females, mean age= 23, standard deviation= 2), the "mature" group (15 males, 3 females, mean age= 44, sd= 10), the "elderly" group (6 males, 12 females, mean age= 76, sd= 10). All participants received an information letter and provided written informed consent. All participants performed the task with their right hand and reported having normal or corrected-to-normal vision. The protocol received approval by the local ethics committee in Human Sciences of the University of Lille 3.

1.2.2 Material & Stimuli

A picture composed of six black targets was displayed on a touch screen Elo Touch 19" 1915L. The targets (10 mm diameter, 100 mm apart) were placed around a virtual circle of 100 mm radius. The participants were invited to sit on a chair, in front of the screen that was placed upon a table and titled at 45 (see Figure III.1).

Figure III.1: Representations of the experimental protocol

1.2.3 Task and procedure

The subjects' task was to touch each visual target one after the other, starting from the bottom right target, and moving counter-clockwise using the right index finger (fist closed). Participants were instructed to synchronize each pointing action to a series of regular auditory tones (beep duration = 100 ms) that was played through computer speakers. Participants were encouraged to let their left arm relaxed upon their left leg. They were clearly instructed that the goal of the task was to be synchronized with the metronome. Each subject performed a total of eight trials. The initial tempo was an inter-onset interval (IOI) of 1100 ms. The temporal interval was increased by 100 ms after each trial until the fastest tempo of 400 ms. Participants were required to produce sixty taps for each trial. The total duration of the session was 10 minutes, approximately.

1.2.4 Measured response parameters

Performance errors were measured in space (area of spatial ellipses) and in time ($\mathrm{IRI}_{\mathrm{error}}$, asynchronies, contact times) and as a function of each spatial position to identify possible anchor points in the spatial trajectories. Autocorrelation functions of inter-response intervals and angular orientations of the spatial ellipses were also measured as indicators of the planning strategies.

Interval timing errors. Inter-response intervals (IRIs) were first measured as the time intervals between the onsets of successive taps. The $\mathrm{IRI}_{\mathrm{error}}$ was then computed as the percentage of difference between each IRI and the reference inter-onset interval (IOI, metronome period) of a given trial ($\mathrm{IRI}_{\mathrm{error}}(i) = (\mathrm{IRIi}-\mathrm{IOI})/\mathrm{IOI}*100$). The $\mathrm{IRI}_{\mathrm{errors}}$ were then averaged for each position, IOI and participant. This measure served as an indicator of the timing error.

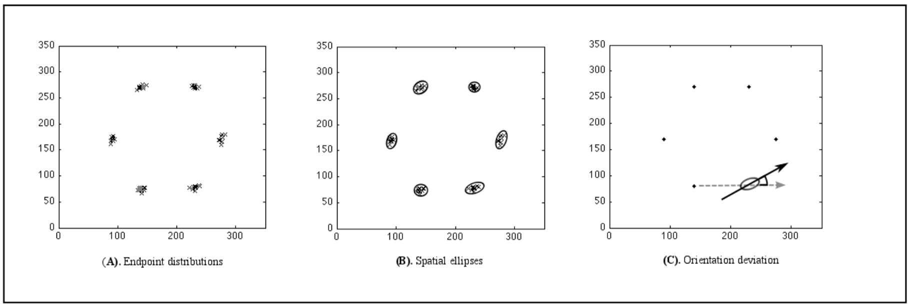
Asynchronies. Asynchronies were calculated as the difference in time between the onset of a tap and the start of the nearest auditory tone. Asynchronies were averaged for each position, IOI and served as an indicator of the participants' capacity to synchronise their pointing action with the external metronome.

Contact times. The Contact time (CT) was defined as the time of finger contact with the touch screen. This measure (in ms) was used to assess the level of control of the motor response output, with shorter CTs being related to a more fluent gesture.

Spatial errors. The endpoint distributions of the tapping actions were plotted for each target position (Figure 3). Using principal component analysis, spatial ellipses were then fitted to the movement endpoint distributions (Figure III.2b, for details on the calculations, see Gordon, Ghilardi, & Ghez, 1994). The confidence intervals were set to 95% on axis length. The area of spatial ellipses was then computed and used as an indicator of the spatial error.

Autocorrelation measures. After omitting the first six IRIs of each trial, autocorrelation values were calculated up to six lags (see Vorberg & Wing, 1996 for details on these measures). The AC values observed at lag-1 and lag-6 only were considered for statistical analysis. These measures served as an indicator of the presence or absence of action control through timekeeping mechanisms.

Trajectory planning strategies. The orientations of the main axis of each ellipse were computed. An orientation deviation (OD) was then calculated as the angular difference between the orientation of the main axis of each ellipse and three referential orientations computed as the orientation of (1) the line linking the current target (n) to the previous (n-1), (2) the line linking the current target (n) to the next (n+1), (3) the tangent to the virtual circle computed for each target position (see Figure III.2). These measures were used as indicators of the spatial planning strategies used to control hand trajectory.



(A). Endpoint distributions

(B). Spatial ellipses

(C). Orientation deviation

Figure III.2: Visual illustration of the three methodological steps that were implemented to calculate the orientation deviation (OD) of the endpoint scatterplots

1.2.5 Statistical analyses

Analyses of variance (ANOVAs) for repeated measures were performed on each variable with GROUP as an independent factor (STATISTICA). Repeated parameters were IOI, Target Position (TP), Interval Position (IP), or Planning MODELS (for the orientation deviation). Fisher LSD post hoc tests were used when required. The alpha level was set to 0.05. The TP and IP position are presented in Figure III.3.

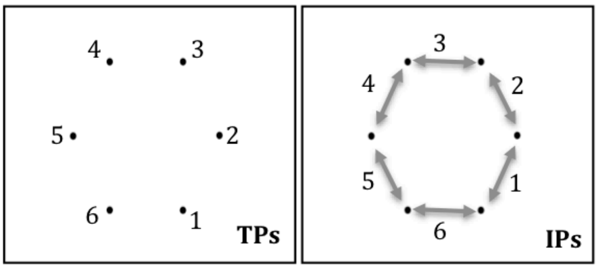


Figure III.3: Schematic description of the target positions (left) and the interval positions (right)

1.3 Results

1.3.1 Asynchronies

A main effect of Tempo was revealed (F(7, 357)=3.054, $p<0.01$). The asynchronies were in average negative between periods 1100 to 600 ms and were close to zero at faster tempi in all groups (see Figure III.4a). No main effect of Group (F(2, 51)=0.638, ns.), and interaction effect of Group*Tempo were found (F(14, 357)=1.189, ns.). A main effect of Target Position (TP) was revealed (F(5, 255)=9.567, $p<0.001$). The asynchronies were significantly larger (more negative) at TP-1 especially as compared to other TPs. No significant interaction effect s of Tempo and TP was found (F(35, 1785)=1.192, ns.). However, a significant interaction effect of Group and TP was revealed (F(10, 255)=26.671, $p<0.001$). The larger error found at TP-1 was in fact explained by the elderly group only (see Figure III.4b). Finally, a significant interaction effect of tempo, group and TP was revealed (F(70, 1785)=2.796, $p<0.001$). The effect observed at TP-1 in the elderly group was true at all tempi, except at 500 ms of IOI (see Figure III.6c, TP-1). More interestingly, the present interaction effect revealed that in the young group, the asynchronies were negative between 1100 to 600 ms of IOI at all TPs and were closer to zero at other tempi. In the mature group, asynchronies were in average less negative as compared to the young group between 800 to 600 ms of IOI. Finally in the elderly group, asynchronies were negative at TP-1 at all tempi, at TP-2 and TP-6 between 1100 to 600 ms of IOI, and were close to zero at all other TPs at all tempi except around periods of 600 ms (see Figure III.4c, with a representative example, TP-4).

1.3.2 $\mathrm{IRI}_{\mathrm{error}}$

A main effect of Tempo was revealed (F(7, 357)=3.589, $p<0.001$). The $\mathrm{IRI}_{\mathrm{error}}$ was significantly larger at the fastest tempo of 400 ms as compared to other tempi. No significant effects of Group were revealed (F(2, 51)=1.333, ns.). However, a significant interaction effect of Tempo and Group was found (F(14, 357)=3.538, $p<0.001$). The $\mathrm{IRI}_{\mathrm{errors}}$ were on average small and negative across all tempi in the mature and young groups, and was significantly larger between 500 to 400 ms in the elderly group as compared to the young group (see Figure 5a). A significant effect of Interval Position (IP) was also revealed (F(5, 255)=30.907, $p<0.001$). On average, the $\mathrm{IRI}_{\mathrm{errors}}$ at IP-1 and IP-4 were nega-

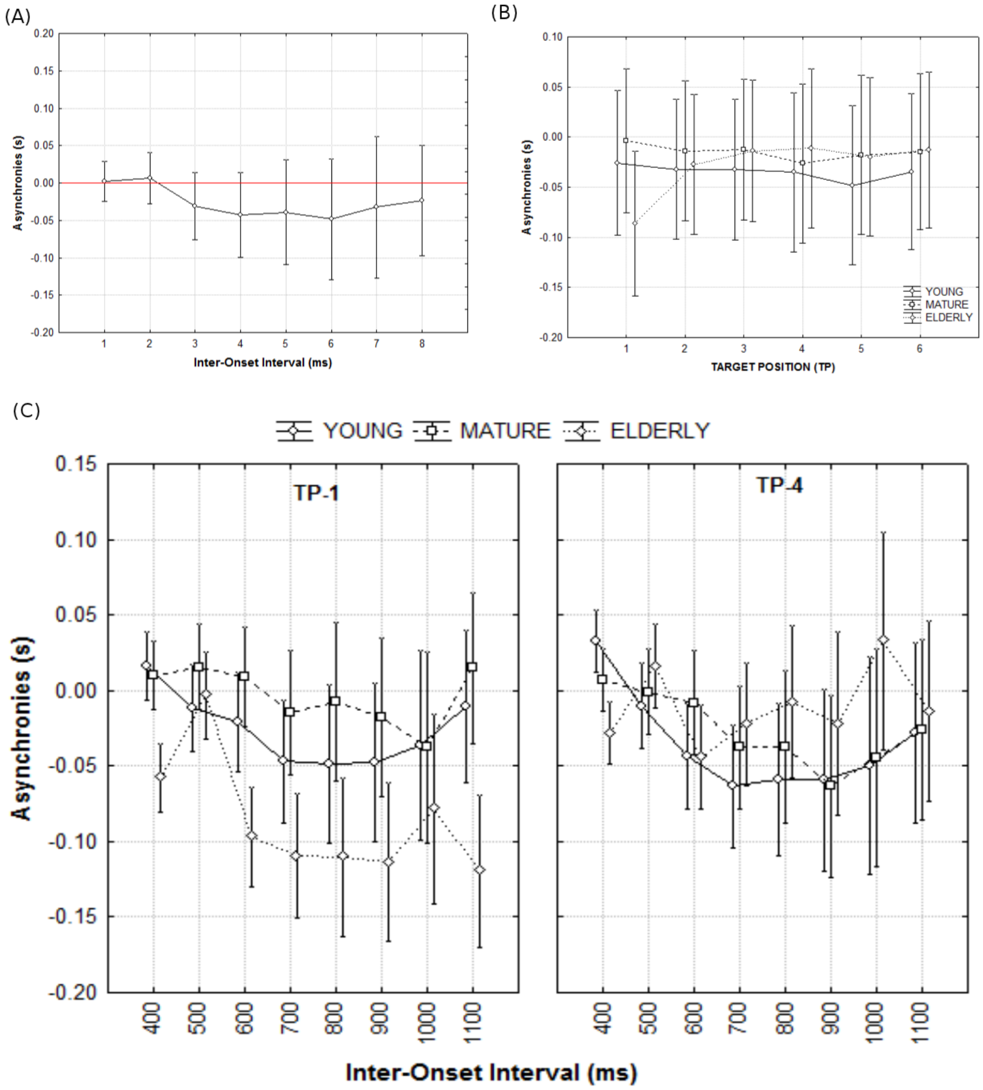


Figure III.4: (A) Asynchronies are presented as a function of the tempo (inter onset interval – IOI) imposed by an external metronome; (B) for each target position (TP); (C) at TP-1 and TP-4 for each group and at each tempo

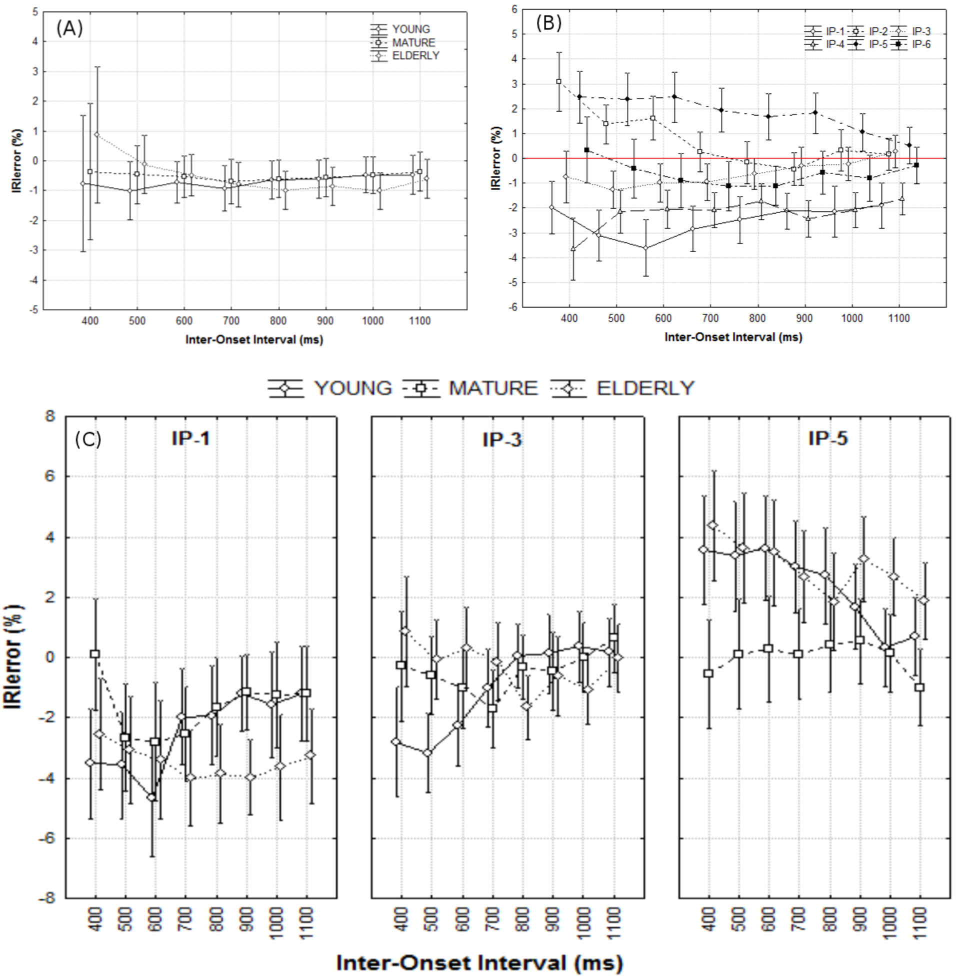


Figure III.5: (A) Temporal errors (inter response interval error – $\mathrm{IRI}_{\mathrm{error}}$) are presented as a function of the tempo (inter onset interval – IOI) imposed by an external metronome; (B) as a function of the tempo for each interval position (IP); (C) at IP-1, IP-3 and IP-5 for each experimental group and at each tempo tive, the $\mathrm{IRI}_{\mathrm{errors}}$ at IP-2 and IP-5 were positive, and the $\mathrm{IRI}_{\mathrm{errors}}$ at IP-3 and IP-6 were close to zero. A significant interaction effect of IP*Tempo was further revealed (F(35, 1785)=3.823, $p<0.01$). The direction of the $\mathrm{IRI}_{\mathrm{error}}$, i.e. positive or negative, did not change in function of tempi. However, the amplitude of the errors was significantly larger from periods of 900 ms at IP-5, from periods of 600 ms at IP-1 and IP-2, and from periods of 400 ms at IP-4. Changes in the amplitude of the $\mathrm{IRI}_{\mathrm{error}}$ were also reported at IP-3 and IP-6, i.e. our two transition points from extension to flexion movements in the present task. The $\mathrm{IRI}_{\mathrm{error}}$ became significantly more negative between periods of 700 to 400 ms at IP-3 and between periods of 800 to 600 ms at IP-6. Hence, anchor points in time were reported in average in the spatial trajectory. Finally, a significant interaction effect of Target, Tempo and Group was reported (F(70, 1785)=1.746, $p<0.001$). In the elderly group, the $\mathrm{IRI}_{\mathrm{error}}$ was in fact significantly more negative at IP-1 and IP-4 and more positive at IP-2 and IP-5, at slow tempi especially (i.e. between 1100 to 700 ms of IOI with variations according to IPs, see Figure III.5c). In the mature group, the $\mathrm{IRI}_{\mathrm{error}}$ was also smaller at IP-5 (i.e. less positive) between 800 to 400 ms of IOI as compared to the two other groups. At IP-3, i.e. at the location of our potential anchor point in time, the $\mathrm{IRI}_{\mathrm{error}}$ was in fact more negative between periods of 700 to 400 ms in the young group. The same anchor point in time was significant at periods of 700 ms only in the mature group and was finally not present i in the elderly group.

1.3.3 Contact times

A main effect of Tempo was revealed (F(7, 357)=30.836, $p<0.001$). On average, the contact times were longer in the slower tempi as compared to faster ones. A significant effect of Group was also revealed (F(2, 51)=5.114, $p<0.001$). Contact times were on average longer in the elderly group as compared to the two other groups. An interaction effect of Tempo*Group was also found (F(14, 357)=2.659, $p<0.01$). Contact times were longer in the elderly group especially between 1100 to 700 ms of IOI (without however significant differences between the mature group and the elderly group at 700 ms of IOI especially, see Figure 6a). A main effect of TP was also found (F(10, 255)=4.179, $p<0.001$). The contact times were in average significantly longer at TP-1, TP-2, and TP-3 as compared to other TPs. A significant interaction effect of Tempo and TP was also found (35, 1785)=1.571, $p<0.05$). On average, between TP-2 to TP-6, the CTs were shorter with changing tempo. Changes were reported at TP-1 and TP-6 in function of tempi, with TP-1 showing equals values than TP-4 between periods of 1000 to 600 ms. The contact times at TP-6 were equals to those observed at TP-1 at periods of 400 ms especially (See Figure III.6b). A significant interaction effect of Group*Target was also revealed (F(10, 255)=4.179, p<0.001) and reflected that CTs were in fact longer at TP-1, TP-2 and TP-3 as compared to other TPs in the elderly group only. In the mature group, the CTs were significantly smaller at TP-5 as compared to other TPs. Finally, in the young group; the CTs were significantly smaller at TP-5 and TP-6 as compared to other TPs. No significant interaction effects of Tempo, Group and TP were found (F(70, 1785)=0.946, ns.).

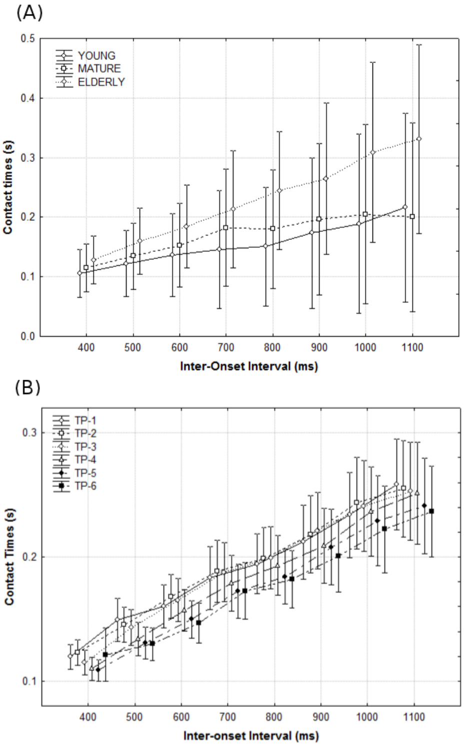


Figure III.6: (A) Contact times are presented as a function of the tempo (inter onset interval – IOI) imposed by an external metronome; and (B) for each target position and at each tempo

1.3.4 Spatial error

A main effect of Tempo was revealed (F(7, 357)=100.76, $p<0.001$). The area of spatial ellipses was in fact significantly smaller at slow tempi, i.e. between 1100 to 700 ms of IOI as compared to faster ones (see Figure III.7a). No significant effect of Group (F(2, 51)=0.795, ns.) or interaction effect of Group*Tempo were revealed (F(14, 357)=.97441, ns.). However, a main effect of target position (TP) was found (F(5, 255)=29.919, $p<0.001$). The spatial area was the smaller at TP-4, i.e. at the location of our potential spatial anchor point, with significant differences with all other TPs. The spatial error was slightly larger at TP-3, larger again at TP-2 and TP-5, and was finally the largest at TP-6 and TP-1. A significant interaction effect of Tempo*TP was also revealed (F(35, 1785)=3.991, $p<0.001$). Differences in the spatial error were in fact more pronounced with increasing tempi, e.g. at periods of 1100 ms the spatial area at TP-4 was significantly smaller as compared to TP-1 only, without changing the relative pattern of errors between TPs, see Figure III.7b. A significant interaction effect of TP and Group was also found (F(10, 255)=4.014, $p<0.001$). At TP-1, the spatial area was larger in the elderly group as compared to the mature group. At TP-6, the spatial area was smaller in the mature group as compared to the two other groups. Finally, no significant interaction effects of Tempo*Group*TP were found (F(70, 1785)=0.899, ns.), see Figure III.7c.

1.3.5 AC-1 values of IRIs

A main effect of Tempo was revealed (F(7, 357)=10.207,$p<0.001$). The AC-1 values of IRIs were in average larger and negative at slow tempi, i.e. between periods of 1100 to 900 ms as compared to faster tempi. A significant effect of Group was also revealed (F(2, 51)=4.297, $p<0.05$). The AC-1 values of IRIs were significantly smaller in the elderly group as compared to the mature group. No significant interaction effect of Group*Tempo was found (F(14, 357)=0.585, ns.). To note however, that differences were more pronounced between periods of 800 to 600 ms in the elderly group as compared to the two other groups (see Figure 1.4.3a).

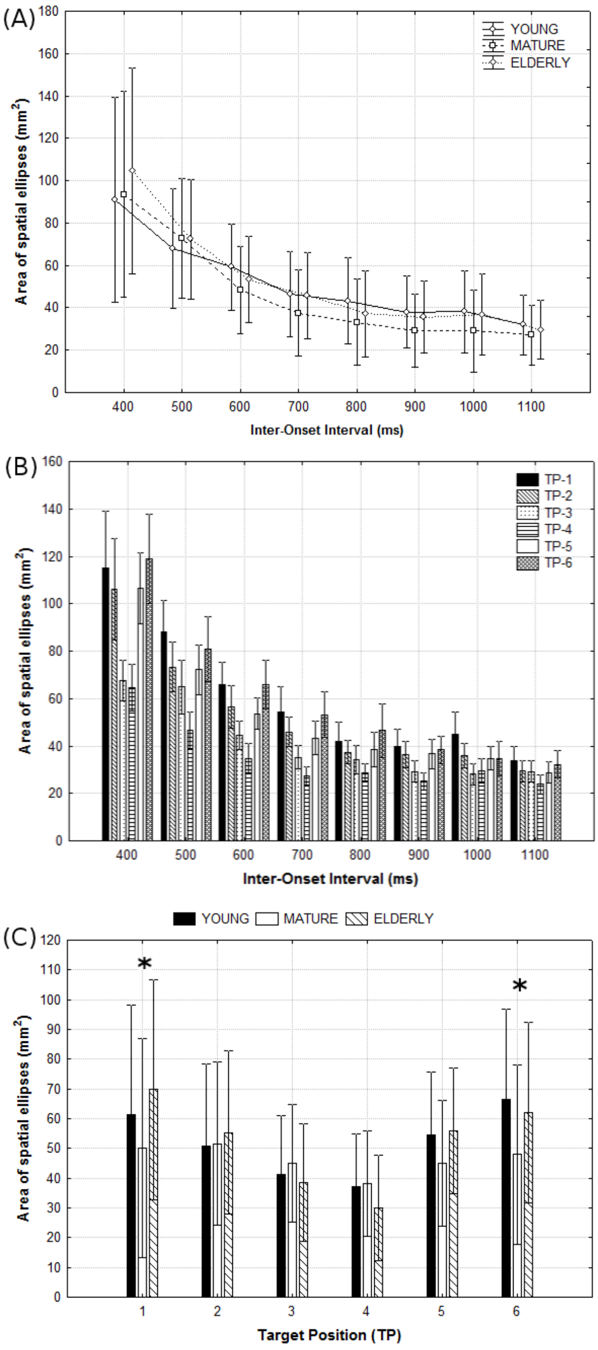


Figure III.7: (A) Spatial errors (area of the endpoint scatterplots) are presented as a function of the tempo (inter onset interval – IOI) imposed by an external metronome; (B) in function of each target position (TP) and at each tempo; (C) in function of each TP and for each group

1.3.6 AC-6 values of IRIs

A significant effect of tempo was revealed (F(7, 357)=17.143, p<0.001). The AC-6 values of IRIs were on average positive and larger at faster tempi (from periods of 600 ms especially) as compared to slower ones. A significant effect of Group was also revealed (F(2, 51)=6.221, p<0.01). AC-6 values of IRIs were significantly larger in the elderly group as compared to the two other groups across all tempi (see Figure 1.4.3b). No significant effect of Tempo*Group was revealed (F(14, 357)=0.652, ns.).

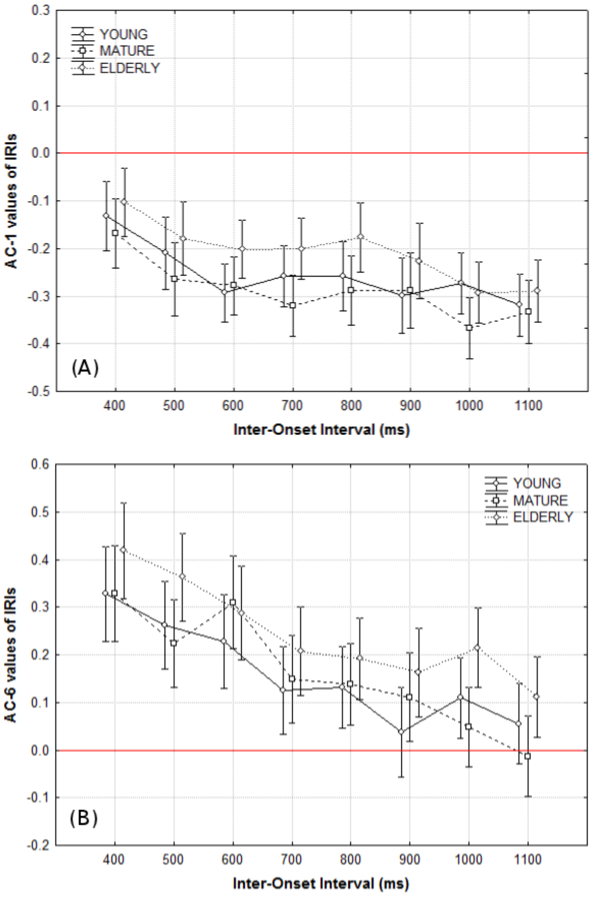


Figure III.8: Autocorrelation functions of the inter-response intervals (IRI) are presented as a function of the tempo (inter onset interval – IOI) imposed by an external metronome. The legends specify for each figure the considered time lags

1.3.7 Planning models

Effects that average the two models tested are not interpreted in the present analysis. A significant interaction effect of tempo and models was revealed (F(7, 357)=9.689, $p<0.001$). On average, the ellipses were significantly more oriented in function of the tangent to the circle from periods of 600 ms, while no differences were observed in average according to an orientation towards the next target (see Figure III.9a). A significant effect of models, tempo and TP was also revealed (F(35, 1785)=1.462, $p<0.05$). The orientation towards the next target was the better fit at TP-1 only. In fact the ellipses at TP-1 were significantly more oriented towards the next target between periods of 1100 to 600 ms. At TP-3, no differences were found between the two models, but ellipses were significantly more oriented towards the next target or the tangent of the circle from periods 600 ms especially. At TP-6, the better fit was the tangent to the circle across all tempi. At other TPs, no differences were reported between the two models at slow tempi, and the circle model became dominant from periods of 600 ms on average (see Figure III.9b). Finally, a significant interaction effect of models, target and group was revealed (F(10, 255)=4.553, $p<0.001$). In fact, the ellipses were significantly more oriented towards the next target at TP-3 and were significantly less oriented towards the next target at TP-4, in the elderly group as compared to the two other groups (see Figure III.9c and III.9d). No significant differences between groups were reported for the other model (tangent to the circle). No additional interaction effect of model, group, tempo and target position was found (F(70, 1785)=1.029, ns.).

1.4 Discussion

In the present study, we used the spatial-tapping task (Dione et al., 2013a, 2013b), a simple visuo-motor task, to test the hypothesis of a general decline in the executive functions with normal ageing (West, 1996). The three main executive functions of planning, i.e. updating in working memory, inhibition and switching were assessed. In the spatial-tapping task, updating functions are required at slow tempi (between periods of 1100 to 900 ms) to maintain timing accuracy; inhibition of the motor response is required at intermediate tempi (between periods of 800 to 600 ms) to keep maintaining the beat in spite of an increasing pressure to anticipate forthcoming events; switching is required at fast

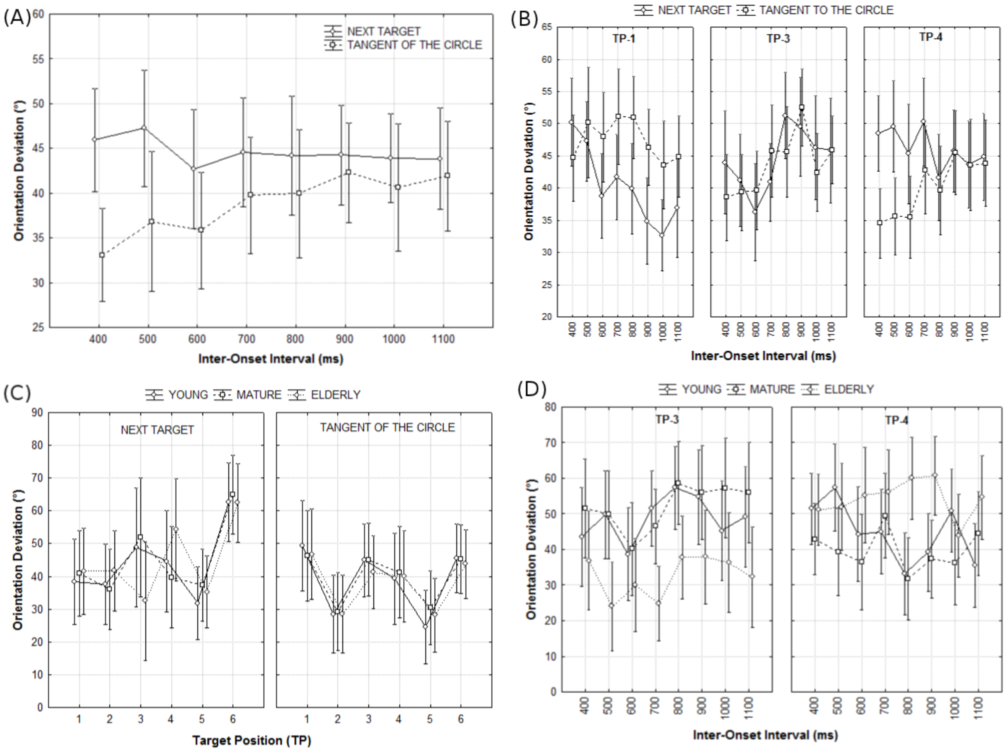


Figure III.9: (A) Orientation deviations of the endpoint scatterplots are presented as a function of the tempo (inter onset interval – IOI) imposed by an external metronome for each model; (B) at TP-1, TP-2 and TP-3 at each tempo; (C) for each target position and each model (TP); (D) at TP-3 and TP-4 especially in function of the tempo and for a fit to the next target only. The legends specify the two selected models that are considered: fit to the tangent to the circle; fit to the next target tempi (between periods of 500 to 300 ms), when the actions are produced more continuously, to reduce a transition cost relative to the production of the two sub-movement patterns of extension and flexion that emerges in the production of a circular action.

Our results revealed a preservation of the updating and switching mechanisms with ageing and significant impairments in the inhibition processes. In fact, elderly participants presented a pronounced difficulty to produce a motor response according to a certain delay. In particular, when the timing was computed on a predictive basis, their responses were always too fast (motor level of the inhibition impairment). However, they were aware of this too fast production and used of compensation mechanisms to maintain high levels of performance in the task. In spite of the use of these compensation mechanisms, performance was affected in the inhibition phase of the task in particular, with a more direct transition from time-based to space-based strategies from the intermediate tempi (cognitive level of the inhibition impairment). Hence, our results do not support the hypothesis of a general decline in the executive functions with ageing but suggest predictive timing deficits impacting abnormal cognitive inhibitory control.

1.4.1 Synchrony performance: motor timing is less produced on a predictive basis with ageing and elderly participants have difficulties to inhibit their first tap

The instruction provided to our participants was to be at best synchronized with the external metronome at all tempi. Analysis of the error of synchrony (asynchronies) revealed that on average, participants successfully followed the tempo with errors comprised between -100 ms to +50 ms across tempi. Note that expert musicians typically present a negative error of 50 ms in classical tapping tasks (Repp, 2005). Asynchronies were on average negative between periods of 1100 to 600 ms and became close to zero at faster tempi, suggesting that the timing was computed on a predictive basis at slow and intermediate tempi especially. However, significant differences were reported in function of age. In the group of young adults, predictive timing strategies were revealed between periods of 1100 to 600 ms. In the mature group, negative asynchronies were as large as in the young group between periods 1100 to 900 ms and were closer to zero at other tempi. In the elderly group, asynchronies were negative and larger as compared to the two other groups at the first target position (TP-1) especially. They were as large as in the young group between periods of 1100 to 700 ms at TP-2 and TP-6 only. They were finally close to zero at other TPs across most of the tempi (except at periods of 600 ms). These results suggest a progressive diminution with age in the capacity to use anticipatory strategies for predictive timing for synchrony purposes. In addition, these results reflect an additional difficulty in the elderly group to inhibit the first tap of an action sequence. This first tap was always produced too fast or largely before beep.

1.4.2 Production of intervals of time: predictive timing strategies are impaired with ageing but elderly participants use of compensation strategies to maintain the correct intervals of time

In the present study, the percentage of $\mathrm{IRI}_{\mathrm{error}}$ was used as an indicator of the ability to produce accurate intervals of time. Results revealed that on average, the timing intervals were accurately produced, with deviations from the mean of 1% approximately, except at the fastest tempo of 400 ms at which larger errors were produced. A specific structuring of the timing intervals was revealed as a function of spatial position. The $\mathrm{IRI}_{\mathrm{error}}$ reflected an alternation of short/long intervals, for all positions except at IP-3 and IP-6, so the intervals of time were alternated one short-one long-zero-one short-one long-zero through space. As expected, with increasing tempi, here from periods of 700 ms, anchor points in time emerged in the spatial trajectory, i.e. at the specific transition point from extension to flexion movements (IP-3 and IP-6). Hence, the movements became more continuous with increasing tempi and accordingly novel tasks constraints emerged in the task. Significant differences were revealed in the production of time intervals with age. Between periods of 1100 to 700 ms, the amplitude of the timing errors was significantly larger in the elderly group as compared to the two other groups while the structuring of the intervals according to spatial position was preserved. The $\mathrm{IRI}_{\mathrm{error}}$ was in fact more negative at IP-1 and IP-4 and more positive at IP-2 and IP-5 in the elderly group as compared to the two other groups. Hence, when the intervals of time were produced in a predictive way (IP-1 and IP-4), the performance was affected in the elderly group that produced too short intervals. However, this error was compensated by larger errors produced on the subsequent interval (IP-2 and IP-5). This result suggests that elderly participants have difficulties to produce a motor response according to a precise delay: they go too fast. However, compensation mechanisms that could be automatic or due to a certain awareness of their error allowed to produce accurate intervals of time on average. The timing performance was also less reliable on average in the elderly group as compared to the young group at fast tempi especially (i.e. between periods of 500 to 400 ms). Moreover, while the presence of an anchor point at IP-3 was significant between periods of 700 to 400 ms in the young group, this anchor point was significant at 700 ms only in the mature group and was not revealed in the elderly group. To note however that in the mature group, additional corrections on time were seen at IP-5. This result could be interpreted as an additional effort in the mature group to compensate for the ineffective correction produced at IP-3. Overall, the timing differences reflected on average in the elderly group could be explained by the absence of timing corrections at the level of the transition point from extension to flexion movements. This result confirms the presence of difficulties to produce a motor action according to a certain requirements for timing control with ageing. While these difficulties were seen at fast tempi only in the mature group (at the level of the first transition point), they were seen across all tempi in the elderly group, suggesting a progressive decline in the ability to smooth a circular movement under temporal constraints.

1.4.3 Autocorrelations values of IRIs revealed a preservation of updating mechanisms but impairments in inhibition mechanisms with ageing

Autocorrelation (AC) values of IRIs are usually used in the motor timing domain to reveal whether the actions sequences are guided through an event-based strategy, i.e. by maintaining the referential interval in memory for comparisons to the produced intervals, or through emergent strategies, i.e. the movement is produced as a spatial displacement from a starting point to an arrival point and the timing error is corrected at posteriori in subsequent movements (Zelaznik, Spencer, & Ivry, 2002). While AC values of IRIs measured at lag-1 are commonly negative in the case of event-based timing, they are generally more positive in the case of emergent timing. In previous studies using the spatial-tapping task, significant autocorrelation values were revealed at lag-1 and at lag-6 (Dione et al., 2013a, 2013b). AC-1 values of IRIs were negative at slow tempi and became significantly less negative from periods of 700 ms. AC-6 values of IRIs, that reflect dependencies in the series going on after having produced an entire cycle (composed of six taps), were positive but small at slow tempi were significantly more positive from periods of 700 ms, and finally reached their larger values from 500 ms of IOI and faster. These results suggest that in the spatial-tapping task, the timing was controlled through an event-based strategy at slow tempi; was then switched towards an emergent strategy at faster tempi, with a phase of transition observed at intermediate tempi.

In the present study, a similar pattern of results was seen on average with AC-1 values of IRIs being negative at slow tempi and becoming more positive at fast tempi, and AC-6 values of IRIs being small and positive at slow tempi and becoming more positive at fast tempi, confirming a transition from event-based to emergent strategies in the task. However, significant differences were observed with age. AC-1 values of IRIs were significantly smaller in the elderly group as compared to the mature group, especially between periods of 800 to 600 ms (see Figure). This result suggest that in the elderly group the timing was efficiently guided through an event-based strategy between periods of 1100 to 900 ms, and was then switched towards an emergent strategy, whereas event-based timing guided the action sequence in the two other groups until periods of 600 ms. These results suggest that updating mechanisms were preserved with ageing while inhibitory mechanisms allowing to transition from a high-level planning strategy to another was impaired. AC-6 values of IRIs were significantly larger in the elderly group as compared to the two other groups across all tempi. The presence of positive dependencies in time series analyses suggests that an error that is produced at the start of the trial is propagated until the end of the cycle (Torre & Delignières, 2008). Hence, more long-term corrections were present in the elderly group across all temp in order maybei to maintain sufficient levels of accuracy through time.

1.4.4 More inhibition of the motor response was required in the elderly group at slow and intermediate tempi

Contact times were measured in the present study as an indicator of motor inhibition. Indeed, in a previous study using the spatial-tapping task, it was shown that long contact times in the intermediate phase of the task were correlated to better abilities to inhibit a motor response towards an irrelevant stimulus in a go-no-go task (smaller number of false alarms). In another study, it was shown that the production of longer contact times in an action sequence allowed isolating each action sub-component as a discrete action (Adam et al., 2000). Our results revealed that contact times were on average longer at slow tempi, and were decreased with increasing tempi, hence confirming that actions were more discrete at slow tempi and more interdependent at faster tempi. However, significant differences were reported as a function of age. Contact times were significantly longer in the elderly group as compared to the group of young adults between periods of 1100 to 700 ms. The contact times were slightly longer in the mature group as compared to the young group at intermediate tempi, with no differences revealed between the mature and the elderly group at periods of 700 ms. This result does not suggest that motor inhibition was impaired with ageing, but rather suggest that more voluntary control of the motor response was required with ageing especially at slow and intermediate tempi. Additional effects revealed that contact times were longer again on the three first spatial positions as compared to other positions in the elderly group. Hence, it is probable that the too fast responses that were produced on the first target (TP-1), as suggested by the results obtained on asynchronies, were compensated by longer waiting times on the screen especially on the first part of the movement (three first target) in the elderly group. A similar but less important effect was reported in the mature group. Indeed, while in the young group, contact times were always shorter at the end of each cycle (TP-5, TP-6); they were shorter at TP-5 only in the mature group. Hence, more inhibition was provided at TP-6 in the mature group as compared to the young group. This result confirms (as seen for the IRIs at IP-5) that a specific attention was provided on the end of each cycle in the mature group as compared to the two other groups. This result could be interpreted as a first entry towards difficulties in producing the first tap of a sequence in the mature group. Or alternatively could be an effect specific to the sample we tested. Hence, it could be interesting to test again a group of mature individuals in the spatial-tapping task to see whether this effect observed on the end of a cycle persists or not.

1.4.5 No differences in the spatial error were revealed as a function of age supporting a preserved switching strategies in space with normal ageing

The spatial error was measured in the present study as the area of spatial ellipses drawn around the endpoint distributions of taps surrounding each target. The spatial error was on average small at slow tempi (between periods of 1100 to 700 ms) and was significantly larger at faster tempi. A specific reduction in the spatial error at the point of transition from extension to flexion movement, i.e. at TP-4, suggesting the presence of an anchor point (Roerdink et al., 2008). However, these differences were more pronounced with increasing tempi. Significant differences were also revealed as a function of age. The spatial error at TP-1 was in fact significantly larger in the elderly group as compared to the two other groups. This result confirms the difficulties in the elderly group to inhibit the first movement of the sequence with here a specific impact found on the spatial performance. In spite of these differences, these results suggest an absence of differences in the strategies of error reduction that takes place in space with age, hence a preservation of switching abilities on space in with ageing.

1.4.6 Planning strategies in space: anticipation mechanisms oriented on the transition point between extension to flexion movements are more pronounced in the elderly group as compared to the two other groups

According to a number of studies interested in the movement planning and execution of spatial trajectories of the hand, the orientation of spatial ellipses drawn around endpoint distributions could inform about the contextual planning strategies that was used to guide the production of repeated actions (Desmurget, Jordan, Prablanc, & Jeannerod, 1997; Desmurget, Pélisson, Rossetti, & Prablanc, 1998; Rossetti & Régnier, 1995). In the present study, we computed the orientation of the main axis of each ellipse. Then, an angular deviation from pre-specified orientations were measured. Two orientation models were used to test whether: (1) the next event was anticipated from the current movement (deviation from the vector linking the current and the next target); (2) the action sequence was produced as a global circle (deviation from the tangent to the circle). Our assumption was that movements should become more circular at fast speeds in the spatial-tapping task, with the need to smooth the trajectory at the place of the transition point from extension to flexion movements through the use of anticipatory mechanisms. Our results revealed that the movements were significantly more oriented according to the tangent to the circle from periods of 600 ms especially, confirming that movements in the spatial-tapping task became more circular and continuous with increasing tempi. Ellipses were oriented towards the next event at specific spatial locations only: at TP-1 between 1100 to 600 ms, and at TP-3 between periods of 600 to 400 ms. This result suggest that anticipation mechanisms were focused on the sequence initiation at slow tempi, while they were geared towards the needs of anticipating the transition point from extension to flexion movements at faster tempi (anticipation of TP-4 from TP-3). Significant differences were revealed in orientation deviations as a function of age and in regards to an orientation towards the next target only. Indeed, in the elderly group, spatial ellipses were significantly more oriented towards the next target at TP-3 across all tempi (see Figure III.9d). This result suggests that a specific attention was geared on the needs to anticipate the point of arm movement transition (TP-4 anticipated from TP-3) across the entire rhythmic range in the elderly group (with however more anticipation required produced at faster tempi, see Figure III.9d). The processes probably impeded them to anticipate the position of other targets (TP-4) to enable good levels of performance at intermediate tempi especially.

1.5 Conclusion

To conclude, our results suggest a preservation of the updating and switching mechanisms with ageing and the presence of specific impairments related to inhibition processes. At many levels, elderly participants were in difficulty to produce a motor action according to a certain delay. More precisely, they were too fast in producing the first action of the sequence, and the first interval of time to produce on each hemi-field (IP-1 and IP-4). In addition, they did not reduce their error in timing at the level of the location of the anchor point. In spite of these deficits in “motor inhibition”, elderly participants were seen to use compensatory mechanisms both in space and time that helped them to reach the same levels of performance than younger participants. Indeed, at slow tempi, too short intervals of time were followed by too long intervals, suggesting a compensation mechanism. On average, no differences were found in their timing error ($\text{IRI}_{\text{error}}$) as compared to the two other groups. These mean $\text{IRI}_{\text{errors}}$ were revealed in our previous study to be the core performance indicator for the updating mechanisms at slow tempi especially (Dione et al., 2013a). Hence, we suggest that updating strategies were preserved with ageing. Moreover, no differences were seen in autocorrelations values of IRIs at lag-1 at slow tempi (between periods of 1100 to 900 ms), which indicates that the actions were guided through an event-based strategy or according to a temporal referential which was maintained in working memory for all experimental groups.

In space, while the spatial error on the first tap was significantly larger as compared to other taps, no group differences were revealed on average. This finding suggests that participants compensated their spatial error by focusing more attention on next taps to maintain overall high-levels of precision in space. Mean spatial error was revealed in our previous study to be the core performance indicator for the switching mechanisms at fast tempi especially (Dione et al., 2013a). Hence, we suggest that switching strategies were preserved with ageing. Furthermore, an anchor point was seen in the spatial trajectory in all groups, confirming that independently of their age, participants used the correct switching strategies at fast tempi, in the spatial-tapping task. To note however that more anticipation or attention of the anchor point was required in the elderly group as compared to other group, as revealed through the analysis of trajectory information. Confirming again the requirement of compensation mechanisms to support the global performance with ageing. These strategies were certainly present to compensate for the absence of reduction of the switching cost in time, as it was found in the elderly group. Reduction of the cost in space was seen in a previous study to depend upon visual strategies (Roerdink et al., 2008). By contrast, the switching cost was reduced in time when participants flexibly flexed or extended their wrist before crossing the transition point (musculoskeletal strategy). Hence, these findings suggest that difficulties to produce flexible motor responses dependent upon timing mechanisms were revealed with ageing. Although these deficits did not impaired the switching function which was rather dependent upon the integrity of anticipation mechanisms that take place on space, they could be incapacitating on a number of daily motor activities, i.e. cooking, driving, sewing, walking, etc. So, it could be important in future research to look deeper into this question and to assess how vision helps compensating for this problem and how these compensatory mechanisms are resource consuming.

Finally, compensatory mechanisms were not sufficient to maintain acceptable levels of performance in the inhibition phase of the spatial-tapping task. Indeed, while the timing was controlled through an event-based strategy at slow tempi, elderly participants were not able to continue using such strategies at intermediate tempi, as reflected in AC-1 values of IRIs. They switched directly towards an emergent or space-based strategy, leading to observe significant differences with the two other groups. Hence, they were impaired to inhibit a given high-level strategy to maintain the good strategy according to task demands (cognitive inhibition). Moreover, differences were observed on contact times. Mean contact times was revealed in our previous study to be the core performance indicator for the inhibition mechanisms at intermediate tempi especially (Dione et al., 2013a). In the present study, elderly participants presented significantly longer contact times as compared to the other groups at the mean levels, suggesting that more voluntary inhibition was required in these participants to deal with the task constraints according to their own difficulties. Hence, we suggest that inhibition abilities were not preserved with ageing.

Overall, the spatial-tapping task allowed in the present study to point out the presence of specific deficits emerging with ageing and to attenuate the hypothesis of a general decline in the executive functions with ageing (West, 1996).

Study 2

Executive functioning in schizophrenia

Abstract

Executive deficits are among the more invalidating symptoms in schizophrenia. Difficulties have been reported in the three main executive functions of updating, inhibiting and switching using traditional neuropsychological assessment. However, traditional tasks lack of specificity and thus can render the interpretation of research results complicated. Here we used the spatial-tapping task to test whether a specific function was impaired in schizophrenia. In this task, finger taps are produced at distinct tempi towards six visual targets that are arranged in space as a circle. In controls, results show that, at slow tempi, the actions were produced in a discrete way, i.e. in isolation from the previous actions and required the use of updating strategies to maintain accurate timing. At fast tempi, the actions became more circular, and thus required smooth integration of the actions within a global circular pattern. At intermediate tempi, the urge to go faster was inhibited in order to maintain the timing accuracy in spite of an increasing pressure to produce a circular movement. Our results revealed that patients with schizophrenia over-switched in the spatial-tapping task, i.e. their movements were circular across all tempi, and as a consequence, they had to correct for a switching cost related to the production of such action pattern. By contrast our results revealed that the updating and inhibiting strategies were preserved in patients, i.e. the timing was correct and the rhythmic pattern was controlled by producing longer contact times than that observed in controls.

2.1 Introduction

Executive deficits are among the more invalidating symptoms in schizophrenia and are often considered as the best predictor of functional outcome (Barch, Moore, Nee, Manoach, & Luck, 2012; C S Carter, Minzenberg, West, & Macdonald, 2012; Holt, Wolf, Funke, Weisbrod, & Kaiser, 2013). Updating in working memory, inhibition and switching abilities are the three main executive functions described in the literature (Miyake & Friedman, 2012). Impairments in all three functions have been revealed in schizophrenia.

Working memory (WM) deficits, i.e. the ability to maintain relevant information in WM and to update this information with changing constraints, is the most common deficit seen in this pathology and have been associated at the brain level to a failure to activate the dorsolateral prefrontal cortex (Carter et al., 1998; Glahn et al., 2005). N-back tasks are often used to reveal WM deficits (Jonides & Smith, 1997; Smith & Jonides, 1997, 1999). In these tasks, a series of one-digit numbers are presented on a computer screen one after the other. Participants are asked to press on the response button when the item displayed is the same than the item presented n times before. Difficulties in these tasks are often revealed with increasing load (n=2) in schizophrenia patients (Bleich-Cohen et al., 2013; Carter et al., 1998; Koike et al., 2013), suggesting a preservation of the basic maintenance abilities and dysfunctions rather centred in the capacity to reload the relevant information in WM (Smith et al., 1998). Concerning the inhibition functions, abnormal patterns are also reported in schizophrenia with failure in inhibiting responses to repetitive stimuli, i.e. latent inhibition (Leung, Killcross, & Westbrook, 2013; Stadlbauer, Langhans, & Meyer, 2013; Stevens, Zheng, & Abrams, 2013; Yogev, Sirota, Gutman, & Hadar, 2004), or to produce a motor response for a specific item among distractors, such as in antisaccade or in go-no-go tasks (Harris, Reilly, Thase, Keshavan, & Sweeney, 2009; Katsanis, Kortenkamp, Iacono, & Grove, 1997; Vercammen et al., 2012) are also seen in schizophrenia. Finally, difficulties in attention switching, i.e. the ability to alternate between stimulus-response rules or instructions in function of changing context have also been found in this pathology (Carter et al., 2012; Egan et al., 2011; Smith et al., 1998). These research findings considered together suggest a central rather than a specific deficit of action planning in schizophrenia (Holt et al., 2013).

There is nevertheless some evidence that the traditional neuropsychological tests used to reveal executive deficits, e.g. the WSCT or N-back tasks, are too complex to target basic cognitive functions (Burgess, 1997, 1997; Miyake et al., 2000; Phillips, 1997; Sood & Cooper, 2013). For example, N-back tasks are usually used as indicators of WM deficits (Conway et al., 2005; Kane & Engle, 2002) but have been shown to require both inhibition, interference resolution and WM demands (Hockey & Geffen, 2004; Jaeggi, Buschkuehl, Perrig, & Meier, 2010; Jonides & Smith, 1997). In N-back tasks, the current item can match a previous item which is not the N item asked for. To solve such sort irrelevant binding, additional inhibition and interference resolution mechanisms are required in this task (Kane, Conway, Miura, & Colflesh, 2007; Oberauer, 2005). Moreover, always concerning the N-back task, the decrease in performance commonly observed with increasing load could be interpreted both because: (h1) the current item requires more working memory abilities, e.g. to hold a memory trace of an item until n+3, or because (h2) a larger number of intermediate items require suppression. Moreover, in schizophrenia, patients exhibit a consistent tendency to over-process random and/or irrelevant details of the environment (Yogev et al., 2004), and it has been suggested that this tendency could be at the origin of the hallucinations observed in this pathology (Frith & Done, 1989; Hemsley, 1976). These arguments rather comforts h2, i.e. a tendency to overprocess distractors in schizophrenia than a disability to maintain a given item across long periods of time in memory. The classical N-back task does not allow testing these two hypotheses separately. Hence, there is a need today to propose tasks that are able to assess the three executive functions separately. This enterprise could allow assessing whether schizophrenia is better defined as a central deficit in action planning (Holt et al., 2013) or as a specific deficit in the switching functions with a tendency to over-switch, which would impact as a consequence the WM abilities (Yogev et al., 2004).

In the present study, rather than using a battery of complex neuropsychological tasks to evaluate the executive functions of planning, we used the spatial-tapping task, a visuo-motor task that has the potential to target each executive function separately (Dione, Ott, & Delevoye-Turrell, 2013a). In the spatial-tapping task, discrete tapping actions are produced on a tactile screen following a circular trajectory and across distinct tempi (Dione, Ott, & Delevoye-Turrell, 2013b). At slow tempi (between periods of 1200 to 900 ms), the actions are typically produced in an isolated fashion while at faster tempi (periods of 500 to 300 ms) the actions became more grouped and circular. At intermediate tempi (periods of 800 to 600 ms) a progressive transition from discreetness to circularity in the gesture is seen. By comparing classical updating, inhibiting and switching tasks to the spatial-tapping task through multiple regression analyses it was showed that: (1) updating functions were required at slow tempi especially to maintain timing accuracy for the production of long intervals of time between taps; (2) switching functions were required at fast tempi, i.e. when the movements were more circular and a switching cost had to be reduced to produce smooth circles; (3) inhibition functions were finally required at intermediate tempi in order to keep the timing accuracy in spite of a pressure to produce a more circular movement. Hence, a fine analysis of timing and spatial dependent parameters are available in the spatial-tapping task to identify the higher-level strategies engaged to control for the action sequences in function of tempi. In the present study, we propose conducted this detailed analysis on the performances data obtained in a group of patients with schizophrenia. We suggest that our results will allow assessing whether schizophrenia should be considered as a central deficit in action planning or as specific deficit in the one or the other of the three executive functions.

2.2 Method

2.2.1 Participants

Thirty-six right-handed individuals participated voluntarily in the study. Eighteen patients (14 males, 4 females, mean age = 43.7) were compared to their age and sex matched controls (mean age = 42.5). Patients were recruited at the day hospital of the civil hospital of Strasbourg, or in ESAT structures in Strasbourg. All participants received an information letter and provided written informed consent. All participants performed the task with their right hand and reported having normal or corrected-to-normal vision. The protocol received approval of the INSERM CPP committee of Strasbourg.

2.2.2 Material and stimuli

A picture composed of six black targets was displayed on a touch screen Elo Touch 19” 1915L. The targets (10 mm diameter, 100 mm apart) were placed around a virtual circle of 100 mm radius. The participants were invited to sit on a chair, in front of the screen that was placed upon a table and tilted at 45(see

Figure III.10).

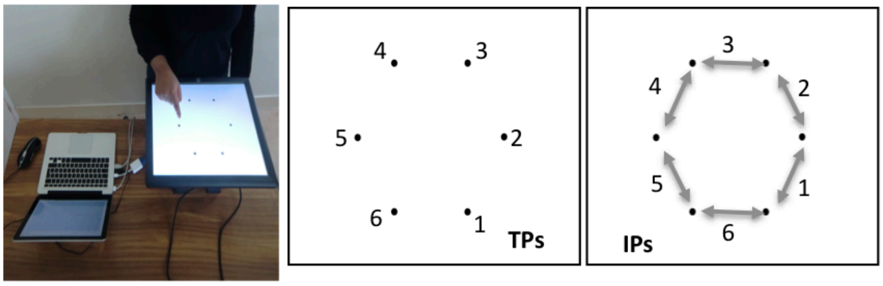


Figure III.10: Picture of the visual display, Target and Interval positions

2.2.3 Task and procedure

The subjects' task was to touch each visual target one after the other, starting from the bottom right target, and moving counter-clockwise using the right index finger (fist closed). Participants were instructed to synchronize each pointing action to a series of regular auditory tones (beep duration = 100 ms) that was played through computer speakers. Participants were encouraged to let their left arm hang relax upon their left leg. They were clearly instructed that the goal of the task was to be synchronized with the metronome. Each subject performed a total of eight trials. The initial tempo was an inter-onset interval (IOI) of 1100 ms. The temporal interval was increased by 100 ms after each trial until the fastest tempo of 400 ms. Participants were required to produce sixty taps for each trial. The total duration of the session was 10 minutes, approximately.

2.2.4 Measured response parameters

Performance errors were measured in space (area of spatial ellipses) and time ($\mathrm{IRI}_{\mathrm{error}}$, asynchronies, contact times) and in function of each spatial position to identify eventual anchor points in the spatial trajectories. Autocorrelation functions of inter-response intervals and angular orientations of the spatial ellipses were also measured as indicators of the planning strategies.

Interval timing errors. Inter-response intervals (IRIs) were first measured as the time intervals between the onsets of successive taps. The $\text{IRI}_{\text{error}}$ was then computed as the percentage of difference between each IRI and the reference inter-onset interval (IOI, metronome period) of a given trial ($\text{IRI}_{\text{error}}(\text{i}) = (\text{IRIi-IOI})/\text{IOI}*100$). The $\text{IRI}_{\text{errors}}$ were then averaged for each position, IOI and participant. This measure served as an indicator of the timing error.

Asynchronies. Asynchronies were calculated as the difference in time between the onset of a tap and the start of the nearest auditory tone. Asynchronies were averaged for each position, IOI and served as an indicator of the participants' capacity to synchronize their pointing action with the external metronome.

Autocorrelation measures. After omitting the first six IRIs and asynchronies of each trial, autocorrelation values were calculated up to six lags. The AC values of IRIs observed at lag-1 and lag-6 only were considered for statistical analysis. The AC values of asynchronies observed at lag-1 only were considered for statistical analysis. These measures served as an indicator of the presence or absence of action control through timekeeping mechanisms.

Contact times. The Contact time (CT) was defined as the time of finger contact with the touch screen. This measure (in ms) was used to assess the level of control of the motor response output, with shorter CTs being related to less inhibitory control.

Spatial errors. The endpoint distributions of the tapping actions were plotted for each target position. Using principal component analysis, spatial ellipses were then fitted to the movement endpoint distributions (for details on the calculations, see Gordon, Ghilardi, & Ghez, 1994). The confidence intervals were set to 95% on axis length. The area of spatial ellipses was then computed and used as an indicator of the spatial error.

Trajectory planning strategies. The orientations of the main axis of each ellipse were computed. An orientation deviation (OD) was then calculated as the angular difference between the orientation of the main axis of each ellipse and three referential orientations computed as the orientation of (1) the line linking the current target (n) to the previous (n-1), (2) the line linking the current target (n) to the next (n+1), (3) the tangent to the virtual circle computed for each target position. These measures were used as indicators of the spatial planning strategies that may have been used to control hand trajectory.

2.2.5 Statistical analyses

Analyses of variance (ANOVAs) for repeated measures were performed on each variable with GROUP as an independent factor (STATISTICA). Repeated parameters were IOI, Target Position (TP), Interval Position (IP), or Planning MODELS (for the orientation deviation). Fisher LSD post hoc tests were used when required. The alpha level was set to 0.05. The TP and IP position are presented in Figure III.10.

2.3 Results

2.3.1 Performance measures: $\mathbf{IRI_{error}}$, asynchronies, contact times, spatial error

2.3.1.1 Inter-response interval error

A significant main effect of IOI was revealed (F(7, 238)= 9.927, $p<0.001$). On average, the IRI_{error} was significantly larger at the fastest tempo, i.e. 400 ms of IOI as compared to slower IOIs. No main effect of group was revealed (F(1, 34)=1.087, ns.). However, a significant interaction effect of IOI and group was revealed (F(7, 238)= 5.242, $p<0.001$). The IRI_{error} was larger in the patient group as compared to the control group at 400 ms of IOI only (see Figure III.11a). A significant effect of Interval Position (IP) was also found (F(5, 170)=5.195, $p<0.001$). The IRI_{error} was on average negative at IP-1, IP-3 and IP-4, and positive at IP-2, IP-5 and IP-6. Hence, the errors were varying as a function of their spatial position. No significant interaction effect of IP and group was found (F(5, 170)=1.478, ns.). However, a significant interaction effect of IP and IOI was revealed (F(35, 1190)= 2.118, $p<0.001$). The IRI_{error} was in fact significantly larger at IP-3 (more negative) from 700 ms of IOI and significantly larger at IP-5 (more positive) from 800 ms of IOI as compared to the IRI_{error} measured at the slowest tempo. At other IPs, no differences were revealed between 1100 to 500 ms of IOI, but the IRI_{error} was on average more positive at the fastest tempo of 400 ms as compared to slower tempi for all IPs (see Figure III.11b). No significant interaction effect of IOI, group and IP was revealed (F(35, 1190)=1.125, ns.). Note however, that the IRI_{error} at IP-5 and IP-3 seemed to be larger in the patient group as compared to the control group (see Figure III.11c). Moreover, the IRI_{error} at IP-3 was no different from zero in the control group at slow tempi the same error seemed to be negative in patients (see Figure III.11c).

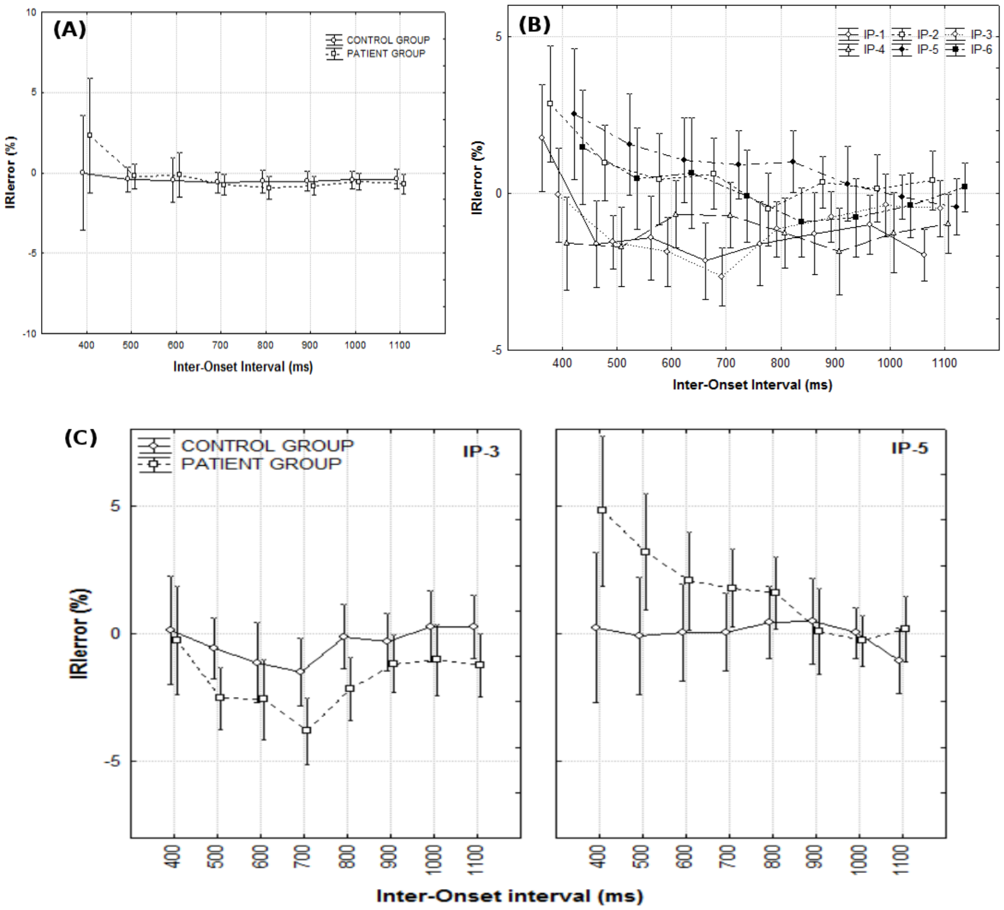


Figure III.11: (A) Temporal errors (inter response interval error – $\text{IRI}_{\text{error}}$) are presented as a function of the tempo (inter onset interval – IOI) imposed by an external metronome for each group; (B) as a function of the tempo for each interval position (IP); (C) at IP-3 and IP-5 for each group and at each tempo

2.3.1.2 Asynchronies

No main effect of IOI was revealed (F(7, 238)=1.404, ns.). Asynchronies were on average close to zero across all tempi. A main effect of Group was revealed (F(1, 34)=5.678, $p<0.05$). Asynchronies were not different in magnitude for the two groups (M= 0.02 s) but were on average negative for the control group and positive for the patient group. No significant interaction effect of group and IOI was revealed (F(7, 238)=1.289, ns.). A significant effect of Target Position (TP) was nevertheless revealed (F(5; 170)= 6.371, $p<0.001$). Asynchronies were on average more positive at TP-1 and TP-2 as compared to other TPs at which they were close to zero. No significant interaction effect of TP and group was revealed. However, a significant effect of TP and IOI was found (F(35, 1190)= 2.055, $p<0.001$). Post hoc tests revealed that differences in asynchronies as a function of TP were revealed between 1100 to 700 ms of IOI only. No significant interaction effect of TP, group and IOI was finally revealed (F(35, 1190)=0.982, ns.). These results are summarized in Figure III.12.

2.3.1.3 Contact times

A main effect of IOI was revealed (F(7, 238)=29.244, $p<0.001$). Contact times were on average longer at slow tempi as compared to faster ones. A main effect of group was also revealed (F(1, 34)=14.184, $p<0.001$). Contact times were significantly larger in the patient group as compared to the control group. Moreover, a significant interaction effect of Group and IOI was found (F(7, 238)=5.267, $p<0.001$). Post hoc tests revealed that contact times were significantly longer in the patient group between 1100 to 600 ms of IOI only compared to that observed in the controls. No other effects were found (TP or interaction effects). These results are summarized in Figure III.13.

2.3.1.4 Spatial error

A significant main effect of IOI was revealed (F(7, 238)= 104.20, $p<0.001$). The spatial error was on average smaller at slow tempi (between 1100 to 800 ms of IOI), as compared to faster tempi. A main effect of Group was also revealed (F(1, 34)= 18.490, $p<0.001$). The spatial error was significantly larger in the patient group as compared to the control group. A significant interaction effect of IOI*Group was also found (F(7, 238)= 5.578, $p<0.001$). In fact, no significant differences were revealed between the two groups at 1000 and 800 ms of IOI, suggesting that differences between groups in the spatial error was more pronounced at faster tempi as compared to slower ones (see Figure III.14a). A significant effect of TP was revealed (F(5, 170)= 4.4156, $p<0.001$). The spatial error was on average the smallest at TP-4 and the larger at TP-2. No interaction effect of TP and Group was revealed (F(5, 170)=0.226, ns.). However, a significant interaction effect of TP and IOI was revealed (F(35, 1190)= 2.238,

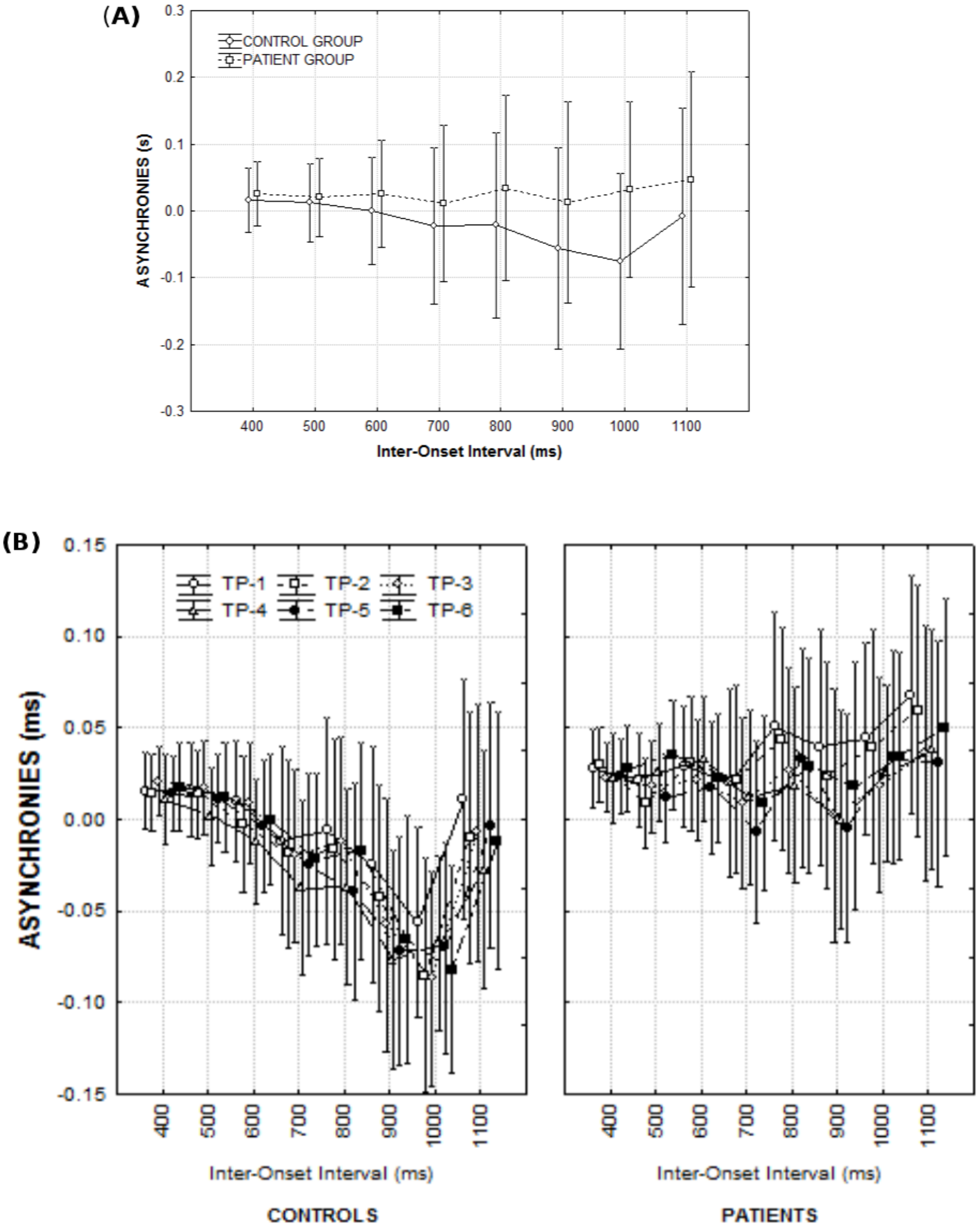


Figure III.12: (A) Asynchronies are presented as a function of the tempo (inter onset interval – IOI) imposed by an external metronome for each group; (B) for each target position (TP) and each tempo for each group

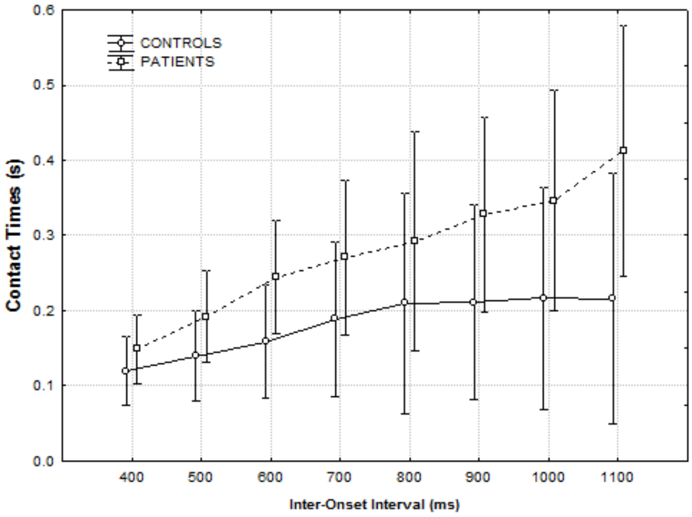
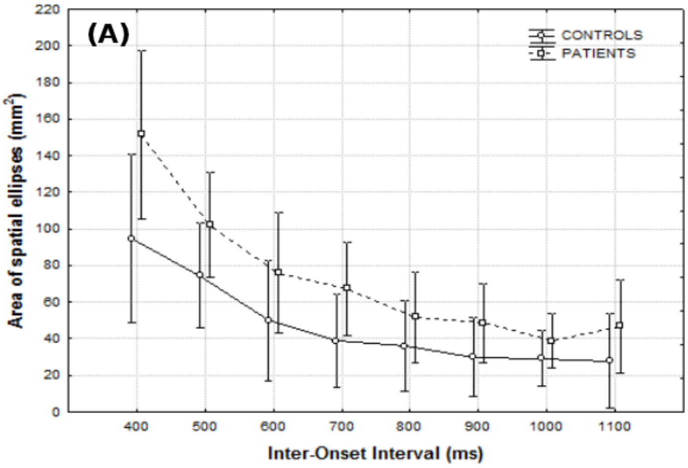


Figure III.13: Contact times are presented as a function of the tempo (inter onset interval – IOI) imposed by an external metronome for each group

$p<0.001$). In fact, differences in the spatial error relative were revealed as a function of spatial position from 700 ms of IOI only. No significant interaction effect of Group, IOI and TP was revealed (F(35, 1190)=0.802, ns.). These results suggest that an anchor point emerged on the spatial trajectory from 700 ms of IOI in both groups (see Figure III.14b).

2.3.2 Planning strategies: orientation deviation from the three models of planning

A main effect of IOI was revealed (F(7, 238)=6.118, $p<0.001$). Deviations to the models were on average smaller at fast tempi (from 600 ms of IOI) as compared to slower ones. A main effect of Model was also revealed (F(2, 68)=70.484, $p<0.001$). Deviations were on average smaller according to the previous target and the tangent to the circle as compared to deviations to the next target. No significant interaction effect of Models and Group were revealed (F(2, 68)=0.177, ns.). However, a significant interaction effect of Models and IOI was revealed (F(14, 476)=6.290, $p<0.001$). Deviations were significantly smaller as compared to the tangent to the circle and as compared to the previous spatial position from 600 ms of IOI especially. No significant interaction effect of Models, Group and IOI was found (F(14, 476)=1.611, ns.). A significant main effect of TP was



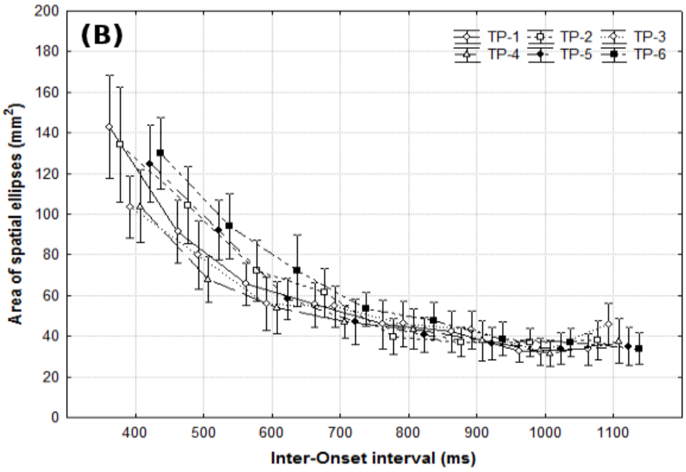


Figure III.14: (A) Spatial errors (area of the endpoint scatterplots) are presented as a function of the tempo (inter onset interval – IOI) imposed by an external metronome for each group; (B) in function of each target position (TP) and at each tempo revealed (F(5, 170)=72.135, p<0.001). Deviations were on average significantly smaller at TP-2 and TP-5 as compared to other TPs. No significant interaction effect of TP and IOI was found (F(35, 1190)=1.373, ns.). However, a significant interaction effect of TP an models was revealed (F(10, 340)=37.021, p<0.001). Ellipses were more oriented towards the next target at TP-1 and TP-4, were more oriented as a function of the previous spatial location at TP-3 and TP-6, and were finally more oriented as a function of the tangent to the circle at TP-2 and TP-5 (see Figure III.15a). A significant interaction effect of TP and Group was also revealed (F(5; 170)= 5.874, p<0.001). Deviations to the models were significantly smaller at TP-2 and TP-5 in the patient group as compared to the control group. No significant interaction effects of TP, IOI and group were revealed (F(35, 1190)=1.305, ns.). A significant interaction effect of Models, TP and group was also found (F(10, 340)=2.079, p<0.05). Post hoc tests revealed that ellipses were less oriented as a function of the previous spatial position at TP-1 and TP-4 in the patient group as compared to the control group. Ellipses were less oriented towards the next target at TP-3 in the patient group as compared to the control group (see Figure III.15c). Ellipses were finally more oriented as a function of the tangent to the circle at TP-5 in the patient group, as compared to the control group (see Figure III.15b). No significant interaction effects of models, IOI and TP were revealed (F(70, 2380)=1.0709, ns.). However, a significant interaction effect of models, TP, IOI and group was found (F(70, 2380)=1.439, p<0.05). The differences revealed at TP-1, TP-2, TP-4 and TP-5 were more pronounced at slow tempi as compared to faster ones. By contrast, the differences revealed at TP-3 were more pronounced at faster tempi.

2.3.3 Autocorrelation values of IRIs (lag-1, lag-6) and asynchronies (lag-1)

2.3.3.1 Autocorrelation values of IRIs at lag-1

A main effect of IOI was found (F(7, 238)=5.493, p<0.001). The AC-1 values of IRIs were negative across all tempi, but were on average larger (more negative) at slow tempi (IOI= 1100 to 1000 ms) as compared to faster ones (IOIs= 600 & 400 ms). A main effect of group was revealed (F(1, 34)=19.050, p<0.001). The AC-1 values in the patient group were on average significantly smaller than that seen in the control group (less negative). No significant interaction effects of Group*Tempo were revealed (F(7, 238)=0.721, ns.), see Figure III.16a.

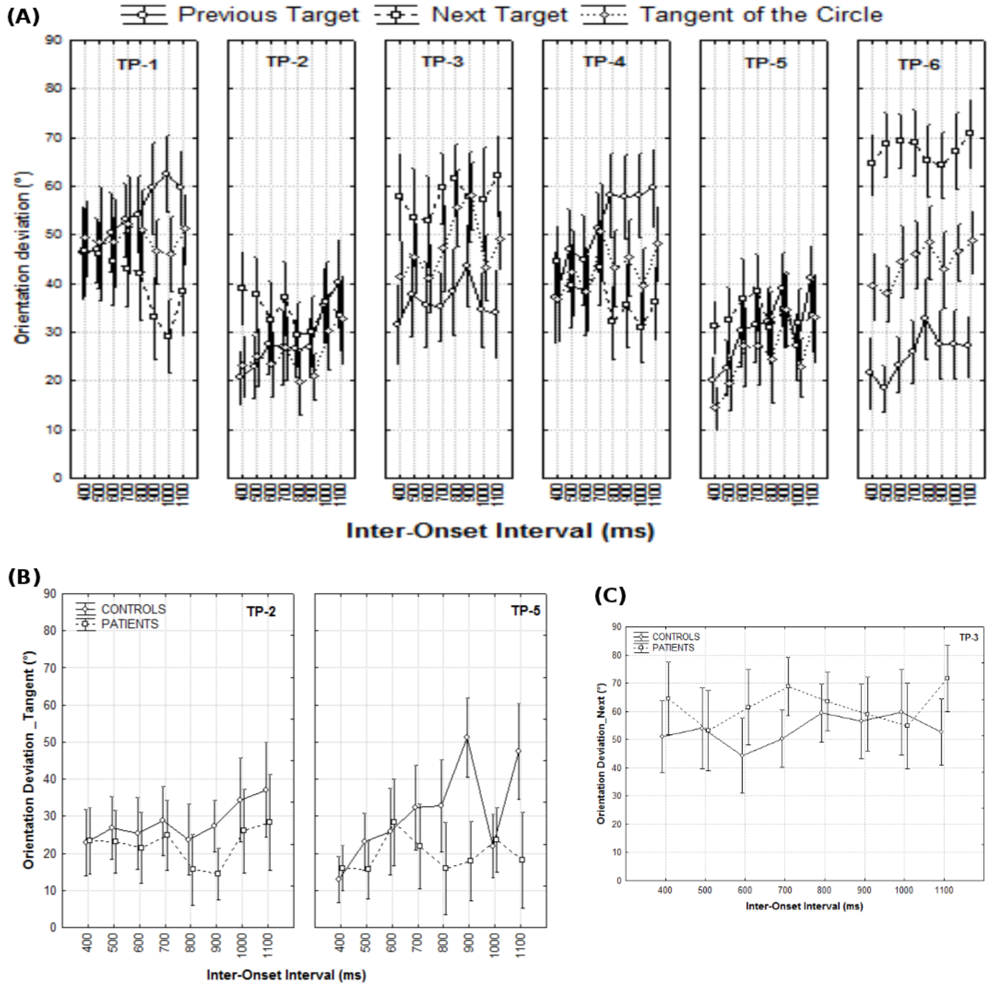


Figure III.15: (A) Orientation deviations of the endpoint scatterplots are presented as a function of the tempo (inter onset interval – IOI) imposed by an external metronome for each model and each IP; (B) at TP-2 and TP-5 for a deviation to the tangent to the circle, (C) at TP-3 for a deviation towards the next target

2.3.3.2 Autocorrelation values of IRIs at lag-6

A main effect of IOI was found (F(7, 238)=16.577, $p<0.001$). The AC-6 values of IRIs were positive across all tempi. However, they were smaller at slow tempi, i.e. between 1100 to 800 ms of IOI, as compared to faster tempi, i.e. between 600 to 400 ms of IOI. A main effect of Group (F(1, 34)=5.287, $p<0.05$) was also revealed. AC-6 values of IRIs were on average larger (more positive) in the patient group as compared to that observed in the control group. No significant interaction effect of IOI and Group was finally revealed (F(7, 238)=1.3162, p=.24320), see Figure III.16b.

2.3.3.3 AC-1 values of asynchronies

No significant main effect of IOI was revealed (F(7, 238)=0.742, ns.). AC-1 values of asynchronies were on average strong and positive with values comprised between 0.40 and 0.50. However, a main effect of group was revealed F(1, 34)= 4.516, $p<0.05$). The AC-1 values of asynchronies were significantly larger for the patient group as compared to the control group. Note however that no differences were found between 500 to 400 ms of IOI (see Figure III.16c).

2.4 General Discussion

Neuropsychological tasks are often used in the literature to assess the executive functions. However, these tasks are known to be too complex, in the sense that multiple functions might be engaged to perform a unique task (see Sood & Cooper, 2013 for an example on the WSCT task). It is then difficult today to understand whether schizophrenia should be described as a central planning deficit or as a specific deficit in the one or the other executive function.

The spatial-tapping task provides the means to assess each function separately: the updating function at slow tempi, the inhibiting function at intermediate tempi, and the switching function at fast tempi. Our results revealed that patients produced more continuous and circular movements than controls across all tempi. However, patients were on average as accurate as their controls to maintain the timing accuracy; and were able to produce longer contact times to inhibit the production of too continuous movements, which suggest a preservation of the updating and inhibiting strategies in the patients. Interestingly, participants had also a tendency to reduce their switching cost in time

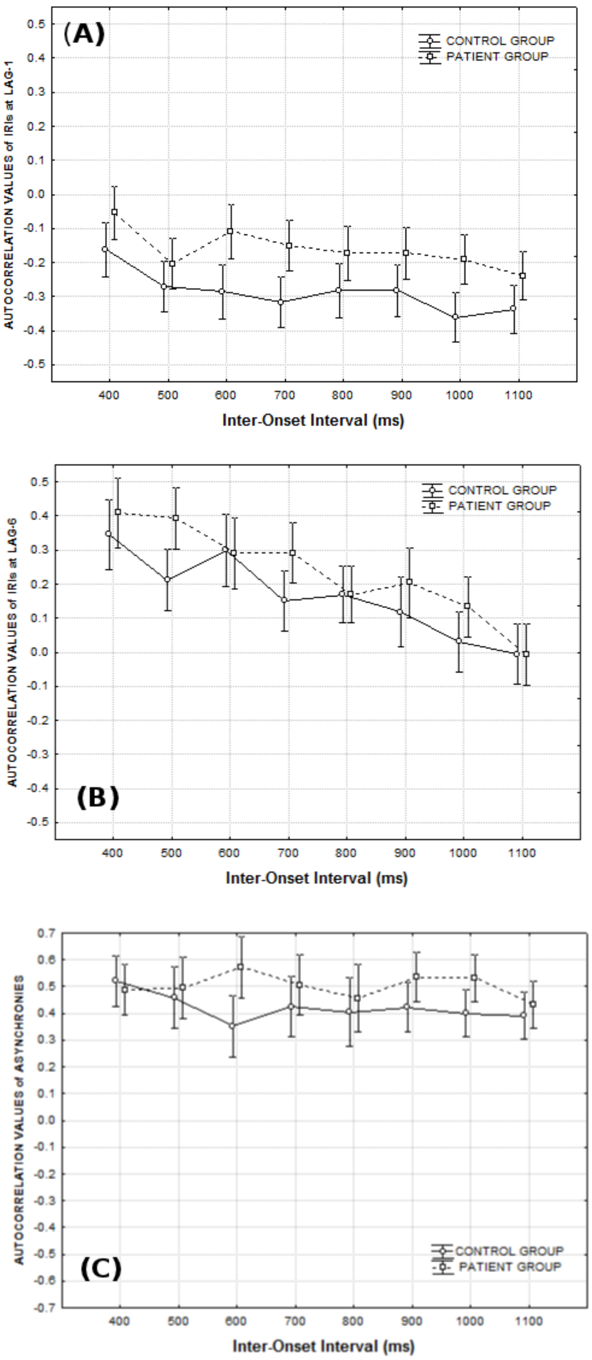


Figure III.16: (A) Autocorrelation functions of the inter-response intervals (IRI) are presented as a function of the tempo (inter onset interval – IOI) imposed by an external metronome at lag-1, (B) at lag-6, (C) Autocorrelation functions of the asynchronies are presented as a function of the tempo (inter onset interval – IOI) imposed by an external metronome at lag-1 rather than in space, which suggested difficulties to focus attention selectively on a discrete event. Hence, we suggest that participants grouped all events between them and over-switched across all tempi, while updating and inhibiting strategies were preserved. These results are detailed in the next sections.

Synchrony performance: the timing was accurate but less produced on a predictive manner in the patient group

The instruction provided to our participants was to be at best synchronized with the external metronome at all tempi. Analysis of the error of synchrony (asynchronies) revealed that on average, participants successfully followed the tempo with errors being close to zero across all tempi. However, the errors were slightly negative in the control group especially 1100 to 700 ms of IOI, while they were positive or null across all tempi in the patient group. These results suggest that the timing was less computed in a predictive manner in the patient group as compared to the control group at slow and intermediate tempi especially (updating and switching phases).

Production of intervals of time: the intervals were as well produced in the two groups, but the requirement of reducing the switching cost on time was more important in the patient group across all tempi

In the present study, the percentage of $\mathrm{IRI}_{\mathrm{error}}$ was used as an indicator of the ability to produce accurate intervals of time. Results revealed that on average, the timing intervals were accurately produced, with deviations from the mean of 1% approximately, except at the fastest tempo of 400 ms at which larger errors were produced. At this tempo, the $\mathrm{IRI}_{\mathrm{error}}$ was also larger in the patient group as compared to that measured in the control group. A specific structuring of the timing intervals was revealed as a function of spatial position. The $\mathrm{IRI}_{\mathrm{error}}$ reflected an alternation of short/long intervals, for all positions except at IP-3 and IP-6. Hence, the intervals of time were alternated one short-one long-zero-one short-one long-zero through space in the control group. As expected, with increasing tempi, i.e. from periods of 700 ms and faster, anchor points in time emerged in the spatial trajectory, i.e. at the specific transition point from extension to flexion movements (IP-3). Hence, with increasing tempi, participants had to deal with the additional constraint of smoothing their movements in time. In the patient group, the $\mathrm{IRI}_{\mathrm{error}}$ was larger at IP-5 (more positive) and at IP-3 (more negative) between 800 to 400 ms of IOI. Moreover, as it can be seen when plotting the $\mathrm{IRI}_{\mathrm{error}}$ at IP-3 as a function of IOI and group, the $\mathrm{IRI}_{\mathrm{error}}$ at IP-3 was also slightly negative in the patient group between 1100 to 900 ms of IOI, while this error was equal to zero in the control group. These results suggest that more demand to smooth the movements on time was required in the patient group as compared to the control group across all tempi. Thus, movements were probably more continuous in the patients as compared to the controls across all tempi, as revealed by the increasing demands to smooth their gesture through time. Hence, the production of the timing intervals was accurate on average (preservation of the updating strategies), while more demands were required to smooth the gesture through time as soon as the slowest tempi (over-switching).

More inhibition of the motor response was required in the patient group at slow and intermediate tempi especially

Contact times were measured in the present study as an indicator of motor inhibition. Indeed, in a previous study using the spatial-tapping task, it was shown that long contact times in the intermediate phase of the task were correlated to better abilities to inhibit a motor response towards an irrelevant stimulus in a go-no-go task, i.e. smaller number of false alarms) (Dione et al., 2013a). In another study, it was shown that the production of longer contact times in an action sequence allowed isolating each action sub-component as a discrete action (Adam et al., 2000). Our results revealed that contact times were on average longer at slow tempi, and were found to decrease with increasing tempi, hence confirming that actions were more discrete at slow tempi and more interdependent at faster tempi. The main finding here was that contact times were on average longer at slow and intermediate tempi in the patient group as compared to the control group. This result does not suggest that motor inhibition was impaired in the patient group, but rather suggest that more voluntary inhibition was required in this group at slow and intermediate tempi especially. It is probable that these contact times were longer in order to inhibit the production of a too fast or continuous action in the patient group (Dione et al, 2013a).

Spatial errors were larger in the patient group as compared to the control group across all tempi; however, actions were well smoothed in space in the two groups

The spatial error was measured in the present study as the area of spatial ellipses drawn around the endpoint distributions of taps surrounding each target. The spatial error was on average small at slow tempi (between periods of 1100 to 800 ms) and was significantly larger at faster tempi. An anchor point was revealed in the spatial trajectory at all tempi, i.e. a specific reduction in the spatial error at the point of transition from extension to flexion movement (Beek, Turvey, & Schmidt, 1992; Roerdink, Ophoff, Peper, & Beek, 2008), here from 700 ms of IOI, at TP-4. Significant differences were revealed as a function of group. The spatial error was significantly larger in the patient group as compared to the control group across most of the tempi (in fact more differences were revealed at fast tempi). Hence, the spatial error was larger in the patient group, without affecting their abilities to reduce a switching cost in space. Note here that two distinct strategies are available to reduce a switching cost in the spatial trajectory: a visual one, by which visual attention is focused at the location of the transition point, and a musculoskeletal strategies by which the movements are flexed or extended in advance at the transition point (Roerdink et al., 2008). While the first strategy typically lead to a reduction of the error in space, the second strategies could reduce the errors both in space and in time. Thus it is probable that the anchor point that emerged here was only reflecting the use of the second strategy. This would suggest that participants would have difficulties to focus their gaze (or visual attention) on the anchor point. In other words, the fact that the spatial error was always larger in the patient group could reveal a difficulty to focus attention in a selective manner in patients.

Movements planning strategies: movements were more circular in the patient group at slow and intermediate tempi, the transition point of flexion/extension was less reliably anticipated in the patient group at fast tempi

According to a number of studies interested in the movement planning and execution of spatial trajectories of the hand, the orientation of spatial ellipses drawn around endpoint distributions could inform about the contextual planning strategies that guides the production of repeated actions (Desmurget, Jordan, Prablanc, & Jeannerod, 1997; Desmurget, Pélisson, Rossetti, & Prablanc, 1998; Rossetti & Régnier, 1995). In the present study, we computed the orientation of the main axis of each ellipse. Then, an angular deviation from pre-specified orientations were measured. Three orientation models were used to test whether: (1) the current movement was produced as a function of the previous spatial location (deviation from the vector linking the previous and the current target),

(2) the next event was anticipated from the current movement (deviation from the vector linking the current and the next target); (3) the action sequence was produced as a global circle (deviation from the tangent to the circle). Here, we focussed only on the second and third models. Our assumption was that movements become more circular at fast speeds in the spatial-tapping task, with the need to smooth the trajectory at the location of the transition point from extension to flexion movements through the use of anticipatory mechanisms. Our results revealed that the movements were significantly more oriented according to the tangent to the circle from periods of 600 ms especially, confirming that movements in the spatial-tapping task became more circular and continuous with increasing tempi. Ellipses were on average oriented towards the next event at specific spatial locations only: at TP-1 and TP-4 between 1100 to 800 ms, and at TP-3 between periods of 600 to 500 ms. This result suggest that anticipation mechanisms were focused on the sequence initiation at slow tempi, while they were geared towards the needs of anticipating the transition point from extension to flexion movements at faster tempi (anticipation of TP-4 from TP-3). Significant differences were revealed as a function of group. Ellipses were in fact more oriented as a function of the tangent to the circle at TP-2 and TP-5 at slow and intermediate tempi in the patient group. Moreover, ellipses were less oriented towards the next target at TP-3, i.e. at the location preceding the position of the anchor point at fast tempi especially. These results suggest that participants produced more circular actions than controls at slow and intermediate tempi especially. This more circular production could explain why contact times were longer and more demands to reduce a cost in space was needed in this group at slow and intermediate tempi. Moreover, the anchor point was less reduced in an anticipatory manner in the patient group at fast tempi. Hence, these results tend to confirm that the anchor point was reduced in time rather than in space in the patient group, suggesting a difficulty especially related to the switching function in the patient group.

Autocorrelations values of IRIs and asynchronies confirmed that the movements were more continuous in the patient group across all tempi as compared to the control group

Autocorrelation (AC) values of IRIs are usually used in the motor timing domain to reveal whether the actions sequences are guided through an event-based strategy, i.e. by maintaining the referential interval in memory for comparisons to the produced intervals, or through emergent strategies, i.e. the movement is produced as a spatial displacement from a starting point to an arrival point and the timing error is corrected at posteriori in subsequent movements (Zelaznik, Spencer, & Ivry, 2002). While AC values of IRIs measured at lag-1 are commonly negative in the case of event-based timing, they are generally more positive in the case of emergent timing. By contrast, autocorrelation values of asynchronies are positive and became more correlated when the timing is computed on the basis of an emergent control strategy. In previous studies using the spatial-tapping task in healthy controls, significant autocorrelation values were revealed at lag-1 and at lag-6 (Dione et al., 2013a, 2013b). Results showed that AC-1 values of IRIs were negative at slow tempi and became significantly less negative from periods of 700 ms. AC-6 values of IRIs, that reflect dependencies in the series going on after having produced an entire cycle (composed of six taps), were positive but small at slow tempi; they were significantly more positive from periods of 700 ms, and finally reached their largest values for tempi faster or equal than 500 ms of IOI. These results suggest that in the spatial-tapping task, the timing controlled through an event-based strategy at slow tempi is then switched towards an emergent strategy at faster tempi, with a phase of transition observed at intermediate tempi.

In the present study, the AC-1 values of IRIs were on average negative and stronger at slow tempi as compared to faster tempi. The AC-6 values of IRIs were on average more correlated at fast tempi as compared to slower ones. On average again, no significant differences were revealed in the AC-1 values of asynchronies as a function of tempi. These results suggest overall, that the task was more guided through an event-based strategy at slow tempi, and through emergent processes at faster tempi. Significant differences were revealed as a function of group. In fact, the AC values were significantly more positive in the patient group as compared to the control group across all tempi and for each dependent variable measured. These results suggest overall that the timing was more computed on an emergent basis or relatively to each cycle (composed of six taps) in the patient group as compared to the control group across all tempi. This result confirms that the movement production was more continuous in the patient group as compared to the control group across all tempi.

2.5 Conclusion

To conclude, in this task, patients had a pronounced difficulty to be accurate in space across all tempi and tended to produce too continuous and circular actions as soon as the slowest tempi. Because their actions were more circular since the slowest tempi, patients were obliged to smooth their action on time sooner as compared to controls and then produced longer contact times to inhibit this too continuous motor production. It is also probable that the differences obtained in AC values (they were more positive in the patient group across all tempi) were due to the additional demand to smooth the action produced within a global circle in the patient group as compared to the control group. Indeed, rather than having timing intervals alternated “short/long/zero/short/long/zero”, structuring that predicts the emergence of negative correlations on the series of IRIs; the structuring of the timing intervals was “short/long/short/short/long/zero” in the patient group, due to the presence of an anchor point in time as soon as the slowest tempi. This specific structuring could have led to observe less negativity or more positivity in the series of IRIs and asynchronies in the patient group as compared to the control group. However, patients were accurate in time and were able to produce longer contact times to voluntarily inhibit their motor response when necessary, hence, suggesting that updating and inhibiting mechanisms were preserved in patients. At faster tempi, participants continued to smooth their action in time rather than in space (i.e. through the use of musculoskeletal strategies). This result suggests a relative preservation of the switching mechanisms in patients. However, they confirm that participants had difficulties to focus their visual attention on the location of the anchor point. Overall, these results suggest a tendency to group successive actions within a global pattern in patients, associated to a difficulty to focus visual attention on specific events. However, patients were accurate on time and were able to produce longer contact times to voluntarily inhibit their motor response when necessary, hence, suggesting that updating and inhibiting mechanisms were preserved in the patients. These results confirms recent findings reported in the literature arguing that patients with schizophrenia are characterized by a problem of over-switching (Yogev et al., 2004) rather than a general deficit in the executive functions (Holt et al., 2013).

Chapter IV

Assessing complexity: the example of bi-manual coordination

Chapter's overview

In the present chapter, we transferred the concept of spatial-tapping to a situation involving bi-manual movements (**Study 1**). This study was conducted in the University of Birmingham (UK), SyMonLab, under the direction of pr. Alan WIng.

We show that distinct executive strategies we involved in the production of simultaneous vs. successive bi-manual movements, i.e. inhibition and updating strategies respectively.

S1: Dione, M., Wing, A. (in prep). Planning, coordinating and executing bi-manual movements through space and time.

Study 1

Planning, coordinating and executing bi-manual movements through space and time

Abstract

The coordination of bi-manual movements can take place according to distinct levels of cognitivo-motor constraints. At low-level, elementary rules of coordination may guide the performance, i.e. there is a preference in the nervous system to send mirror commands when actions are performed with the two arms. With practice, and through the use of cognitive strategies, these natural tendencies may be overcome to enable the production of more skilled performances.

Both selective attention and the use of perceptual binding rules have been suggested as the potential cognitive strategies enabling successful multi-limb coordination. Binding rules might provide an integrated signal towards the two limbs instead of two separate signals representing each limb to give rise to a unified experience of coordination. By contrast, selective attention could assign a specific task goal to each limb and in this manner overcoming the natural tendencies of the system to produce similar action patterns when it is not required in the situation. It has been recently suggested that attention processes may be engaged to help stabilizing basic coordination constraints while perceptual binding may help the coordination in more complex tasks (hierarchical model). However, it is unclear how binding rules may help motor coordination when the task constrain the brain to send two separate signals the each hand, e.g. when the actions are produced the one after the other rather than simultaneously. Hence, we suggest that the one or the other strategy might be involved as a function of the error produced given the task constraints rather than as a function of task complexity.

To test this hypothesis, in the present study, we assessed how the use of a pre-imposed binding rule affected the spatial performance of bi-manual movements produced simultaneously or successively. More precisely, participants had to mentally picture geometrical shapes (e.g. a line, a square, a circle) in the sagittal plan and to produce paced repetitive movements towards the corners of each figure. We analyzed how the spatial variability observed at movement endpoints for each hand was affected by shape complexity (pre-imposed binding rule), task difficulty (movement speed), and vision (eyes open or close). We did not test the full experimental design.

Our results revealed that in the simultaneous task, the error to correct was an error of motor execution requiring selective attention while in the successive task, updating strategies entered into play to help coordinating the current movement as compared to the previous movement performed (binding rule), while the simultaneous task appear as more demanding (or less complex) in terms of cognitive resources than the successive task. The use of a pre-imposed binding rule, did not help stabilizing the motor coordination but helped binding a series of discrete events towards the gestalt when the task demands were high. Hence, our results are not in favor of the hierarchical model but suggest the cognitive strategy engaged may strictly depend upon the error produced to perform a specific motor task.

1.1 Introduction

Bi-manual tasks of coordination are exemplar lab-situations to enable the study of complex motor skills. Many daily tasks require isomorphic movements of the hands that can be produced simultaneously (e.g. clapping hands), or the one after the other (e.g. alternating movements of the arms to support locomotion). In other tasks, each hand may play a differentiated role, e.g. typewriting, playing a music instrument, driving a car, etc. Hence, bi-manual tasks appear as prevailing tasks to better understand: (1) how the brain orchestrates the multiple motor commands relative to each arm in multitasking situations, (3) how the brains deals with the functional, behavioral and anatomical asymmetries relative to the production of each specific movement while ensuring high levels of flexibility and stability in the performance, (2) what are the high-level cognitive functions that enable the production of complex adaptive behaviors. For these several reasons, the study of bi-manual situations has received these last years an increasing scientific interest (see Swinnen & Wenderoth, 2004, for a review on this topic).

Research on bi-manual coordination has been initiated in the light of two distinct theoretical perspectives: the dynamic and the information processing approaches. According to the dynamic approach of motor coordination proposed by Haken, Kelso and Bunz (HKB model, 1985, see Schmidt & Lee, 2011), motor coordination is conceived as a self-organizing system that is subject to destabilization and transitions. The two hands producing repetitive actions are conceived as two oscillators that are prone to be automatically attracted towards a specific physical state of coordination. This decentralized mode of motor coordination is permitted given the many degrees of freedom involved in movement. Two oscillators that have they own variability can be attracted towards a given physical state of common variability. With changes in the environmental constraints, a transition towards a more stable state is expected. This assumption was depicted through comparing the production of in-phase vs. anti-phase movement patterns (Kelso, 1984). While both patterns were shown to be stable at low frequencies, at fast speeds, only the in-phase pattern remained stable and the anti-phase was transitioned towards an in-phase regime. Hence, this approach suggests that motor coordination can be under the control of physical laws that are independent of any supervising brain structure of control.

The information processing approach rather raised the question of how bi-manual coordination can take place when each hand is assigned at the same time to two different tasks. For example, in a study of Goodman et al.(1983), participants had to produce two movements towards same-sized targets placed at the same distance. For one of the two limbs, a hurdle was placed on the spatial trajectory. Several hurdle heights were tested. Results revealed that the movement time of the limb that had to cross a hurdle was larger than the movement time observed for the other limb. More interestingly, the movement time of the limb that had no hurdle was also increased as a function of the hurdle heights. The effect was also seen in the kinematic analyses of the movements, i.e. a tendency in the no hurdle limb to resemble in shape to the other limb. This study illustrates the main assumption defended in this framework, i.e. the neural cross-talk hypothesis, idea following which the brain would send by default some fraction of the motor commands as a mirror image for the two arms (Cattaert, Semjen, & Summers, 1999). In particular when the tasks assigned to each hand are different, e.g. drawing circles clockwise with the one hand and counterclockwise with the other hand, learning is required in order to overcome the natural symmetric tendency (Swinnen, Young, Walter, & Serrien, 1991).

In the last decade, it has been proposed rather than considering the two main perspectives that have guided the understanding of bi-manual coordination as distinct views, that they should be integrated within a unified framework (Swinnen & Wenderoth, 2004). More precisely, the one or the other mode of coordination (supervised vs. unsupervised) might enter into play as a function of the task complexity, difficulty level and experience. When the task is not too complex, low-level neuromuscular patterns of coordination might enter into play. By contrast, with increasing task complexity (e.g. complex spatio-temporal interlimb relationships or performance speed), supervised modes of coordination could enter into play. More precisely, with increasing difficulty, it was shown that the activation of a general sensorimotor network was extended to parietal, temporal and frontal areas. In the review proposed by Swinnen et al.(2004), it was suggested that abstract perceptual binding rules might enter into play within the supervised mode of coordination in order to ensure successful bi-manual coordination when the task became more complex. As compared to selective attention, a cognitive process by which cognitive resources are focused on specific aspects of the motor task, perceptual binding rules would unify the different motor subtasks towards the gestalt. Hence, while selective attention would be engaged to overrule basic coordination constraints, binding rules would be involved in more complex tasks. For an example of binding rule, while it is hard to produce a 90 out of phase finger tapping pattern, the task became easier when referring to the sound made by a galloping horse. Hence, a hierarchical model going from low-level neuromuscular patterns of coordination to higher supervised levels of coordination patterns is assumed.

Interestingly, perceptual binding and selective attention have been recently presented within the influential framework of the predictive coding hypothesis as two opponent computations that share functional properties (Friston, Mattout, & Kilner, 2011; Friston, 2010; Hohwy, 2012). Indeed, within this framework, the main function assigned to the brain is to represent the world so we can act meaningfully on it. Attention and conscious perception have been suggested as two opponent computations allowing representing the world (Hohwy, 2012). While attention is seen as an analyzer that allow optimizing or reducing the variability related to low-level stimulus/response interactions, conscious perception is considered as the opponent computation, i.e. that binds together the multiple information required to understand the world into a meaningful contextual state (Boxtel, Tsuchiya, & Koch, 2010; Hohwy, 2012). In this view, each cognitive strategy, i.e. selective attention and perceptual binding, might be involved as a function of specific task constraints, i.e. to set the sufficient levels of variability to allow integrating the distinct components present in a given task (perceptual binding) vs. to refine specific S-R relationships (selective attention). This approach differ from the hierarchical view of Swinnen et al. (2004) in the sense the use of the one or the other strategy rather emerges as a function of the specific task demand than as a function of the task complexity. In the view of Swinnen et al. (2004), complexity arose when different task goals are assigned to each hand, e.g. producing simultaneous movements at distinct spatial locations or with distinct timing demand (polyrhythms). However, amplitude interference between the two hands was shown to be better reduced when attention (visual cues illuminating the targets) rather than a perceptual binding rule (verbal representation of the movements to produce) was used to guide the movements (Diedrichsen, Nambisan, Kennerley, & Ivry, 2004). Hence, here, a situation that is expected to be complex is better solved through selective attention than through perceptual binding. The same authors suggested that the symbolic cues were resource consuming because in this case, a symbol had to be transformed into a response code to control the action. An alternative to the hierarchical view could be to propose that the cognitive strategy involved is completely dependent upon the error produced by the cognitivo-motor system in a given situation. For example, if we assume that a unique motor command is sent at the same time towards the two arms, e.g. when two movements are produced at the same time towards the same spatial location. Given that each arm has is own motor execution properties (time delays, muscles involved, force demands), one could expect that in this case an error of execution will be produced. In this situation, coordinating the two arms could only rely on reducing the noise due to motor execution, e.g. by inhibiting the too fast course of one of the two hands as compared to the other. Hence, it is more probable in this case that selective attention would enhance the performance. By contrast, when two distinct motor commands are sent the one after the other towards each arm, e.g. when movements are produced successively rather than simultaneously. The differences observed in performance between the two hands could be both due to the variability of the motor commands or to the variability related to motor execution. In this case, the output error would reflect an average of the errors due to the cognitive and motor implementation systems. Hence, compensation mechanisms by which a response is made according to an average of the errors produced across time should be involved. In other words, a perceptual binding rule, which according to Swinnen et al. (2004) might provide an integrated signal towards the two limbs instead of two separate signals representing each limb to give rise to a unified experience of coordination, might be helpful. Overall, considering the expected errors that should emerge according to the task involved rather than the "complexity" or the "difficulty" of the task could be useful to make the appropriate predictions about the engagement of a given cognitive strategy in a given motor task.

In the present study, we tested the effect of the complexity of a pre-imposed binding rule that constrain participants to unify their movements towards the gestalt rather than on each discrete action, on the spatial performance in a simultaneous vs. a successive bi-manual tapping task. More precisely, participants were asked to mentally picture geometrical shapes (e.g. a line, a square, a circle) in the sagittal plan and to produce paced repetitive movements towards the corners of each figure in a simultaneous or in a successive manner. We measured the spatial variability at movement endpoints for each hand separately. We assume that whether the role of a binding rule is to unify the movements of the two limbs towards the gestalt whatever the condition, the differences in spatial variability between the two hands would be decreased with the increase in shape complexity (Swinnen & Wenderoth, 2004). Whether the use of a binding rule just adds a cognitive load to the task, because a symbol has to be transformed into a response code (Diedrichsen et al., 2004), we expect that the mean levels of variability will be increased whatever the task with the increase in shape complexity. In order to test these assumptions, we tested the effect of shape complexity on successive and simultaneous bi-manual tasks (experiment 1). As control conditions, we tested the existence of leaderships effects in the successive condition (experiment 2), the effects of movement speeds in the simultaneous condition (experiment 3), and the effects vision in both conditions (exp1 was performed with eyes close while exp2 and 3 were performed with eyes open). Indeed, in the successive condition, the sequence could start with the right or the left hand, hence, it is important to know whether starting with the one or the other hand had an impact on the performance. Comparing movement speeds, as a function of shape complexity is useful to reveal whether an additive noise due to the spatial directions in which is movement is produced was present in this task. Indeed, one could expect that producing a square is a harder task than producing a line, just because a square requires producing vertical movements that could be under the effect of gravity, and hence became more variable (Papaxanthis, Pozzo, Vinter, & Grishin, 1998; Virji-Babul, Cooke, & Brown, 1994). Whether such differences exist, they should be visible and distinguishable from binding effects at very slow tempi, i.e. when attention can be focused on each sub-movement. If there are no additional demands to produce the square (a shape composed of four discrete lines), no differences might be revealed between the square and the line at very slow tempi.

1.2 Methods

1.2.1 Participants

Ten right-handed students (8 females, 3 males) between 18 to 28 years of age (mean age = 24) and recruited from the University of Birmingham participated in the study. They were paid 9 for their participation. All participants received an information letter and provided written informed consent. One participant's set of data was excluded from all analyses because he was showing difficulties in following the instructions and stopped the test before the end.

1.2.2 Material

Motion data were collected using an Oqus Qualysis motion capture system of twelve cameras. Ten passive sensors were used to constitute a complete model of the arms (see Figure IV.1). However, for the purposes of the present study, the two markers placed on the index fingers of the right and left hands only were used for the data analysis.

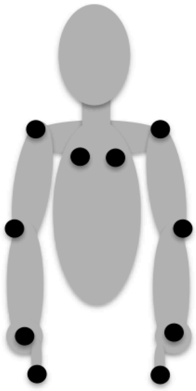


Figure IV.1: Four markers were placed on each arm and two on the torso

1.2.3 Procedure

Participants had to mentally picture 2D geometrical shapes in the sagittal plan and were asked to tap repetitively at the corners of the imaginary shapes with their two index fingers and along with a metronome. Three shapes were used: (1) a line constituted of two virtual targets, (2) a square constituted of four virtual targets, (3) a circle constituted of six virtual targets (see Figure IV.2). The index fingers were oriented perpendicular to the palm and participants were asked to bring the two fingers as close as possible without however contact between the two fingers. The rest of the fist was closed. Displacements from target-to-target were not straight but slightly curved. Twenty taps by targets were produced in each condition.

Concerning the size of the shapes, participants were asked to condition the motor task between their navel and their eyes and to try producing equal-sized movements across conditions. Participants were also instructed to never produce the largest movement possible in the sagittal direction. A familiarization phase was first conducted in which the experimenter was holding pictures of the three shapes in the participant's sagittal plan to ensure that the instructions were well understood. In this familiarization phase, the motor tasks were produced at distinct tempi, with the eyes closed or opened, simultaneously or successively (i.e. each hand had to reach the same target location the one after the other). Just after the familiarization session, the experiment started. Participants were invited to stand up on the center of the motion capture system, behind a line that was drawn on the floor. Three experimental phases were then performed. In phase 1, participants were asked to close their eyes and produced three trials of the simultaneous tapping task and three trials of the successive tapping task for the line and the square in an alternated fashion (Su-Si-Su-Si-Su-Si or Si-Su-Si-Su-Si-Su). Periods were set to 600 ms of IOI, and participants were always starting with the right hand in the successive task. In phase 2, participants were asked to perform a successive tapping task of the two hands for each of the three shapes. Periods were set to 600 ms. Three trials were performed starting with the right hand, and three others starting with the left hand, in an alternated fashion (R-L-R-L-R-L or L-R-L-R-L-R). The hand initiating the action sequence to produce will be referred to the "leader" hand in the next sections. In phase 3, participants were asked to perform a simultaneous tapping task of the two hands for the line and the square across ten distinct tempi (from periods of 1200 to 300 ms). The tempo was the slower in the first trial and was speeded up of 100 ms of periods at each trial. In all phases, participants always started performing the line, then the square and finally the circle. The three phases were counterbalanced with changing participants and the entire experiment lasted 1 h 30 min at all.

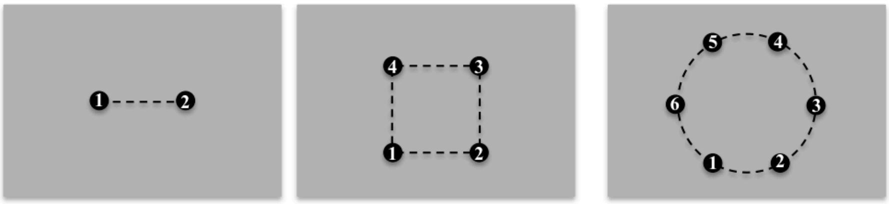


Figure IV.2: Three imaginary geometrical shapes produced in the sagittal plan

1.2.4 Measures

All analyses were conducted in Matlab. Local minima and maxima were extracted from the x-axis displacement data as movement endpoints. The endpoints were then plotted for each target position on the sagittal plan. Using principal component analysis, spatial ellipses were then fitted to the movement endpoint distributions (Figure IV.3, for details on the calculations, see Gordon, Ghilardi, & Ghez, 1994). The confidence intervals were set to 95% on axis length. The area of spatial ellipses was then computed and used as an indicator of the spatial variability.

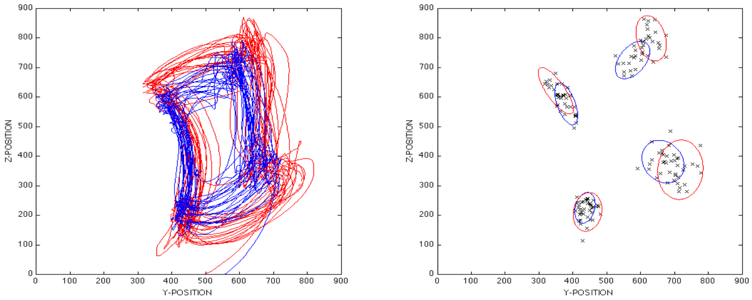


Figure IV.3: Examples of trajectories (left-panel) and spatial ellipses (right-panel) for a participant performing the successive tapping task (phase 2) starting with the left hand. In blue, the position data of the right hand, in red, the position data of the left hand

1.2.5 Statistical analyses

Analyses of variance (ANOVAs) were performed with TASK {successive; simultaneous}, LEADING {right hand; left hand}, TEMPO from 1200 to 300 ms}, SHAPE {line; square; circle} and HAND {right; left} as repeated measures. Fisher LSD post hoc tests were used when required. The alpha value was set to 0.05. The three experimental phases are referred to as experiment 1, 2 and 3 in the Results and discussion section.

1.3 Results & discussion

1.3.1 Experiment 1: simultaneous vs. successive tapping (eyes close)

In this experiment, simultaneous and successive tapping tasks were performed with the eyes closed at periods of 600 ms.

1.3.1.1 Results

All participants successfully followed the tempo, i.e. without exceeding deviations of ± 50 ms as compared to the referential period of 600 ms. The experimental design was 2(TASKS)*2(SHAPES)*2(HANDS).

A main effect of task was revealed (F(1, 8)=10.168, $p<0.05$). The spatial variability was significantly larger in the simultaneous tapping task as compared to the successive tapping task. There was also a reliable effect of shape (F(1, 8)=57.147, $p<0.001$). With the square, the spatial variability was significantly larger than with the line. A significant interaction effect of task and shape was also revealed (F(1, 8)=15.762, $p<0.01$). The spatial variability was in fact larger with the square in the simultaneous task as compared to the successive task. There was no main effect of hands (F(1, 8)=0.468, ns) but there was a reliable interaction effect with the tasks. In the simultaneous task, the spatial variability was larger for the left hand as compared to the right hand. There was no interaction effect of hands and shape. However, a significant interaction effect of task, shapes and hands was found (F(1, 8)=7.086, $p<0.05$). The spatial variability was larger for the left hand as compared to the right hand with the square in the simultaneous task. In the successive task, the spatial variability was significantly larger for the right hand as compared to the left hand with the line (see Figure IV.4).

1.3.1.2 Discussion

In this experiment, simultaneous and successive tapping tasks were performed with the eyes close at periods of 600 ms. Our results revealed that the performance was on average more variable in the simultaneous task as compared to the successive task. The larger variability observed in the simultaneous task could be due to the higher level of cognitive demand that was required to control the movements in this specific task. Indeed, in the successive tapping task,

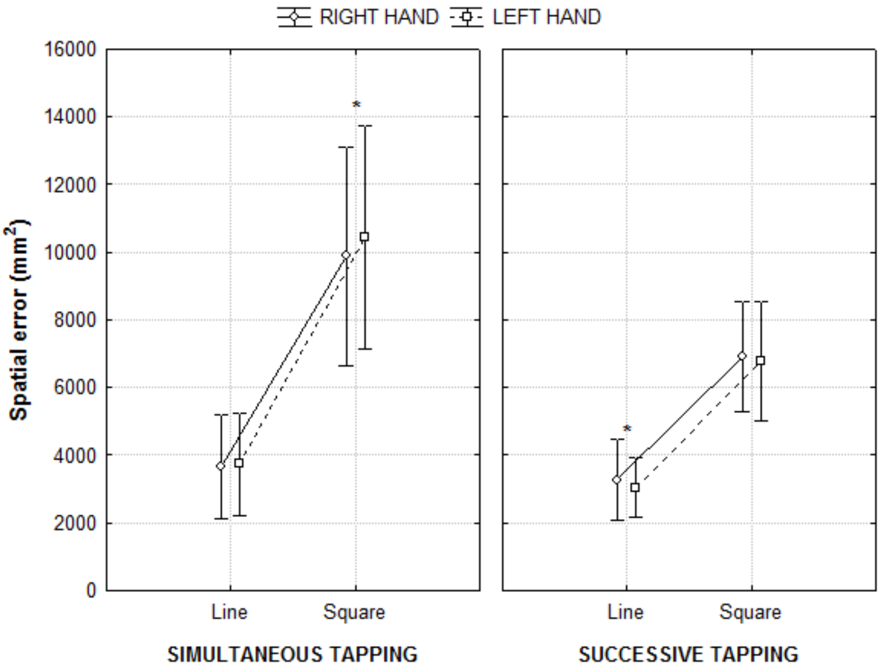


Figure IV.4: The spatial variability is represented for the simultaneous vs. the successive tasks, for the line or the square, and separately for the right and the left hand each action was produced the one after the other, hence, more cognitive resources were available to produce each action separately, ensuring higher levels of performance; while in the simultaneous task attention resources were divided between the two arms.

In both tasks, the spatial variability was larger with the increase in shape complexity. As regards to our assumptions, this result could suggest that the use of a binding rule did not united the two arms towards the gestalt but had just a cognitive cost that rendered the task harder to produce on average. However, the spatial variability was further larger in the simultaneous task as compared to the successive task. One could then argue, that the task was harder to perform in both conditions for reasons that are external to the use of a binding rule, e.g. because of the spatial configuration, and that the binding rule per se had additional deleterious effects on the simultaneous tapping task and maybe beneficial effects in the successive tapping task. It is also possible that the advantage seen in the square in the simultaneous condition was just due to the fact that the actions were produced discretely in this condition; hence, more attention was available to produce accurate actions as compared to the other condition.

Whatever the real causes that may explain these results, the shape complexity increased the cognitive load in both tasks. If we just focus on these differences, our results suggest that two distinct types of error correction processes were revealed in each condition. Indeed, in the simultaneous condition, with the increase in cognitive load, reliable differences were found between the two hands. The variability of the left hand was in fact significantly larger than the variability of the right hands. These differences might reflect a dominance effect in right-handed participants, i.e. who developed across ages a specialization to produce daily motor tasks with their right hand. These differences were not present when the cognitive load was lower (i.e. with the line), which suggests that with attention, the R/L differences were significantly reduced. Hence, it is probable that in simultaneous tapping, an error of execution have to be reduced.

By contrast, in the successive condition, with the increase in cognitive load, reliable differences that were initially found between the two hands disappeared. Indeed, in this condition the variability of the right hand was significantly larger than the variability of the left hand when the cognitive load was low (i.e. with the line). It is probable that such differences do not reflect an increase in the difficulty to execute the movement with the right hand, but rather reveals a correction process that operated to optimize the motor performance. Indeed, in the successive tapping task, the right hand was initiating the action sequence, and the left hand was following. Hence, it is probable that the error produced by the leading hand according to the expected spatial location to reach (or internal spatial referential) was used as a corrective signal to plan the movement of the follower hand towards the same referential in an optimal way. Then the motor planning of the following hand was each time updated from the error produced by the leading hand, resulting in an optimization of the motor performance in the follower hand as compared to the leader hand. These R/L differences disappeared in the same task successive with the increase in shape complexity, which suggests that this strategy was dependent upon the availability of cognitive resources.

Overall, our results suggest that two distinct mechanisms of error correction entered into play in the simultaneous and successive tapping tasks. While motor execution errors were corrected in the simultaneous task, a sort of updating process entered into play in the successive task to make each action matching the previous one. Interestingly, the use of a binding rule in this case affected more the simultaneous condition than the successive condition. Hence, if one considers that the mean levels of variability increased first because of the spatial configuration of the task (gravity effects may be expected with the square as compared to the line), and second, that a binding rule affected the performance in an additive way, we could suggest that the performance was enhanced in the successive task and reduced in the simultaneous task with the use of a binding rule. In this case, one could also counter-argue that the beneficial effect seen in the successive task as compared to the simultaneous task was just due to the fact that more resources were available in this task to produce each action. In this case, only a deleterious effect of the binding rule would be highlighted in the simultaneous task, while more research should be required to know how the results were affected by the binding rule in the simultaneous task.

1.3.2 Experiment 2: successive tapping starting with the right or the left hand (eyes open)

In the present experiment, we tested the effects of leadership in the successive tapping task, i.e. by asking participants to start the sequence with the right or with the left hand, for the line, the square and the circle. Inter-onset periods were set to 600 ms and the eyes were opened.

1.3.2.1 Results

All participants successfully followed the tempo, i.e. without exceeding deviations of ± 50 ms as compared to the referential period of 600 ms. The experimental design was 2(LEADING)*2(SHAPES)*2(HANDS). A main effect of shape was revealed (F(2, 16)=27.317, $p<0.001$), the spatial variability was increased with shape complexity see Figure 5. There was also a reliable main effect of hands (F(1, 8)=11.359, $p<0.01$). The spatial variability was on average larger for the left hand as compared to the right hand. A significant interaction effect of shapes and hands was also revealed (F(2, 16)=6.198, $p<0.05$). The spatial variability was in fact significant larger for the left hand as compared to the right hand with the square in particular. There was no main effect of hands (F(1, 8)=11.359, $p<0.01$), however a significant interaction effect of leading and hands was revealed (F(1, 8)=26.990, $p<0.001$): the spatial variability was significantly larger for the leader hand as compared to the follower. There was no significant interaction effect of leading and shape (F(2, 16)=1.0073, ns). Finally, there was no significant interaction effect of leading, shapes and hands (F(2, 16)=3.501, ns).

1.3.2.2 Discussion

In the present experiment, we tested the effects of leadership in the successive tapping task, i.e. by asking participants to start the sequence with the right or with the left hand, for the line, the square and the circle. Inter-onset periods were set to 600 ms and the eyes were opened. Hence, in this task, the leader hand always provided a potential visual target to reach for the follower hand.

The important points of comparisons here as compared to the first experiment concern the effect of vision and the leading effects. Interestingly, we found that the spatial variability was always larger with the increase in shape complexity. Which confirms as compared to experiment that the cognitive load was larger as the function of the shape complexity, even with eyes open. To note here that the mean levels of variability were the same in the two tasks, although this effect was not tested statistically, i.e. around 3000 mm^2 for the line and around 7000 mm^2 with the square, which suggests that vision had only a small effect on the mean levels of spatial variability. By contrast, vision had a large effect on the R/L differences between hands. Indeed, the effects seen in the first experiment, i.e. the right hand being more variable than the left hand when the sequence

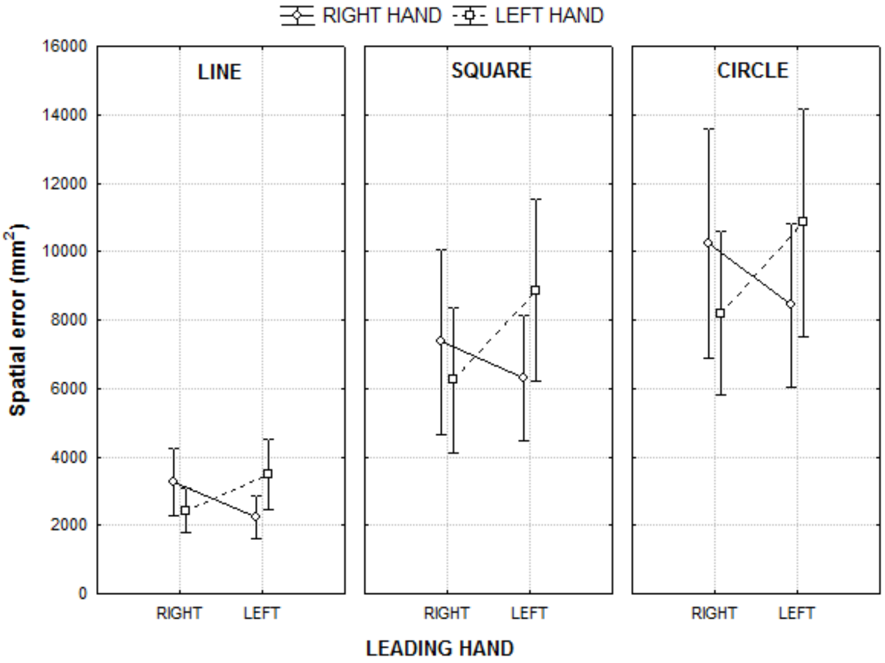


Figure IV.5: The spatial variability is represented in function of tempi for the line, the square and the circle shapes, for the right and the left hands separately, and with the right or the left hand leading was started with the right hand, were enlarged and became visible for all shapes. Moreover, an effect of leadership was found. Whatever the leading condition, the leading hand was always showing higher levels of variability that the following hand. This result confirms, as regards to experiment 1, the presence of predictive strategies by which the corrective signal emitted by the leading hand was used to update the motor plan that guided the execution of the movement of the following hand in the successive task, and suggest that this process is enhanced by vision.

Another effect related to R/L differences was also found: the spatial variability was larger for the right hand as compared to the left hand in the square as compared to the other shapes. This result suggests that the square was a more difficult shape to produce as compared to the two other shapes. This result can be interpreted as a gravity effect. Indeed, effect of gravity is assumed to be stronger for the production of a vertical movement as compared to a horizontal movement (Papaxanthis, Pozzo, Vinter, & Grishin, 1998; Virji-Babul, Cooke, & Brown, 1994). Given that the square contained two vertical movements to produce while the line and the circle contained only horizontal or diagonal movements to produce, this hypothesis seem reliable. Nevertheless, as already reported, the mean levels of variability were larger for the circle as compared to the square. This result could suggest that the cognitive load was even though larger for the circle. The strong differences between the two shapes might then rely on the fact that four taps were to be produced within a cycle with the square while six had to be produced with the circle. Hence, it is probable that the motor plan to load before to produce the action sequence or in other words the cognitive load was kept higher in the circle as compared to the square.

Overall, our results confirm the presence of an updating strategy in the successive tapping condition in particular, i.e. cognitive process that is independent from the hand initiating the sequence and that is enhanced by vision.

1.3.3 Experiment 3: simultaneous line and square tapping at distinct tempi (eyes opened)

In this experiment, a simultaneous tapping task was produced at distinct tempi (from slow to fast tempi) with the eyes opened.

1.3.3.1 Results

One participant failed to follow the tempo at all inter-onset periods. Two participants failed to follow the tempo at 1200 ms, 600, 400 and/or 300 ms. Hence, the data of these three participants were excluded from the present analysis. The six remaining participants successfully followed the tempo, i.e. without exceeding deviations of ± 50 ms as compared to the referential period. The experimental design was finally 8(TEMPI)* 2(SHAPES)* 2(HANDS).

A main effect of shape was revealed (F(1, 5)=76.557, $p<0.001$). The spatial variability was significantly larger with the square as compared to the line (see Figure 6). There was also a significant effect of hands (F(1, 5)=17.973, $p<0.001$). The spatial variability was on average larger for the left hand than for the right hand. No significant interaction effect of hands and shapes was revealed (F(1, 5)=0.133, ns). There was also a reliable main effect of tempo (F(7, 35)=2.676, $p<0.05$). The spatial variability was on average larger at fast tempi, i.e. between periods of 500 to 400 ms as compared to slower tempi. There was also a significant interaction effect of shape and tempo (F(7, 35)=4.818, $p<0.001$). The spatial variability was in fact larger at faster tempi (between periods of 500 to 400 ms) with the square only. There was also a significant interaction effect of hands and tempo (F(7, 35)=2.866, $p<0.05$). The spatial variability was in fact larger for the left hand as compared to the right hand between periods of 600 to 400 ms in particular. Finally, no significant interaction effect of hand, shape and tempo was revealed (F(7, 35)=0.794, ns).

1.3.3.2 Discussion

In this last experiment, a simultaneous tapping task was produced at distinct tempi (from slow to fast tempi) with the eyes open. Our results reveal overall that this task was hard to perform, because three of our participants failed to follow the tempo. In the present experiment, only one trial was performed by tempo, while in the two other experiments of the present study three trials were performed by condition. Hence, it would be better in the case of a replication of the present experiment to perform at least three trials by tempo, to test more participants, or to familiarize the participants with the entire task before to do the test. However, significant and meaningful differences were obtained according to the conditions manipulated for the six participants included in the present analysis.

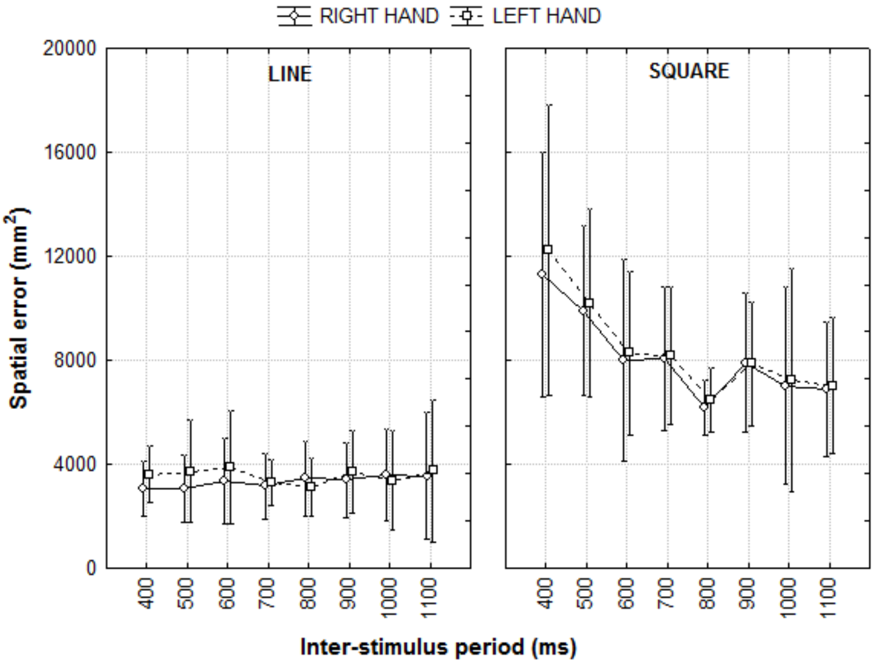


Figure IV.6: The spatial variability is represented in function of tempi for the line and the square shapes and separately for the right and left hand

In the present experiment, differences in spatial variability were revealed both at the levels of the mean variability and at the levels of the differences between hands as a function of the tempo. Interestingly, the mean levels of variability were larger in the square as compared to the line at slow tempi, i.e. between periods of 1100 to 700 ms. At slow tempi, participants had the sufficient time to focus attention of each movement, hence the series can be considered as series of discrete events. Differences emerged in the spatial variability in spite of this possibility. This result suggests that differences related the spatial configuration of the square, a shape that was more difficult to produce as compared to the line, affected the spatial variability in the significant manner. Hence, the square was definitely more difficult to perform, certainly because of the vertical movements involved in the sequence to produce.

At fast tempi, i.e. from periods 600 ms, R/L differences were found in both shapes. In fact, the spatial variability of the left hand was always significantly larger than the spatial variability of the right hand. Hence, the same "dominance" effect than in experiment 1 was revealed here with increasing speeds whatever the shape complexity. This result confirms that differences related to motor execution difficulties are revealed in our tasks by a dominance effect, and in the same vain, that the simultaneous task required to overcome a noise related to motor execution. Furthermore at fast tempi, i.e. from periods of 500 ms, the mean levels of variability were increased with the square only. This result suggests that with fast tempi, the cognitive load became higher in the square but not in the line. To explain these results, we suggest that the square was planned as a series of four discrete lines at slow tempi, and as a global square at faster tempi, i.e. with the involvement of a more complex motor plan that was loaded before the initiation of the action sequence and maintained throughout. This strategy could be require to ensure higher levels of performance given the task constraints (high speed) that let no time to re-build a motor program after the execution of each action.

Concerning the effect of vision, if we focus on the tempo of 600 ms, as compared to experiment 1, both the main levels of spatial variability and the differences between hands seemed to be lower with vision (8000 mm^2) than without vision with the square (10000 mm^2), although no statistics were conducted to compare these results. This result suggests that it was easier to reduce the differences between hands and to keep the actions discrete with vision. With the line, the same levels of variability were revealed with or without vision (4000 mm^2

approximately). However, no differences were revealed between hands without vision. This result could simply be due to the fact that participants were less trained the present experiment (one trial by tempo with vision), as compared to the other experiment.

Overall, the results of the present experiment reveals that binding strategies that consisted here in programming by advance the entire motor sequence rather than focusing attention on each discrete action was required when the shape was more complex than a line only and at fast speeds only. While binding strategies affected the mean levels of variability, difficulties to execute the actions were revealed by R/L differences reflecting a dominance effect. This effect was seen whatever the shape with the increase in movement speeds. With these results in mind, if we come back to the two previous experiments, these results suggest that binding effects were present in the simultaneous task with the square (mean var ¿ 8000 mm^2 in exp1) and were certainly absent in the successive condition (mean var ? 8000 mm^2 in exp 2 and exp3). The possible absence of these effects in the successive condition could be due to the fact that binding in this case takes place from movement to movement, the planning of the present movement being affected by the execution of the previous one. Hence, no needs to bind the spatial shape within a global structure were required in the successive task. Spatial binding took place with increasing difficulty (movement speeds) in the simultaneous task only. It could be interesting in future studies to know whether spatial binding should be involved in successive tasks produced at fast speeds. One could expect that in this case the updating strategy would be lowered.

1.4 General Discussion

In the present series of experiments, we tested the possible effects of shape complexity, vision and movement speed on the spatial variability of goal-directed actions produced with the two arms in a simultaneous or a successive manner. Shape complexity was initially considered as a way to impose a binding rule to the motor task. Our initial aim was to test whether these rules helped coordinating the actions of the two hands between them, as suggested in Swinnen et al. (2004), or just adds a cognitive load to the task because a symbol has to be transformed into a response code (Diedrichsen et al., 2004). Our results strongly comfort the second hypothesis. Indeed, shape complexity rendered the task more difficult to perform in all experiments (higher spatial variability).

Our results revealed first that the simultaneous task was on average harder to produce than the successive tapping task, task for which the spatial variability was smaller. This finding corroborates the results of previous neuro-scientific studies that compared brain activations during bimanual coordination vs. single-limbs tasks (Toyokura, Muro, Komiya, & Obara, 2002; Tracy et al., 2001; Ullén, Forssberg, & Ehrsson, 2003). These studies revealed that more brain regions were involved in the production of bi-manual as compared to uni-manual tasks, i.e. the primary motor cortex, the premotor cortex, the SMA and the cerebellum. Hence our results suggests that an additional load or effort in the nervous system is required when two movements are produced at the same time rather than one at a time, effect that was reflected in the present study in the spatial variability.

Interestingly, by comparing the successive bi-manual task to the simultaneous one, our results revealed that the two tasks were different in nature and involved distinct sort of cognitive strategies to be coordinated. While an error related to motor execution was revealed in the simultaneous condition, with R/L differences suggesting a dominance effect being always revealed with the increase in task difficulty, a sort of updating process by which the error correction signal produced in the leader hand bias the planning and execution of the follower hand was seen in the successive condition when the task was not too hard to perform (i.e. with vision, or with the line in absence of vision).

The use of a pre-imposed binding rule did not favor motor coordination in any task but systematically increased the mean levels of spatial variability. Here, these rules were rather a constraint increasing the cognitive load than a support to motor coordination. However, our results suggest that binding effects emerged as a function of the task difficulty. Indeed, in experiment 3, in the square and with increasing speeds (i.e. from periods of 500 ms), a noise that was neither only due to motor execution and nor to the spatial configuration of the task was revealed. Because producing the task at slow tempi allow focusing attention on each discrete sub-movement, while such strategy is not possible with the increase in movement speeds, it is probable here that the actions were bound within a global shape. Hence, binding rules emerged when the task had to be produced continuously rather than as a series of discrete actions.

This result means that binding effects were not forcefully present in the two other experiments that were produced at periods of 600 ms. Hence, it is possible that in these experiments, only the amount of cognitive load was manipulated. Thus, it could be interesting in a further study to compare the successive and the simultaneous condition with eyes close or open distinct tempi, including tempi faster than 600 ms to really test the effect of a binding rule on the two distinct tasks. However, it is hard to expect that with the increase in task difficulty, the pattern of result will completely be switch and reveal different effects, i.e. supporting in the better way the motor coordination. It is more probable that the binding rules per se as they were manipulated did not support the coordination in terms of shape of the movement. Hence, it could be interesting in the future version of the document to measure how the timing was affected by the use of such rule. It is possible that the spatial binding rule in fact helped coordinating the action on time rather than on space.

Our results also revealed that vision comes at a support to optimize the conditions by which the updating mechanism entered into play (exp1-exp2). Vision rendered cognitive resources available whatever the shape complexity. This result corroborates with the most recent findings concerning the role of vision in locomotion. Indeed, vision was shown to have the ability to regulate location on a local level (step-by-step) or at a more global level (route planning) (Patla, 1997). Visual information is also known to constitute one of the most salient source of information to control walking (Bank, Roerdink, & Peper, 2011) or to avoid obstacles in healthy participants (Patla & Vickers, 1997) and to help maintaining dynamic stability in walking in elderly subjects (Bank et al., 2011), in Parkinson's disease (Azulay et al., 1999; Vitório et al., 2012), or following a stroke (Hollands et al., 2013; Hollands, Pelton, Tyson, Hollands, & van Vliet, 2012). Here, the role of vision is generalized to other kinds of movements, i.e. bi-manual movements and is presented as an optimizer rather than as the original executive updating mechanisms.

The results of the present study allow us to bring arguments concerning the debate of the meaning of this spatial variability, computed as ellipses around the endpoint distributions surrounding each virtual target. Indeed, while the precursor view was to suggest spatial variability informs us about the nature of the planning strategies that are in use to guide action sequences (Desmurget, Pélisson, Rossetti, & Prablanc, 1998; Gordon et al., 1994; Rossetti & Régnier, 1995), an opponent view suggest that spatial variability can simply reflect noise relative to movement execution (Van Beers, Haggard, & Wolpert, 2004). Indeed, if we consider that action execution takes place following at least three stages, i.e. localization, planning and execution, it is important to consider that the variability observed in hand pointing movements could depend upon each of these three stages. In the context of bi-manual coordination, our results revealed that both difficulties related to the amount of cognitive demand or to motor execution difficulties affected the spatial variability. However, spatial variability was affected in two distinct ways. Indeed, when cognitive demands were high, here with shape complexity or more continuous movements, the spatial variability was increased in average. By contrast, when execution demands were high (here at faster tempi), spatial variability was affected as a deviation from the mean. Indeed, in all three tasks, the spatial variability was equals to 4000 mm^2 in average with the line, to 8000 mm^2 in average with the square, and to 10000 mm^2 in average with the circle and were in average deviated from 500 mm^2 from the mean when the execution demands became larger. Hence we conclude that spatial variability can inform us both about the amount of cognitive load that is required to produce a given motor task (mean levels of variability), but also about the motor execution demands that are required to produce a given task (standard deviation from the mean). We promote the use of this variable for a better understanding of the high-level cognitive functions and low-level dynamics that enables the coordination of bi-manual movements.

Overall, our results confirm that bi-manual tasks are prevailing paradigms to study the nature of the high-level mechanisms of action planning. These tasks allow an ecological study of these processes in the sense that there are no needs to use a secondary verbal task to explore these mechanisms. The interpretation we adopt is in line with the predictive coding hypothesis according to which attention is assumed to enter into play to optimize the accuracy of already stable patterns of action while binding strategies rather help structuring multiple information into a coherent context to support the production of less stable patterns (Friston, Daunizeau, Kilner, & Kiebel, 2010; Hohwy, 2012). Accordingly, our results are against the hierarchical view according to which the more complex the task, the more binding could intervene to help the coordination, and rather suggest that the cognitive strategy involved is completely dependent upon the error produced by the cognitivo-motor system in a given situation. Classifying the motor tasks as regards to the potential error that they produced rather than as the function of their “complexity”, could help future research to draw more accurate predictions about the cognitive strategies involved to support the coordination of tasks.

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Chapter V

General discussion

1.5 Results summary

In the present thesis, we introduced the spatial-tapping task as a novel paradigm to assess the high-level executive functions. This task was designed as a hybrid of finger tapping and circle drawing tasks. More precisely, participants were asked to produce repetitive taps of the index finger on six discrete visual targets that were arranged around a virtual circle following distinct tempi (from slow to fast tempi). This task was shown to share similar properties than finger tapping tasks at slow tempi (between inter-taps periods of 1200 to 900 ms) and than circle drawing tasks at faster tempi (between inter-taps periods of 500 to 300 ms). At intermediate tempi (periods of 800 to 600 ms) a specific phase of transition of control strategies was revealed. The task constraints pressured participants to go faster, and hence to start anticipating forthcoming events. Participants inhibited the production of too fast movements in order to deal with the task instructions, i.e. to keep in synchrony with the external metronome (see Chapter2-Study1). This pattern of behavioral results led us to divide the task between three behavioral phases; following the hypothesis that updating strategies were required at slow tempi (phase 1) to maintain the timing accuracy, that inhibiting strategies were required at intermediate tempi (phase 2) in order to keep high levels of timing accuracy in spite of an increasing pressure to anticipate forthcoming events, that switching strategies were required at faster tempi (phase 3) in order to smooth the actions that were now more circular and then to correct the timing errors a posteriori, i.e. after having produced an entire circle. This specific hypothesis was tested (see Chapter2-Study3). In this study participants were asked to perform three traditional neuropsychological tasks that aimed at tapping the three executive functions of updating, inhibiting and switching, and the spatial-tapping task. In order to obtain performance scores in the spatial-tapping task, the data obtained for each dependent variable (spatial error, temporal error, contact times) was averaged by phase. Multiple regression analyses were then conducted between these scores and the scores obtained in the classical tasks. Our results confirmed our hypotheses by revealing that the performance scores in the updating task (n-back) were correlated with the timing errors that were measured as a percentage of deviation to the referential interval of time that was to be produced in the slow phase of the spatial-tapping task only. The scores obtained in the inhibiting task (go-no-go) were correlated with the contact times in the intermediate phase of the task only. The scores obtained in the switching task (letter number task) were finally correlated with the spatial error in the faster phase of the task only. These results suggest that the spatial tapping task is able to target independently the three main executive functions, with the cognitive task goal being changed as a function of task demands (here the temporal constraints).

The relationships between the high-level executive functions and attention are intriguing. The concepts seemed to cross over at many levels. Indeed, in the literature, selective attention is often opposed to the ability to inhibit distractors. In switching tasks, it is often stated that one needs to switch "attention" from a relevant aspect of the task to another. In Chapter2-Study2, we assessed the relationships between attention, its opponent computation, i.e. conscious perception and the high-level executive functions. More precisely, we used distractors that have the potential to trigger the automatic orientation of attention towards specific spatial locations during the spatial-tapping task. Our results revealed that attention and conscious perception entered respectively into play to optimize the accuracy of the timing performance, and to better define the contextual information needed to produce embedded sequences of actions. However, these psychological mechanisms did not interfere with the planning strategies by which the actions were controlled: autocorrelation values of inter-response intervals were not changed according to the experimental conditions that were manipulated. These results suggest that the attention and conscious perception acts as mediate between perception-action links by selecting, improving and reinforcing S-R relationships without affecting in a direct way the time dependencies between successive motor actions.

Determining executive profiles according to specific pathologies is seen as a hard task in the literature, mainly because the classical neuropsychological are too complex and hence does not allow to test specific hypotheses. These difficulties were seen in the literature in the context of normal ageing and schizophrenia. These selected pathologies are often interpreted in terms of a general decline in the executive functions. However, it seems clear that the declines observed with ageing and in schizophrenia are not dependent upon similar mechanisms. In Chapter 2, we asked young, mature and elderly participants (Study1) and patients with schizophrenia (Study2) to perform the spatial-tapping task. More specific executive profiles were drawn for these two populations. In Study 1, we revealed that elderly individuals suffer of a specific deficit of inhibition, with updating and switching strategies being preserved. The deficits encountered were mainly due to a difficulty to generate a motor response according to a certain delay. Elderly participants were in fact always too fast to produce an action according to a certain delay. However, they compensated this default by producing longer contact durations. These mechanisms of compensation allowed them to be on average accurate in time and to maintain the good strategies of updating (as revealed through the autocorrelation functions of IRIs at slow tempi). Nevertheless, it was not possible for them to maintain these strategies when the tempo became significantly faster, i.e. from inter-tap periods of 800 ms. Hence, they switched too fast from an event-based strategy to an emergent strategy (as revealed through the autocorrelation functions of IRIs at intermediate tempi) as compared to their controls, who were able to maintain the timing event-based until inter-tap periods of 600 ms. Thus, the specific inhibition phase of the spatial-tapping task (phase 2) was impaired with ageing. The main deficit presented by elderly participants, i.e. producing too fast actions when they are produced on a predictive manner also interfered with the integrity of their switching strategies, but at a timing level only. Indeed, elderly participants were impaired in switching from extension to flexion movements according to musculoskeletal strategies, i.e. by flexing or extending in advance at the level of the transition point. However, they were not impaired to put in place a switching strategy depending upon vision, i.e. fixating the gaze at the transition point. It was further shown that they focused more their visual attention on the transition point as compared to other participants (as seen according to the planning strategies they used to control the spatial trajectory of their movements: more anticipation was produced at the specific level of the anchor point). Hence, our results are not in agreement with the actual hypothesis of a general decline in executive functions going on with ageing. We suggest that their deficits were especially related to abnormalities in motor and cognitive inhibition. In study 2, schizophrenia patients were compared to age-matched controls in the spatial tapping task. Results were more complex. In these patients, the spatial error and the contact times were larger at all tempi as compared to their controls. Moreover, the movements were more circular especially at slow tempi as compared to their controls. These results suggest that patients grouped within global sequences of actions across all tempi (more circular movements and larger spatial variability). This global strategy was however inhibited through the production of longer contact times especially at slow and intermediate tempi. In spite of these differences, actions were well timed at all tempi, without significant differences revealed as compared to controls. These results suggest that patients used a switching-like strategy across all tempi to guide their actions. According to these results, two hypotheses can be drawn: (1) it is possible that participants over-switched, i.e. all their movements were under the control of the basal ganglia without possibilities to change of strategy according to the task demands, (2) it is also possible that patients suffered from a cerebellar dysfunction and hence compensated these difficulties by producing more continuous actions (depending upon the basal ganglia). Stated differently, the disabilities observed in these patients could be due to difficulties to focus attention on each discrete action, or to an over-ability to group many independent events between them. More research is needed here to disentangle between these assumptions. In any case, these results are against the idea of a general decline in the executive functioning. At least, the switching function may be preserved. The results obtained in these two distinct populations confirm the potential of the spatial-tapping task to draw new arguments to understand how executive functions are impaired according to specific pathologies.

In the last experimental chapter of the present thesis (Chapter 4), we tried to transfer the concept of spatial tapping to more complex motor control situations, i.e. bimanual coordination. Participants were asked to point to the corners of virtual geometrical shapes they had to mentally picture in their sagittal plan. We tested the possible effects of the nature of the motor task (successive vs. simultaneous movements), the shape complexity (by using different sorts of geometrical shapes, i.e. a line, a square, a circle), vision (eyes close vs. eyes open) and task difficulty (movement speed) on the spatial variability measured at movement endpoints. Our results revealed that the conditions manipulated affected the spatial variability measured at endpoint locations in two distinct ways: while the increase in cognitive complexity affected the mean spatial variability, the increase in motor demands affected the standard deviation of the spatial variability. Moreover, visual attention and grouping-like strategies entered into play depending on the task constraints to support a successful bi-manual coordination, i.e. to help reducing a motor error, and to help maintaining an acceptable context (well drawn geometrical shape) when the task became more difficult. Hence, the concepts related to the spatial-tapping task can be transferred to more complex situations to understand how multi-limb coordination takes place.

Overall, our results revealed that a simple motor task, namely the spatial-tapping task, provided the means to explore and to get sensitive measures of the executive functions and hence could be used as a replacement of complex neuropsychological works. Implications and limitations of the present research work are discussed in the next sections.

1.6 Implications and limitations of the present work

1.6.1 A new tool to assess the executive functions

In the present work we introduced the spatial-tapping task as a novel task to assess the executive functions. We showed that this task has the potential to overcome the difficulties that are commonly reported with classical executive tasks, i.e. task impurity and complexity (Burgess, 1997; Phillips, 1997; Rabbitt, 1997). Indeed, in the spatial-tapping task the same contents were used to assess the three executive functions, i.e. six visual targets arranged along a virtual circle. As a function of the temporal constraints, the task goal was implicitly turned towards specific constraints: maintaining accurate timing at slow tempi, inhibiting the motor response at intermediate tempi, switching between motor sets at fast tempi. Moreover, the correlations revealed with classical neuropsychological tasks were also very specific, which confirms that the spatial-tapping task was not complex in nature. A unique function was tapped as a function of the temporal constraints. It is also very important to note here that schizophrenia patients used a bad strategy according to the task constraints, i.e. switching in the place of updating. It is probable that this pattern of result was very specific to this population. This could be a sort of complexity issue visible in the spatial-tapping task. However, through the use of a specific spatio-temporal analysis that was extracted at an individual level, we were able to identify the strategy in use. Hence, even if some sorts of complexity can be seen in the spatial-tapping task, we dispose of the necessary measures to identify and control them.

The spatial-tapping task also allowed positing about the function served by inhibitory mechanisms. This executive function has a confusing status in the actual literature. While it is presented as the most highly inheritable factor that is the only factor common to the switching and the inhibiting tasks according to Miyake's view (Friedman et al., 2008; Friedman, Miyake, Robinson, & Hewitt, 2011; Miyake & Friedman, 2012), this function was completely left out in cognitive control studies (Colzato, Waszak, Nieuwenhuis, Posthuma, & Hommel, 2010; Cools, 2006). In the spatial-tapping task, two sorts of inhibitory mechanisms were revealed: cognitive inhibition, i.e. the ability two transition from a high-level strategy of motor control (event-based timing) to another one (emergent timing), and motor inhibition, i.e. the ability to produce a motor response according to a specific motor delay. It is the case that inhibition seen as a common factor could refer to the motor level. Indeed, in the study in which elderly participants were compared to young and mature controls, motor inhibition was required but not necessary at all tempi, hence affecting in some secondary ways the updating and the switching functions. By contrast, cognitive inhibition was required only in the intermediate phase of the task (phase 2), when the temporal constraints began pressuring the subjects to start anticipating forthcoming events. There are certainly tight relationships between motor inhibition and cognitive inhibition. Indeed, elderly participants had the tendency to produce too fast actions and were using compensating mechanisms in order to retain this too fast production. Hence, it is probable that since they had no more reasons to use these compensatory mechanisms, because the environmental constraints pressured them to go faster (phase 2), they stopped compensating, leading them to impaired performances in the inhibiting high-level function. Hence, we suggest that motor inhibition could constitute a common factor between the three high-level executive functions of updating, switching and inhibition. We further suggest that cognitive level of inhibition should be taken into account as an executive function per se, which could serve the specific role of inhibiting a routine according to task instructions. Because, the spatial-tapping task was able to provide measures for each specific function and for each individual subjects (as seen with the correlation with classical tasks), we suggest that the task could be used in clinical settings in replacement of classical complex tasks. Nevertheless, some remaining work is required. Indeed, we should dissociate more clearly between the cognitive and motor levels in the task and their relationships with the dependent measures used. We should probably compare more neuropsychological tasks than just the three to each function and sub-function. We should test whether the task could be transferred to smart technologies (e.g. i-pads) with all performance measures being automatically generated for clinical facilities.

1.6.2 Role of the cerebellum in the executive functioning

The executive functions have been considered a long while as depending upon frontal mechanisms (Luria, 1966; Norman & Shallice, 1986). Today, there is growing evidence that sub-cortical functions are also involved in the executive functioning. In recent models of executive functioning, a focus has been set on the role of the basal ganglia in the executive functioning (Cools, 2011; Miyake & Friedman, 2012). Our results further highlighted the role played by the cerebellum in the executive functioning. The implication of this sub-cortical structure in the executive functions has already been established in the literature, however, the nature of cerebellar involvement is not well understood (Bellebaum & Daum, 2007; Timmann & Daum, 2007). At the light of our results, we suggest that the cerebellum could first play the role of a pacemaker in executive control (Ackermann, Grber, Hertrich, & Daum, 1997; Keele & Ivry, 1990; Trenkner, Smith, & Segil, 1984). Indeed, in the motor control domain, the cerebellum is more expected to intervenes in tasks that require accurate timing, such as finger tapping tasks as compared to tasks in which the timing is treated secondarily, e.g. in circle drawing tasks (Ivry & Spencer, 2004; Ivry, Spencer, Zelaznik, & Diedrichsen, 2002; Spencer & Ivry, 2005; Spencer, Zelaznik, Diedrichsen, & Ivry, 2003). In the spatial-tapping task, the task resembled a finger tapping task at slow tempi and a circle drawing task at fast tempi. At slow tempi, updating strategies were required to maintain accurate timing while at fast tempi switching strategies were required to produce a smooth action pattern. Accordingly, another potential role for the cerebellum in the executive functions could be to provide the necessary brain circuitry to allow setting up the correct updating strategies. Indeed, such strategies require holding a referential item in long-term memory, and concurrently to maintain an active representation of the results of the current action produced for comparison to the referential. Both the cerebellum and hippocampe regions have been shown in the literature to largely contribute to the setting up of updating strategies (Gluck, Allen, Myers, & Thompson, 2001) but also to the encoding of information in long-term memory (Andreasen et al., 1995; Ito, 1986; Maren & Baudry, 1995). The cerebellum could in particular play the role of reinforcing and conditioning discrete behavioral responses (e.g. updating of the current action), while the hippocampus would be involve in activating a memory that is more explicit, experiential and time-independent, e.g. to maintain the referential available (Thompson & Kim, 1996). Overall, we suggest that the cerebellum could play a core role in the executive functioning and more particularly in the updating mechanisms. It could be interesting for future research to test patients suffering from cerebellar and striatal diseases with the spatial-tapping task.

1.7 Conclusion

The executive functions are commonly described as the abilities to plan, coordinate and execute our daily activities and behaviors. Frontal patients were the first to show disabilities in these functions. More specifically, patients were not impaired to produce simple motor tasks or single motor-sets but were in difficulty to produce sequences of ordered actions. Moreover, patients seemed to have changed personality, showed more impulsive behaviors, and were found to suffer from emotional deregulation. These observations conducted clinician and researcher to infer than the functions served by the frontal lobes were high-level in nature, allowing the control of regulation of complex activities and determining the basis of one's personality (Luria, 1966). This initial assumption led researchers and clinicians to develop complex tasks to reveal such complex functions, e.g. WSCT, Tower of London, etc. (Milner, 1963; Shallice, 1982). This deductive approach led the field to suffer from a number of difficulties: (1) the tasks were shown to lack of construct validity, (2) to be impure, (3) to lack of specificity and to be too complex (Burgess, 1997; Phillips, 1997; Rabbitt, 1997). An analysis of the commonalities and differences underlying the complex task led however researchers to draw clearer assumptions (Miyake et al., 2000). Multiple executive functions that were independent from each other were revealed, i.e. the switching-specific and updating-specific functions (Miyake & Friedman, 2012). A common factor between these functions, namely inhibition, was also described (Friedman et al., 2008, 2011). Potential relationships between the executive functions were also stated: inhibition and switching seem to depend on each other. Indeed, switching abilities were broadly defined as the capacities to generate a routine behavior and then, to switch from a routine to another one. In the other way, inhibition was defined as the ability to inhibit a routine behavior. Inhibition could also play the role of avoiding switching to put in place a more elaborate strategy dependent upon updating strategies, and in relation with past experiences (Miyake & Friedman, 2012; O'Reilly & Frank, 2006). Furthermore, through years of studies of the executive functioning it was shown that the frontal lobes were not the unique cerebral structures involved in executive functioning. In particular, fronto-striatal networks were shown to play an important role in the executive functioning (Cools, 2011; Miyake & Friedman, 2012). Finally, while knowledge about the executive functions is growing in the last decade, there are remaining difficulties that are especially related to the assessment tools (e.g. Charlot & Feyereisen, 2005). No paradigm has yet been proposed in the literature. Providing such task was the main objective of the current thesis work.

Our main assumption was that simple motor tasks could be used in replacement of complex reasoning tasks to assess the executive functioning. Indeed, although task could seem easy to produce, they do rely on high-level strategies. For example, simple tapping tasks have been found to engage updating like-mechanisms while circle drawing tasks have been found to engage switching-like mechanisms. In order to provide a single paradigm to assess the executive functions, we designed a hybrid of finger-tapping and circle-drawing tasks, namely, the spatial-tapping task. In this task, participants were asked to produce finger taps on six targets arranged as a circle, at distinct tempi. This task, in which simple actions are executed the one after the other, hence requiring motor planning, was found to resemble finger tapping at slow tempi, and circle drawing at faster tempi. Moreover, at intermediate tempi, inhibition mechanisms entered into play to maintain the tasks as a finger-tapping task while the temporal pressure encouraged participants to go faster, and hence to start drawing circles. We also reported data suggesting that the task was dependent upon updating mechanisms at slow tempi, inhibition mechanisms at intermediate tempi and switching mechanisms at fast tempi. Indeed, significant and specific correlations with classical tasks and the spatial-tapping tasks were revealed as a function of tempo changes. Psychological mechanisms such as attention and conscious perception were seen to be involved in the definition of the task context independently of the temporal constraints. Attention helped producing discrete actions while conscious perception through core binding functions helped produce more circular trajectories. These results demonstrate that the task could be used in clinical settings to assess each executive function in a specific way.

Our results also allowed us to suggest some theoretical assumptions about the executive functioning. First, two sorts of inhibitory mechanisms were revealed in the task. Inhibition may concern a single motor action (motor inhibition), and may concern the transition from one executive strategy to another (cognitive inhibition). It is probable that the common factor between the three executive strategies of updating, switching and cognitive inhibition is motor inhibition. Second, we infer that two distinct subcortical mechanisms seem to play a crucial role in the executive functioning: the cerebellum, and the basal ganglia. Indeed, in the motor control literature, it has been shown that the cerebellum intervenes especially in finger tapping tasks, while the basal ganglia intervenes essentially in circle drawing tasks. Accordingly, we suggest here that the specificities related to the executive functions could be due to the involvement of specific subcortical regions as a function of task goal. Updating strategies could depend upon the cerebellum while switching strategies could depend upon the basal ganglia. These two structures were shown to subserve the specific roles of reinforcing abstract stimulus-response associations (cerebellum, updating function) vs. reinforcing more concrete stimulus-outcome associations (striatum, switching functions). Hence, we assume here that specific subcortical structures might be involved as a function of task demands. In the light of our experimental results, task demands could be defined as the ability to produce a discrete action in a predictive manner (updating function), vs. to produce a continuous action in which the trajectories are planned primarily, i.e. time corrections are applied secondarily (switching functions). Thirdly, we revealed that psychological processes such as attention and conscious perception helped to define the context without inferring directly on the underlying executive mechanisms. We suggest that these processes helped maintaining active the task goal to support the global perception. While attention may be important to better define the context in the case of updating, conscious perception through his binding function could be an optimizer of the switching function. Our main findings are summarized in table V.1. Finally, we showed that the concept of spatial-tapping per se could be used to study more complex situations that uni-manual tapping in the motor control domain, i.e. bi-manual coordination. Hence, we hope that the hybrid method of producing and planning actions both in space and in time rather than in time only (information-processing approach) or in space only (dynamical perspective), will be used in future studies for a better understanding of neuropsychological basis of the executive functions. We also propose that studying bi-manual situations and more complex ones (multi-limb coordination or social interaction) may be a powerful way to gain a better understanding of how executive strategies could be combined to deal with complex situations.

1.8 Future directions

For future directions, we promote first transdisciplinarity for future studies of the executive functions, i.e. between the fields of neuropsychology and the motor control domain. Within the motor control domain, we also hope to bridge the gap

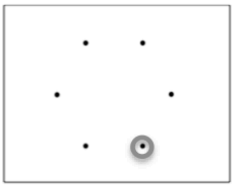
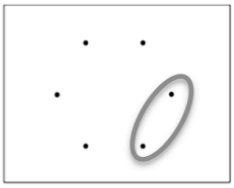
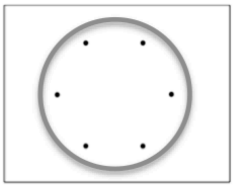
Task instructions	Synchrony		
Task constraints	Slow tempi (1200 to 900 ms)	Intermediate tempi (800 to 600 ms)	Fast tempi (500 to 300 ms)
Context definition			
Attention orienting	Focused attention	Anticipation of the next spatial location	Conscious perception (full anticipation)
Attention resources	+++	++	+
Spatial variability	Small	Slightly larger	Very large
Contact times	Long	Intermediate	Short
Motor actions	Discrete	Discrete/Continuous	Continuous
Implicit task goal	Timing accuracy	Timing accuracy	Gesture fluency
Timing mode of control	Event-based	Event-based	Emergent
Executive functions	Updating	Inhibiting	Switching
Secondary demands	Inhibiting the presence of irrelevant visual targets	Inhibiting the production of too fast actions	Timing accuracy
Main Brain mechanisms	Cerebellum Hippocampus (LTM)	Frontal lobes Cerebellum Basal ganglia	Basal ganglia
Norman and Shallice model (1986)	SAS	SAS	CS
Classification of Pathologies	??	Ageing (inhibition)	Schizophrenia (over-switching)

Table V.1: Main findings

between information-processing approaches and the more dynamical approach. In a more specific way, it could be interesting in future research using the spatial-tapping task to:

- Test the relationships between a larger number of classical tasks and the spatial-tapping tasks,
- Develop an application of the spatial-tapping task for an easy use in clinical settings,
- Assess Parkinsonian patients and cerebellar patients in the spatial-tapping task,
- Study the eye-hand dependencies going-on in the spatial-tapping task using for example an eye-tracker in combination to a motion capture display,
- Continue studying bimanual coordination, but also to try transferring the concept in an even more complex situation that bi-manual coordination, e.g. social interaction
- Evaluate the specific impact of motor feedback (or proprioception) in the spatial-tapping task,
- Study whether learning to patients or healthy subjects to coordinate actions between them could have beneficial effects on the executive functioning (cognitive remediation by movement).

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