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L'encodage de la forme par le toucher haptique.

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Université de Montréal
Faculté des études supérieures

Cette thèse intitulée:

L'encodage de la forme par le toucher haptique

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RÉSUMÉ

L'habileté humaine à reconnaître entre des formes par des mouvements exploratoires actifs dépend des signaux sensoriels originant des mécanorécepteurs cutanés et profonds, c'est le toucher haptique. Les mécanismes d'intégration de ces différents signaux en une perception unifiée sont peu connus. Avec l'idée d'étudier ces mécanismes centraux, nous avons développé un test de discrimination de formes basé sur l'exploration active d'un composant géométrique, les angles en deux dimensions (2D).

Les sujets devaient utiliser un mouvement d'aller et retour sur deux angles successifs afin d'identifier (paradigme de choix forcé) le plus grand entre un 90° (Standard) et un angle de comparaison entre 91° et 103°. Le seuil de discrimination (75%) était de 4.7° (fraction de Weber, 5%). La performance était peu affectée par les mouvements d'exploration, ni par des petits changements dans l'orientation générale. Exprimés en degré à l'épaule, ces seuils (moyenne=0.54°) étaient plus petits que les estimés précédemment publiés, suggérant ainsi une contribution additive des informations cutanées et proprioceptives.

Ces implications ont alors été testées directement par la suppression sélective de chacune, soit par anesthésie locale distale ou par déplacement des objets sous le doigt immobile des sujets (appareillage sous contrôle informatique). Les seuils étaient significativement augmentés par la suppression de chaque source, et au niveau du hasard en cas de suppression double, montrant ainsi la nature intégrative et haptique de ce type de tâche.

Finalement, l'impact des conditions d'exploration sur la performance a été évaluée. De manière consistante avec nos résultats précédents, nous montrons une diminution de performance lorsque les informations sensorielles cutanées ou périphériques sont affectées, confirmant une fois encore la nature haptique de la tâche. En revanche, nous n'avons pas retrouvé de différence significative entre les performances lorsque les explorations impliquent des mouvements distaux (poignet) versus proximaux (épaule). De manière intéressante, des informations au sujet des cadres de références centraux utilisés pour représenter les formes ont pu être obtenues en manipulant les mouvements d'exploration (délai entre les explorations de deux angles à comparer et direction du regard par rapport aux angles). En particulier, nous avons montré que les seuils étaient augmentés en diminuant le délai (de 15s à 5s) entre les explorations de deux objets à comparer, mais cet effet, présent pour des objets en position excentrique, disparaissait lorsque le regard (tête et yeux liés) était dirigé vers les objets (non visibles).

Deux modèles alternatifs pourraient rendre compte de ces résultats. 1) Tout d'abord, les informations seraient représentées dans un cadre de référence égocentré, basé sur les coordonnées des yeux et des mains. Avec le temps, une réorganisation orienterait les informations vers un cadre de référence allocentrique, et possiblement centré sur les objets. 2) Les informations haptiques seraient codées dans deux cadres de référence égocentriques, un visuel (à longue latence et centré sur le regard) et un moteur (de courte durée et centré sur la main). Certaines expériences pouvant trancher entre ces deux modèles sont par la suite suggérées.

MOTS CLEFS: Main, tactile, proprioceptif, somatosensoriel, représentation, pariétal, humain, liage, egocentré, allocentré, Haptique.

ABSTRACT

The human ability to recognize objects on the basis of their shape, as defined by active exploratory movements, is dependent on sensory feedback from mechanoreceptors located both in the skin and in deep structures (haptic feedback). Surprisingly, we have little information about the mechanisms for integrating these different signals into a single sensory percept. With the eventual aim of studying the underlying central neural mechanisms, we developed a shape discrimination test that required active exploration of objects, but was restricted to one component of shape, two-dimensional (2D) angles.

Subjects used a to-and-fro movement to scan a pair of angles with the index finger of the outstretched arm (standard 90°; comparison 91 - 103°), identifying the larger of each pair (two alternative-forced choice paradigm). Discrimination threshold (75% correct) was 4.7°, giving a Weber fraction of 5%. Performance was relatively independent of the exploratory movements, and was not modified by slightly rotating the orientation of one angle in the pair. Both cutaneous (digit) and proprioceptive (shoulder) feedback likely contributed to the results, since thresholds expressed in terms of shoulder angle were lower (mean 0.54°) than previous estimates of position sense at the shoulder.

The importance of cutaneous and proprioceptive feedback for 2-D angle discrimination was subsequently investigated by selectively suppressing each source of afferent feedback, respectively, digital anaesthesia and passive displacement of angles under the immobile digit using a computer-controlled device. Discrimination threshold was significantly increased in both cases, and performance was only at the chance level when both sources of feedback were suppressed. Thus, 2-D angle discrimination is an integrative task, and truly haptic in nature.

Finally, we studied the impact of the exploratory conditions on task performance. We showed that changes in the quality of either cutaneous or proprioceptive feedback modified task performance, consistent with the haptic nature of the task. Discrimination threshold was, moreover, similar for distal (wrist) and proximal (shoulder) articulations. Insight into the central frames of reference underlying haptic shape was obtained by modifying the scanning conditions (delay between successive scans, direction of gaze relative to the angles). Interestingly, when the angles were explored in an eccentric position (60° to the right), threshold was increased when the delay between scans was decreased from 15 to 5 s. The increase disappeared when gaze (head + eyes) was turned in the direction of the (unseen) angles.

Two alternate models that could account for the results are discussed. 1) The information is initially represented in an egocentric frame of reference, using both hand and eye coordinates. With time, a remapping of the sensory information into an allocentric (possibly object-centred) frame of reference occurs. 2) The haptic information is coded in two egocentric frames of reference, one visual (long lasting; gaze-centred) and one motor (short lasting; hand-centred). Further experiments are suggested to distinguish between these two models.

KEY WORDS: Hand, tactile, proprioceptive, somatosensory, frame of reference, parietal, human, binding, egocentric, allocentric, haptic.

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CR	Champ Récepteur
FNM	Fuseau Neuromusculaire
IRED	InfraRed Emitting Diode
LED	Light Emitting Diode
MCP	Métacarpophalangia
MSSM	Modified-Standard-Standard-Modified
OTG	Organe Tendineux de Golgi
PC	Corpuscule de Pacini
PV	Aire Pariéto-Ventrale
RA	Adaptation Rapide
SI	Cortex Somatosensoriel Primaire
SII	Cortex Somatosensoriel Secondaire
SA	Adaptation Lente
SEM	Standard Error of the Mean
VPL	Ventro Postérieur Latéral

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CHAPITRE I - INTRODUCTION

La somesthésie est un sens essentiel, qui est impliqué autant dans la perception que dans le contrôle moteur. Ainsi, la somesthésie est indissociable de la préhension, de l'exploration et de la manipulation d'objets, mais aussi du contrôle de l'équilibre, de la posture et de la locomotion, ainsi que de tous les mouvements d'orientation du regard et de l'audition. Au point de vue neurophysiologique, il s'agit donc d'un modèle privilégié de l'intégration sensorielle et de la coordination sensorimotrice. Etant donné la difficulté d'aborder en même temps toute la richesse de ces phénomènes, une première étape consiste toutefois à décomposer la somesthésie en habiletés plus élémentaires. En particulier, nous nous intéresserons dans cette thèse aux habiletés sous-tendant la perception des formes explorées par le toucher, sans vision. Trois questions spécifiques structureront notre approche de cette thématique : *Qu'est-ce qu'une forme ? Quelles sont les informations somesthésiques disponibles au sujet de la forme? Comment les formes explorées par le toucher sont-elles représentées ?*

Qu'est-ce qu'une forme ? Ainsi que noté par Goodwin et al. (1991), établir une définition n'est pas simple, car une forme comporte par nature de nombreuses dimensions. En conséquence, la stéréognosie, c'est-à-dire la capacité de perception des formes, diffère probablement de la sensation d'attributs plus élémentaires, comme par exemple la texture qui comporte deux à trois dimensions au maximum (Hollins et al., 1993). Le dictionnaire (Oxford English Dictionary) nous indique que le forme est « ...le contour d'un objet », il existe cependant plusieurs attributs définissant un contour, tel que sa courbure, la structure de son relief, son orientation et ses dimensions. Comme montré par Roland (1987), les mécanismes neurophysiologiques varient en fonction des attributs recherchés. Le premier objectif est donc d'établir une définition de travail pour la forme (chapitre 2.1), ainsi que l'opérationnalisation d'une tâche perceptuelle (chapitres 4).

Quelles sont les informations somesthésiques disponibles au sujet de la forme? Dans un ouvrage classique, Gibson (1966) propose de séparer les habiletés tactiles selon qu'elles se basent 1) uniquement sur des informations cutanées (toucher cutané); 2) sur une combinaison d'informations tactiles et proprioceptives (toucher haptique); et 3) sur une combinaison d'informations haptiques avec un sens de l'effort généré (toucher actif). Suivant cette idée, nous utiliserons l'expression de *toucher haptique* pour référer à l'utilisation combinée d'informations cutanées et proprioceptives. Cette habileté étant particulièrement pertinente pour la reconnaissance d'objets et l'utilisation d'outils, cela justifie ainsi le terme haptique, du grec 'haptikos' signifiant préhensible. Une recension des écrits sera nécessaire afin de déterminer quels récepteurs pourraient effectivement être impliqués dans ce toucher haptique (chapitre 2.2). En effet, nous verrons qu'aucune preuve antérieure de l'implication du proprioceptif à la stéréognosie n'a été publiée, malgré que cela constitue une croyance généralement acceptée. Un objectif majeur de la thèse sera donc de fournir une confirmation expérimentale de cette croyance (chapitre 5), sur laquelle se base notre définition du toucher haptique.

Comment les formes explorées par le toucher sont-elles représentées ? Finalement, la question la plus intéressante reste de déterminer la nature des processus haptiques impliqués dans la stéréognosie. Plusieurs éléments sont fournis par la littérature : d'une part la neurophysiologie apporte plusieurs informations sur la localisation et la structuration des représentations somesthésiques (chapitre 2.3); et d'autre part les études psychophysiques apportent plusieurs informations intéressantes au niveau des cadres de références utilisés pour représenter les formes haptiques (chapitre 2.4). En particulier, nous verrons que ces dernières études fournissent un cadre théorique important pour analyser les résultats neurophysiologiques et poser des hypothèses sur le traitement haptique, que nous testerons par la suite (chapitre 6).

CHAPITRE II - RECENSION DES ÉCRITS

Si la somesthésie a été et reste un sujet largement exploré, en revanche la stéréognosie haptique telle que définie dans l'introduction générale a reçu peu d'attention jusqu'ici. Dans le but d'établir des hypothèses testables, cette revue enchaînera les trois étapes suivantes : 1) choisir une définition de la forme permettant l'étude spécifique de la stéréognosie haptique; 2) établir les sources d'informations disponibles pour la perception haptique des formes; et 3) faire ressortir les évidences publiées concernant la nature des processus haptiques, du point de vue neurophysiologique et psychophysique.

2. 1 DEFINITION ET CHOIX DES FORMES

Tel qu'indiqué dans l'introduction générale, la définition de la forme constitue une question à part entière. En effet, il existe plusieurs types de formes, selon qu'elles soient constituées de courbures locales, de structures en relief (par exemple des lettres en Braille), de segments plats, et en fonction de la façon dont ces composantes sont associées (intersection ou courbure progressive, orientation des composants élémentaires les uns par rapport aux autres). En conséquence, il existe possiblement plusieurs habiletés différentes regroupées sous le terme stéréognosie, associées plus ou moins spécifiquement à chacun de ces types de formes. Un choix attentif dans la définition de la forme employée est donc crucial car le type de forme utilisé va contraindre les traits caractéristiques analysables, la nature des informations disponibles, et potentiellement la nature du traitement central de ces informations. Ainsi, plusieurs études (Roland et Mortensen, 1987, Roland, 1987, O'Sullivan et al. 1994, Roland et al. 1998) ont montré l'implication d'aires cérébrales différentes selon que les stimuli à examiner soient microgéométrique (par exemple des textures) versus macrogéométrique (par exemple des longueurs ou des formes). Une subdivision analogue (géométrie micro- vs macro- spatiale) a par ailleurs été proposée par Stoesz et al. (2003), qui montrent l'implication sélective de structures visuelles potentiellement impliqués dans l'imagerie mentale de la géométrie macrospatiale (voir chapitre 2.3). Notre premier critère pour choisir une définition de la forme est donc que les formes ainsi définies ne soient pas limitées à la microgéométrie. La limite entre micro- et macrogéométrie n'est toutefois pas claire. Cependant, l'analyse des structures proposées comme microgéométrique (ou géométrie microspatiale) montre qu'un simple contact cutané suffit pour les explorer, alors que les structures macrogéométriques génèrent également des informations proprioceptives. Ainsi, la présence d'informations proprioceptives est un des facteurs possiblement impliqués dans la distinction entre microgéométrie et macrogéométrie. Le second critère retenu est donc que les objets choisis permettent l'activation de chacune de ces deux sous-modalités. Finalement, un dernier critère est de fabriquer des formes les plus simples possibles, ce qui facilite l'analyse des performances. Ces critères vont donc aider à choisir un modèle d'étude parmi les différentes formes possibles, revues ci-dessous.

2.1.1 Cas des formes courbes

Une première approche consiste à définir la forme comme l'ensemble des courbures locales, ce qui s'applique très bien aux objets symétriques comme une sphère, une ellipse, ou tout autre objet similaire ne présentant pas de structuration en plusieurs parties. Ce type de forme semble analysé comme une sensation élémentaire comportant peu de dimension. En effet, lorsque des sujets doivent discriminer entre des séries d'objet constitués d'une courbure unique variant en amplitude et en largeur (Louw et al. 2000, 2002, Nefs et al., 2001), alors les performances sont liées au ratio amplitude/largeur selon une loi valable quelle que soit la taille des objets (de 1 micromètre à un mètre). Il s'agit d'un avantage en terme de réduction de la complexité de l'objet d'analyse, mais également un inconvénient si le but de la recherche est d'étudier la stéréognosie, c'est-à-dire la perception d'une forme structurée à partir de ses sous-parties. De plus, il est également possible que les informations proprioceptives ne soient pas utilisées pour ce type d'objet, puisqu'il n'y a pas de changement qualitatif des performances entre le cas du mètre (où les informations proviennent possiblement des modalités proprioceptive et cutanée) et le cas du micromètre (sans information proprioceptive possible). Ce type de forme n'est donc pas a priori un choix optimal pour l'étude de la stéréognosie haptique.

2.1.2 Cas des structures en relief

Une seconde façon de constituer des formes passe par l'établissement de structures en relief comme des lignes ou des points. Un cas particulièrement intéressant vient de l'exemple des lettres en Braille. Ces lettres sont constituées de points dont la disposition spatiale constitue un code représentant en relief les différentes lettres de l'alphabet, utilisé pour la lecture par les aveugles. La question de savoir si la stéréognosie cutanée diffère ou est identique à la stéréognosie haptique n'est toutefois pas claire. Ainsi, ce type de stimuli ne semble pas activer les mêmes aires que les formes plus larges (macrogéométriques) impliquant des mouvements d'exploration et/ou des informations proprioceptives (Roland et Mortensen, 1987, Roland, 1987, O'Sullivan et al. 1994, Roland et al. 1998, Stoesz et al., 2003). Finalement, l'examen de ce type de forme ne génère probablement aucune information proprioceptive, ce qui les disqualifie au regard des critères exprimés ci-dessus. La comparaison entre la stéréognosie haptique et la stéréognosie cutanée serait toutefois un prolongement intéressant des recherches présentées dans cette thèse.

2.1.3 Cas des barres orientées

L'utilisation de lignes présentant différentes orientations, taille et espacement est courante dans le cadre des études portant sur la perception de textures (Darian-Smith et Oke, 1980, Lamb, 1983, Sathian et al., 1989, Connors et al., 1990, Sinclair et Burton, 1991, Chapman et al., 2002). Une autre utilisation consiste à s'intéresser à la perception de l'orientation ou de la longueur de ces lignes (Van Boven et Johnson, 1994, Sathian et al. 1997, 2001, 2002, Hsiao, et al. 2002, Kappers, 2003). Du point de vue psychophysique, les performances de discrimination d'orientation présentent la même métrique que la discrimination d'angle –une des structurations possibles de la forme (Fasse et al. 2000). Du point de vue neurophysiologique, des activations hémodynamiques similaires sont retrouvées pour des discriminations de formes macrogéométriques ou de longueur (Roland et al., 1998). Ainsi, le traitement central de l'orientation et de la longueur de barres pourrait constituer un bon modèle pour l'étude des processus centraux liés aux formes macrogéométriques. De plus, l'orientation des parties d'un objet est probablement une composante fondamentale de la forme, qui pourrait donc structurer le traitement des informations tactiles d'une façon similaire à ce qui se passe dans les aires visuelles (Hsiao et al., 2002). Cependant, l'orientation des parties d'un objet ne constitue qu'une information élémentaire, alors que nous recherchons plutôt la nature des traitements spécifiques à la stéréognosie, qui pourraient différer du traitement plus simple des orientations ou de la taille des segments constitutifs de la forme. Enfin, les informations sur l'orientation d'une barre sont détectables par un simple toucher cutané, ce qui complique la séparation des habiletés vers la microgéométrie de celles tournées vers la macrogéométrie. En conséquence, il apparaît préférable de choisir un niveau légèrement supérieur en terme de complexité.

2.1.4 Cas des angles d'intersection

Finalement, une dernière solution, proposé par Ullman (1995) dans le cadre de travaux sur le système visuel, consiste à définir la forme comme une série d'arête (ou de surface) et les relations spatiales (angle d'intersection) entre elles. Bien que cette définition restreigne la stéréognosie à certains types d'objets particuliers, elle présente plusieurs intérêts. Tout d'abord, ce type de forme est fonctionnellement indépendant de chacune de ses parties. Autrement dit, connaître l'orientation d'une des surfaces d'un objet par un simple contact local (structuration microgéométrique) ne permet pas de connaître la structuration entre les parties de cet objet (structure macrogéométrique). Un second avantage est que l'encodage de ce type de forme peut se baser à la fois sur des informations cutanées et des informations proprioceptives. En effet, toutes les caractéristiques macrogéométriques (orientation et longueur des segments, angles d'intersection, positions relatives dans l'espace des différentes parties d'un objet) activent potentiellement les récepteurs cutanés et proprioceptifs, respectivement par contact et par contrainte des positions du doigt explorant la forme. Finalement, ce type de forme peut être grandement simplifié, en utilisant des objets en deux dimensions composé de deux barres de longueur fixe dont les orientations respectives forment un angle d'intersection. Ce type de forme répond alors à l'ensemble de nos critères de sélection exprimé plus haut, et est donc retenu comme modèle de la forme dans nos études sur la stéréognosie haptique.

2.2 LES SOURCES D'INFORMATIONS PERIPHERIQUES

Suivant sa définition, le toucher haptique peut se baser sur une multitude d'informations, en provenance soit des mécanorécepteurs cutanés, soit des mécanorécepteurs proprioceptifs. A notre connaissance, il n'existe toutefois aucune évidence publiée antérieurement de cette double implication dans le cadre de la stéréognosie. Dans cette partie, les mécanorécepteurs potentiellement impliqués seront donc revus, dans le but de déterminer les évidences supportant leur implication à la stéréognosie haptique.

2.2.1 Mécanorécepteurs cutanés

Il existe une grande variété de mécanorécepteurs cutanés dont l'importance varie en fonction du type de peau, notamment les surfaces cutanées glabres vs. poilues (Vallbo et al., 1995). Dans le contexte de l'exploration tactile, Lederman et Klatzky (1987) ont montré que les sujets humains utilisent des mouvements spécifiques en fonction des attributs qui sont recherchés. L'analyse de leurs observations montre qu'aucun des mouvements naturellement choisis ne passe par l'utilisation de la peau poilue, suggérant ainsi que la peau glabre, et en particulier au niveau des mains, constitue en soi une spécialisation du système somatosensoriel tourné vers l'examen tactile. En conséquence, nous nous concentrerons dans cette section sur les mécanorécepteurs présents dans la peau glabre des mains. Il faut toutefois noter que la peau poilue pourrait jouer également un rôle, notamment au niveau de la proprioception.

Les études de microneurographie ont permis de séparer quatre types de fibres afférentes du système somesthésique en provenance de la peau glabre humaine: les RA et les PC, récepteurs à adaptation rapide ; les SAI et les SAII, à adaptation lente. Selon toute vraisemblance, ces fibres seraient respectivement associées aux récepteurs de Meissner, aux corpuscules de Pacini, aux disques de Merkel, et aux terminaisons de Ruffini. De façon intéressante, chacun de ces quatre types de mécanorécepteur cutané semble constituer une voie spécifique, ou canal d'information, dont les stimuli préférentiels diffèrent (Mountcastle et al., 1972, Vallbo et Johansson, 1984). Au point de vue anatomique, des études récentes suggèrent que les fibres de même type tendent à se regrouper en faisceau, puisque les noeuds de Ranvier (point de régénération des potentiels d'actions propres aux fibres myélinisées) des fibres de même type seraient colocalisés (Hallin et Wu, 2001). Au niveau cortical, des évidences indiquent également une séparation des projections des récepteurs de type I, qui projettent sur des bandes corticales alternées pour les RA et les SAI au niveau de l'aire 3b (Sur et al., 1984). Finalement, les résultats montrant qu'il est possible d'adapter un canal cutané par stimulation prolongée sans observer d'adaptation des autres canaux cutanés (Gescheider et al., 1979, Hollins et al ., 1990), l'observation des effets différentiels de l'âge sur les capacités tactiles -et en particulier une augmentation différentielle du seuil de détection des stimuli activant les PC (Verrillo, 1979, Gescheider et al., 1994), sont autant d'indications que les récepteurs cutanés forment effectivement des canaux distincts (revus dans Gescheider et al., 2004).

- Les RA montrent une spécialisation pour certaines propriétés de surface des objets, en particulier grâce à leur adaptation rapide (Johansson, 1978). Ils amènent notamment des informations sur la friction, et donc sur le glissement d'objets tenus en main (Johnson et al., 2001). Ce canal pourrait alors sous-tendre le contrôle des forces de préhension nécessaires pour la manipulation d'objets (Johansson et al., 1992, Monzée et al., 2003), et donc l'exploration de la forme.

- Les SAI semblent spécialisés pour les caractéristiques spatiales, tel que les courbures locales (Goodwin et Wheat, 1992), l'orientation de barres (Dodson et al., 1998), la structure spatiale d'une texture (Connor et Johnson, 1992) ou encore la forme de lettres en Braille (Phillips et al., 1990). De plus, les champs récepteurs des neurones corticaux de l'aire 3b sur lesquels ces récepteurs projettent montrent une sensibilité spatio-temporelle (coexistence de zones excitatrices et inhibitrices dont les activations des succèdent à travers le temps) qui leur permettent de représenter les caractéristiques spatiales indépendamment de la vitesse d'application (Di Carlo et Johnson, 1999). Les mêmes processus expliqueraient également la sensibilité de ces neurones à l'orientation et à la direction d'un stimulus mobile sur la peau (Hsiao et al., 2002). En conséquence, ces récepteurs semblent particulièrement bien adaptés pour fournir des informations sur les caractéristiques spatiales locales des objets, et donc fournir des informations importantes à la stéréognosie.

- Les SAII semblent préférentiellement activés par les forces tangentielles (étirements latéraux) appliquées sur la peau, ce qui leur permettrait un rôle important dans l'encodage des informations proprioceptives permettant le contrôle fin des doigts (Edin et Johansson, 1995, revus dans Johnson et al., 2000). En revanche, ces mêmes propriétés rendent improbable la contribution des SAII à la perception des structures microspatiales, notamment les courbures (Goodwin et al., 1997).

- Au contraire des SAII, les PC sont extrêmement sensibles, au point qu'à peu près tous les types de stimulation mécaniques les activent (Mountcastle et al., 1972). En conséquence, les interprétations proposées varient grandement, de détecteur de force (Adrian et al. 1929, cité dans Johnson, 2000) –hypothèse relativement abandonnée puisque cette sensibilité à la force disparaît dans le cas de contact soutenu, jusqu'à l'idée récemment émise d'une implication spécifique pour l'utilisation d'outils (revus dans Johnson et al., 2000, 2001). En effet, ces derniers auteurs argumentent que les PC sont les seuls à être sensibles aux vibrations propagées par les tissus, tel que celles causée par l'utilisation d'un outil pour l'exploration distante. Il pourrait donc s'agir d'une spécialisation pour l'exploration distante, important d'un point de vue évolutif pour la détection des vibrations émises par l'approche d'un prédateur.

2.2.2 Mécanorécepteurs proprioceptifs

Le domaine proprioceptif peut se baser sur une large gamme de mécanorécepteurs, incluant les récepteurs intramusculaires (fuseaux neuromusculaires -FNM), les organes tendineux de Golgi (OTG), les récepteurs articulaires, ainsi que les récepteurs cutanés et notamment les SAII (voir section précédente et Edin, 1992). Actuellement, la plupart des auteurs s'accordent pour attribuer un rôle central aux récepteurs intramusculaires. La contribution des autres récepteurs ne peut toutefois pas être exclue.

Plusieurs évidences supportent l'implication des FNM à la proprioception, c'est-à-dire à la capacité de connaître les positions et mouvements de son propre corps. Ainsi, des vibrations tendineuses connues pour activer les FNM amènent des illusions de mouvement (Goodwin et al., 1972), proportionnelles à l'écart entre la stimulation d'un agoniste et d'un antagoniste (Gilhodes et al., 1986). De plus, les tests du sens de la position montrent une précision proportionnelle aux changements de longueurs des muscles à travers plusieurs articulations, indiquant le rôle crucial de ces récepteurs à la perception (Hall et McCloskey, 1983). Au point de vue anatomique, les fuseaux neuromusculaires sont constitués de plusieurs parties, classiquement séparée en terminaisons primaires associées à l'innervation Ia (sensibilité à la longueur et à la vitesse d'étirement du muscle) et secondaires associées à l'innervation II (sensibilité à la longueur du muscle, et donc aux positions). Les FNM sont donc capables d'encoder à la fois la position et les mouvements des membres. Finalement, la sensibilité des FNM est sous le contrôle direct d'un système spécifique, l'innervation par des fibres motrices gamma (mais aussi quelques bêta innervant à la fois les fibres extrafusales motrices et intrafusales des FNM), qui permet d'ajuster la sensibilité statique et dynamique des FNM. Ces propriétés, ainsi que les difficultés de tester ces propriétés in vivo chez l'homme en dehors du cas de mouvement lent (Prochazka et Hulliger, 1998), aboutissent toutefois à un schéma d'ensemble difficile à appréhender (Mattews, 1988).

Malgré cette complexité, plusieurs études de modélisation ont montré que le signal des FNM, pris en tant que codage de groupe, permet effectivement de rendre compte de la sensibilité kinesthésique. Ainsi, une précision comparable du sens de la position est prédite pour l'articulation de l'épaule par des modèles indépendants en prenant soit la distribution des FNM à travers les muscles (Scott et Loeb, 1994), soit la distribution des erreurs pour une tâche de pointage sans vision lors d'un mouvement multi-articulaire (Van Beers et al., 1998). Une autre modélisation montre le lien entre la direction d'une force statique exercée au niveau de la main et le signal de population des FNM (Roll et Gilhodes, 1995) pris à travers plusieurs muscles. Dans ce dernier modèle, chaque muscle présente un vecteur préférentiel, considéré comme une combinaison des sensibilités des fibres FNM individuelles. Un modèle d'addition vectoriel, similaire à celui proposé par l'équipe de Georgopoulos pour rendre compte de l'association entre les décharges neurales des cortex moteurs et de la direction des mouvements (Gergopoulos et al., 1982, Kalaska et al., 1983), rend alors très bien compte de la direction réelle. Récemment, ce modèle s'est révélé efficace également dans le codage du mouvement, en particulier la direction tangentielle au mouvement instantané (Bergenheim et al., 2000, Roll et al., 2000). Ainsi, malgré la complexité des FNM, plusieurs indications suggèrent que ces récepteurs suffisent à rendre compte de la précision du sens de la position d'une part, et de la direction des mouvements d'autre part. Finalement, la corrélation entre la cinématique des mouvements et les signaux afférents enregistrés dans différents muscles montrent une contribution additive des FNM situé dans des muscles synergistes, qui rend effectivement compte de la cinématique du mouvement (Verschueren et al., 1998), ainsi que de la position (Cordo et al., 2002).

Longtemps pensés comme les principaux propriocepteurs, les récepteurs articulaires ont toutefois été peu à peu écartés. En effet, la sensibilité de ces récepteurs semble principalement liée aux positions extrêmes des articulations (Clark et al., 1989), et donc possiblement associé à un mécanisme de protection des articulations. La contribution de ces récepteurs ne peut toutefois pas être complètement négligée, puisqu'il est possible de détecter des mouvements aux articulations distales lorsque la contribution des récepteurs musculaires et cutanés est abolie (Gandevia et McCloskey, 1976). Finalement, l'injection d'anesthésique dans ces articulations mène également à une diminution partielle de la détection de mouvement, ce qui soutient l'implication, même mineure, de ces récepteurs à la proprioception (Ferrell et al. 1987; Clark et al. 1989).

Les organes tendineux de Golgi sont activés par la tension musculaire, surtout lorsque générée par une contraction (Jami, 1992). Ces récepteurs pourraient donc être impliqués dans la perception de la force produite, en relation avec une copie d'efférence des commandes motrices (Jones, 1994). De façon intéressante, Gregory et al. (2003) ont montré que les signaux des OTG augmentaient durant et après un exercice prolongé de contractions excentriques. Or, ce type d'exercice amène une augmentation de la tension musculaire passive, susceptible d'endommager les muscles (Whitehead et al., 2001). Ainsi, les OTG pourraient participer à un mécanisme de protection spécifique du tissu musculaire, tout comme les récepteurs articulaires pourraient participer à un mécanisme de protection des articulations.

Les récepteurs considérés comme cutanés peuvent également jouer un rôle dans la proprioception, ce qui est notamment suggéré par les déficits proprioceptifs affectant les grands brûlés (Moberg, 1983). Tout d'abord, les récepteurs SAII revus précédemment pourrait effectivement jouer un rôle, notamment du fait de la sensibilité aux étirements latéraux des SAII. Ces récepteurs pourraient ainsi expliquer en partie les résultats de Gandevia et al. (1976, 1983), qui montrent que la détection de mouvement imposé au niveau de la phalange distale de D3 ou D4 est en partie préservé même lorsque les muscles sont désengagés par une posture particulière (extension de tous les doigts excepté une flexion de l'interphalangienne proximale de D3 ou D4). Soutenant cette vue, l'étirement mécanique de la peau des doigts génère une illusion de mouvement (Edin et Johansson, 1995). Finalement, la peau poilue semble également en mesure de jouer un rôle important à la proprioception, puisqu'une stimulation électrique de ceux-ci donne lieu à des illusions kinesthésiques (Collins et Prochazka, 1996).

Ainsi, on voit que le toucher haptique peut se baser sur une multitude de récepteurs, qui transmettent des informations complexes, partiellement redondantes, et probablement assez bruitées par le contexte d'exploration tactile. Cependant, montrer que chacun des types de récepteurs peut être impliqué dans une tâche haptique ne suffit pas à démontrer effectivement cette implication. Un objectif important de cette thèse est donc de déterminer cette contribution, en particulier l'utilisation d'informations cutanées et proprioceptives durant une exploration de la forme des objets. Finalement, la complexité des signaux haptiques laisse entrevoir un traitement complexe au niveau central. Comme mentionné par Mattews (1988) au sujet des informations proprioceptives, des signaux complexes nécessitent probablement des traitements complexes.

2.3 NEUROPHYSIOLOGIE HAPTIQUE

Dans la partie précédente, il a été mis en évidence que plusieurs canaux d'informations, en partie distincts et en partie redondants, composent les voies afférentes du système somatosensoriel. Dans cette section, nous verrons les structures corticales impliquées dans la modulation et le traitement des informations sensorielles. Les études d'activation et de lésion indiquent un rôle prépondérant du lobe pariétal pour la stéréognosie haptique, en particulier suivant une voie dorsale depuis le sillon central (aires somatosensorielles primaires) jusqu'au sillon intra-pariétal (cortex pariétal postérieur). Il faut néanmoins tenir également compte de l'implication des lobes frontaux au contrôle et à la perception du mouvement, ainsi que des lobes temporaux/occipitaux pour leur rôle éventuel dans l'imagerie mentale des formes haptiques. Les évidences expérimentales suggèrent en effet que la stéréognosie haptique est difficilement dissociable du contrôle moteur d'une part, et de l'imagerie mentale d'autre part, une habileté possiblement visuelle par nature.

2.3.1 Modulation et structuration des informations afférentes

Les afférences cutanées et proprioceptives passent par des fibres myélinisées de gros diamètre (vitesse de conduction 35-70 m/s) et projettent aux noyaux cuneatus et gracilis de la colonne dorsale, avec des somatotopies séparées pour les modalités cutanées et proprioceptives (Jones et Powell, 1969a,b, 1970, Kaas et al., 1979, Jones et Friedman, 1982, Steriade et al., 1997, Jones 2002). Ces structures projettent elles-mêmes au thalamus puis au cortex, du VPL vers les structures somatosensorielles primaires (3b et 1 pour les afférences cutanées, 3a et 2 pour les afférences proprioceptives), et secondaires (SII, redéfinit en SII et PV selon Krubitzer et al., 1986, 1995, Disbrow et al., 2000). Un point important est que les structures sous-corticales, et particulièrement le thalamus, reçoivent également une très large proportion de projections réciproques depuis les aires corticales, ce qui en fait des lieux de modulation beaucoup plus que des simples relais des informations somatosensorielles vers le cortex (Steriade et al., 1997, Zang et Jones, 2004). Ce point devient évident lorsque sont examinés les effets de gating (modulation des informations somatosensorielles par l'occurrence d'un mouvement) d'une part, et d'autre part les expériences de plasticité des représentations corticales et sous-corticales en fonction de la nature et de la quantité de stimulations somatosensorielles.

L'idée d'une modulation des informations somatosensorielles afférentes est tout d'abord supportée par les évidences de gating d'origine centripète (c'est-à-dire causé par une interaction entre les informations périphériques). Ainsi, lorsqu'un sujet doit détecter une stimulation électrique sur le doigt, un mouvement imprédictible imposé à ce doigt provoque une augmentation importante du seuil de détection de ces stimuli (Williams et al., 1998, Williams et Chapman, 2000, 2002). Il existe également des évidences de gating d'origine centrifuge, c'est-à-dire causé par une ou des influences centrales. Ainsi, lorsque les sujets imaginent un mouvement sans le réaliser (Cheron et Borenstein, 1992, Kakigi et al., 1997), ou lorsque les cortex moteurs sont activés (probablement SMA) par stimulation magnétique transcranienne (Haggard et Whitford, 2004), alors une modulation de la transmission des informations sensorielles est observée. En conséquence, une variété de mécanismes semble dédiée à la modulation des informations somatosensorielles afférentes (Chapman, 1994).

Une modulation est également apparente dans la structure des CR corticaux et sous-corticaux. En effet, il est reconnu classiquement (Kalaska et Pomeranz, 1979, Merzenick et al., 1983, Kaas et al., 1983, Clark et al., 1989, Rencanzone et al., 1992a,b,c, revus dans Jones 2001) qu'une perte d'afférence amène une réorganisation au niveau cortical et sous-cortical des représentations somatotopiques (expansion/rétrécissement des représentations corporelles stimulés/déafférentées, différenciation/fusion des représentations somatiques stimulés de manière asynchrone/synchrone). De manière intéressante, une expérience d'anesthésie locale a montré qu'une partie au moins de cette réorganisation est quasi-instantanée, au niveau thalamique comme au niveau cortical (Nicolelis et al., 1993). Cela suggère donc que la structure des champs récepteurs (zone physique dans laquelle une stimulation provoque une réponse neurale) est en fait une propriété dynamique, largement structurée par les informations sensorielles elles-mêmes. Finalement, ce principe d'une structuration dynamique des CR a été proposé depuis longtemps pour rendre compte de la préservation des détails et de l'augmentation du contraste via un mécanisme d'inhibition latéral. En effet, il existe un fort degré de convergence à l'intérieur des voies afférentes au cortex somatosensoriels, ce qui devrait logiquement diminuer le rapport signal/bruit à chaque « relais » sous-cortical. Au contraire, une augmentation progressive du contraste semble la règle. Un mécanisme d'inhibition latéral pourrait alors expliquer ce résultat (Mountcastle et Darian-Smith, 1968). Dans ce schéma, l'information portée par chaque neurone est affiné par la suppression des corrélations entre neurones, ce qui aboutit à une augmentation du contraste (rapport signal/bruit) et une compression de l'information contenue par la population neurale en question. Ce schéma classique indique donc un rôle central à des mécanismes d'autostructuration des champs récepteurs. Un autre exemple a depuis été montré au niveau des propriétés des CR de l'aire 3b (voir chapitre suivant).

2.3.2 Hiérarchie de représentation et stéréognosie haptique

Plusieurs évidences indiquent un rôle central du lobe pariétal à la somesthésie. Ainsi, les expériences lésionnelles indiquent une détérioration voir une destruction des habiletés somesthésiques suite à une lésion du lobe pariétal chez le macaque et l'homme (Randolph et Semmes, 1974, Carlson, 1981, Murray et Mishkin, 1984, Roland, 1987a,b, Caselli, 1993, Reed et al., 1996, Valenza et al., 2001). En particulier, il apparaît que les aires somatosensorielles primaires 3a et 3b constituent un point d'entrée incontournable des informations proprioceptives et cutanées (respectivement). D'une part, elles reçoivent la majorité des afférences thalamiques (Jones et Powell, 1970, Jones 2002), et d'autre part leur destruction ou leur inactivation sélective amène une perte quasi complète de la somesthésie, analogue à une déafférentation majeure (Randolph et Semmes, 1974, Hikosaka et al., 1985). L'analyse exhaustive des CR de neurones de l'aire 3b indique de plus une sensibilité à l'orientation qui pourrait structurer les processus haptiques d'une façon analogue au système visuel (Hsiao, 2002). En effet, ces CR présentent une coexistence de zone excitatrices à courte latence, et de zone inhibitrice à longue latence (DiCarlo et al., 1998, 1999, 2000, 2002). L'effet d'un stimulus appliqué sur le CR de ces neurones dépend donc des stimulations précédentes (codage spatio-temporel), ce qui aboutit à des champs récepteurs sensibles à l'orientation et/ou à la direction d'un stimulus mobile appliqué sur la peau. L'aire 3b pourrait donc avoir un rôle dans l'extraction de l'orientation des stimuli cutanés grâce à un phénomène d'autostructuration des champs récepteurs.

La plupart des auteurs s'accordent pour considérer ensuite une organisation hiérarchique sérielle depuis le sillon central jusqu'au cortex pariétal postérieur (Hyvärinen et Poranen, 1978, Iwamura et al., 1993, revus dans Iwamura 1998, Bodegard et al., 2001). En se déplaçant dans le sens rostro-caudal, on voit ainsi que la structure des CR démontre un élargissement et une complexification dans l'aire 1 par rapport à l'aire 3b (Iwamura et al., 1985a, b, 1993). L'aire 2 présente des neurones activés par la préhension de formes spécifiques (Iwamura et al., 1978), sa destruction chez le singe entraîne des déficit dans la stéréognosie haptique (Randolph et Semmes, 1974, Carlson, 1981), et des activations hémodynamiques spécifiques pour la courbure y sont retrouvé chez l'humain (Bodegard et al., 2000, 2001, 2003). Plus caudal, le cortex pariétal postérieur (aire 5 et 7) reçoit une convergence d'afférence de toutes les aires somatosensorielles primaires (Jones et Powell, 1969a, b). Les subdivisions du cortex pariétal postérieur demeurent toutefois mal connues. L'aire 5 est caractérisée par de grands champs récepteurs somatosensoriels, parfois bilatéraux, alors que l'aire 7 est dominée par des inputs visuels (partie médiale, 7a) ou une combinaison d'inputs visuels et somesthésiques (partie latérale, 7b). Bien que ces aires soient considérées classiquement comme de haut niveau, peu de cellules sensibles aux formes ont été retrouvés dans les aires 2 et 5 (Koch et Fuster, 1989, Gardner et al., 1999), et une claire sensibilité aux formes n'a pu être mise en évidence que dans certains neurones de l'aire 7, probablement en lien avec la préhension (Taira et al., 1990). Le cortex pariétal postérieur pourraient ainsi être d'avantage lié au guidage du mouvement qu'a l'analyse des stimuli tactiles (Gardner et al., 1999, Ro et al., 2000, Debowy et al., 2001, Gardner et al., 2002). Finalement, toutes les aires décrites précédemment projettent également vers SII, qui constitue possiblement une voie ventrale liée à l'apprentissage et la mémoire (Friedman et al., 1986). Cette voie ventrale pourraient également être liée à l'identification: d'une part SII contient des cellules de haut niveau capable de détecter des changement de texture chez le macaque (Jiang et al., 1997, Pruet et al., 2001), et d'autre part Reed et al. (2004) montrent une activation sélective de ces aires chez l'humain pour la reconnaissance d'objet par le toucher.

2.3.3 Autres aires potentiellement impliquées dans la stéréognosie haptique

Plusieurs aires situées en dehors du lobe pariétal pourraient également contribuer à la stéréognosie haptique, notamment les lobes frontaux et occipitaux. Tout d'abord, les études d'imagerie indiquent que le contrôle du mouvement d'exploration passerait par une interaction entre aires frontales et pariétales, mais aussi les noyaux sous-corticaux (thalamus, putamen) et le cervelet (Seitz et al., 1991, Boecker et al., 1995, Stoeckel et al., 2003). Cela est aussi confirmé par des enregistrements unitaires chez le singe, qui démontrent une sensibilité des aires motrices aux formes dessinées (Averbeck et al., 2003a,b). Toutefois, l'interprétation traditionnelle de cette sensibilité comme un support des activités motrices (et probablement du gating associé aux activités motrices) pourrait être incomplète. En effet, la découverte récente d'activation des aires motrices en fonction d'une illusion somatosensorielle (vibration tendineuse) pourrait indiquer également un rôle perceptuel, notamment au niveau des informations proprioceptives (Naito et al., 1999, 2002). Il est d'ailleurs frappant de constater qu'un même codage vectoriel peut rendre compte à la fois des décharges retrouvées dans les cortex moteurs et dans la décharge des FNM (voir chapitre 2.2.2). Finalement, le lobe frontal participe également au maintient en mémoire des informations somatosensoriel (Koch et Fuster, 1989, Romo et al., 1999, Zhou et Fuster, 2000), et est très probablement impliqué dans toute manipulation cognitive de ces informations (revus dans Fuster, 2001, 2002).

Au niveau du lobe occipital, plusieurs évidences montrent l'implication des zones visuelles pendant la lecture du Braille chez les personnes aveugles (Sadato et al., 1996, Cohen et al., 1997, Buchel et al., 1998, Sadato et al., 1998). Bien que ces résultats soient éventuellement liés à une réorganisation absente chez les sujets normaux, cela supporte néanmoins la proximité des systèmes visuels et haptiques dans l'analyse des formes, c'est-à-dire la stéréognosie. De plus, des évidences récentes chez des sujets contrôles suggèrent qu'une partie au moins de la stéréognosie haptique normale passerait par des aires visuelles. En effet, Zangaladze et al. (1999) ont montrés que la disruption par TMS d'aires visuelles extra-striées (possiblement V6 à proximité de la jonction pariétal/temporale/occipitale) provoque un déficit spécifique pour l'analyse de la macrogéometrie (orientation), mais pas de la microgéometrie (texture) –alors que les mêmes objets étaient explorés. Ce point est d'autre part supporté par l'observation d'une activation de cette aire lors de la stéréognosie haptique (Amedi, 2001). Une interprétation possible de ces évidences passerait alors par l'utilisation d'imagerie mentale, qui se baserait donc sur des structures au moins en partie communes à la vision et à la stéréognosie haptique (Sathian et Zangaladze 2002).

2.4 PSYCHOPHYSIQUE HAPTIQUE

Un des points intéressant avec les évidences neurophysiologiques revues plus haut est le lien fort entre stéréognosie haptique et contrôle du mouvement d'une part, stéréognosie haptique et système visuel d'autre part. Dans cette partie, nous verrons que des évidences psychophysiques convergent vers des conclusions similaires. En particulier, plusieurs évidences suggèrent 1) que le toucher est sensible au contexte; et 2) que les cadres de références utilisés pour coder l'orientation de barres explorés manuellement sont identifiables par de simples mesures psychophysiques.

2.4.1 Les habiletés haptiques dépendent du contexte

L'observation de comportement naturels d'exploration d'objet chez l'humain ; ou de posture chez le singe, montrent 1) de procédures exploratoires spécifiques en fonction des caractéristiques recherchées (texture, forme, etc..) chez l'humain (Lederman et Klatzky 1987), et 2) l'utilisation préférentielle d'une partie de l'espace péri-corporel chez le singe (Grazziano et al. 2004). Ces deux expériences suggèrent donc une dépendance au point de vue, c'est-à-dire que les explorations de formes présentent à la fois des procédures spécifiques et des postures préférentielles. Confirmant cette vue, l'analyse des performances de reconnaissance de formes par le toucher haptique montrait un avantage spécifique pour l'exploration par l'arrière des objets, suggérant une complémentarité des systèmes haptiques et visuels (Newel et al. 2001). Il n'est cependant pas clair si ces données s'expliquaient par une optimisation de l'information haptique disponible ou reflétaient réellement les stratégies cognitives d'analyses des formes. Dans la même veine, il existe plusieurs évidences que les habiletés haptiques sont affectées par la posture. Ainsi, toucher le contour d'une table avec les doigts croisés amène la perception de deux contours plutôt qu'un. Une illusion encore plus impressionnante est obtenue par vibration tendineuse du coude (perception d'extension du bras) : si les sujets tiennent leur nez durant cette stimulation, alors ils tendent à percevoir un allongement de leur nez (Lackner et Taublieb, 1983, Lackner, 1988). De manière intéressante, ce type d'influence peut transparaître même en l'absence de perturbation des informations proprioceptives.

Par exemple dans une tâche de classification d'un « J » tactile normal ou inversé en miroir, Pratter et al. (2002) ont montré un temps de réaction proportionnel à l'angle de rotation de ces lettres par rapport à une orientation colinéaire au regard (ou à la tête, ou au corps), montrant ainsi l'utilisation de rotation mentale d'une part, et d'un cadre de référence égocentré d'autre part. Dans la même veine, Soechting (1982) a montré qu'une même tâche d'appareillement des orientations des avant-bras (et donc des angles du coude) amenait des performances différentes selon que l'instruction était d'appareiller les orientations de l'avant-bras vs. appareiller les angles articulaires du coude, alors que ces deux instructions sont équivalentes. Cela pointe que les représentations centrales sont directement affectées par les consignes.

Ainsi, le contexte d'une tâche influe sur son exécution, non seulement par des interférences avec les informations haptiques disponibles, mais probablement aussi en changeant les stratégies perceptuelles des sujets. Il devrait donc être possible d'ajouter des informations sur la nature des cadres de références utilisées par le toucher haptique par de simples manipulations psychophysiques.

2.4.2 Quels cadres de références pour le toucher haptique ?

Un grand nombre d'auteurs ont suggérés qu'une multitude de cadres de référence transparaissait dans l'analyse des performances humaines, au niveau de la somesthésie et du contrôle moteur (Paillard 1991, Bridgeman et al. 1997, Rossetti et al. 1998, Millner et al. 1999), de la vision (Millner et Goodale 1995), ou encore de l'imagerie mentale (Wraga et al. 1999). A titre d'exemple, Carrozzo et al

(2002) montrait récemment que la distribution des erreurs dans une tâche d'atteinte pouvait dépendre de connaissances préalables. Si les sujets étaient informés que les cibles tombaient sur une barre virtuelle (sans qu'aucune vision de cette barre ne soit donnée), alors la distribution des erreurs semblait contrainte par cet objet virtuel. Cela amenait ces auteurs à suggérer l'utilisation d'un cadre de référence allocentré ou non en fonction de la tâche, et donc l'implication de plusieurs cadres de référence possibles pour une même tâche. En plus du caractère multiple de ces cadres de référence, Rossetti et al. (1998) ont montré dans un papier pionnier que l'interaction entre ces cadres de référence pouvait être changée par l'ajout d'un délai. Ainsi, l'ajout d'un délai de 8 secondes dans une tâche de reaching amenait non seulement à une diminution de performance, mais aussi à un changement de la distribution des réponses, suggérant ainsi un changement de la nature d'un ou plusieurs cadres de référence lié à la demande mnésique de cette modification de la tâche. Des conclusions similaires étaient fournies dans une étude clef de Millner et al. (1999), qui observaient que l'ajout d'un délai chez des clientèles souffrant d'ataxie optique menait à une augmentation paradoxale de la précision des saccades. Selon ces auteurs, l'ajout d'un délai (5 secondes) aurait suffi à supprimer l'implication d'un cadre de référence particulier, supposé à courte latence et distordu chez les clientèles étudiées, ce qui expliquerait ainsi l'amélioration paradoxale des performances avec l'ajout d'un délai entre la présentation d'une cible et l'initiation de la saccade.

Dans le domaine du toucher haptique, une interprétation similaire à été proposée pour rendre compte des performances d'appariellement des orientations de barres. En effet, dans une série d'étude sur la perception de l'orientation de barres par le toucher haptique à travers l'espace péri-corporel, Kappers et al. ont montré un biais systématique dans la perception du parallèlisme (Kappers 1999, 2002, Kappers et Koenderink 1999). Une explication simple était alors de postuler que le biais provenait de l'interaction entre deux cadres de référence, dont un serait centré sur le bras et de courte durée, et un serait allocentré et capable de se maintenir plus longtemps en mémoire à court et moyen termes. Supportant cette interprétation, Zuidhoek et al. (2003), en ajoutant un délai de 10 secondes entre la présentation d'une orientation devant être reproduite et sa reproduction, ont vu une diminution de ce biais systématique affectant la perception du parallèlisme. En conséquence, ces auteurs démontrent l'intérêt des études psychophysiques pour questionner la nature des cadres de référence utilisés par le système haptique, en proposant une double implication d'un cadre egocentré avec un cadre allocentré.

CHAPITRE III - PROBLÉMATIQUE

L'objectif général de cette thèse est d'étudier la stéréognosie haptique chez l'humain via une série d'expérience psychophysique. En particulier, nous proposons une tâche simple de stéréognosie haptique (premier article), que la stéréognosie haptique se base effectivement sur une combinaison d'information cutanées et proprioceptives (second article), et que les cadres de références utilisées pour représenter les formes pourront être mis en évidence par de simple manipulation des conditions expérimentales (troisième article).

Dans le premier article, nous verrons tout d'abord l'opérationnalisation d'une tâche de discrimination de formes simples, ainsi que les relations entre la performance de discrimination d'une part, le mouvement, la répétition de sessions expérimentale, l'orientation de l'appareillage, les caractéristiques des sujets et leur stratégies. Nous nous attendons à ce que les sujets se basent effectivement sur l'angle d'intersection formé par nos formes, et non pas simplement sur l'orientation d'un des segments.

Dans le second article, nous testerons en particulier l'effet de supression sélective des informations cutanées ou proprioceptives. Notre seconde hypothèse est que chaque suppression d'information se traduira par une diminution (mais pas une suppression) des capacités de discrimination.

Finalement, le troisième article sera consacré à 1) déterminer si la stéréognosie haptique est dépendante du point de vue; 2) déterminer l'origine de cette dépendance (périphérique ou centrale); et 3) utiliser la dépendance au point de vue pour ajouter des informations sur la nature des cadres de référence utilisés pour coder les formes haptiques. Spécifiquement, notre hypothèse est que la stéréognosie haptique dépende du point de vue à la fois par des manipulations de la qualité de l'information haptique (origine périphérique) et par des manipulations du contexte n'affectant pas la qualité des informations périphériques

CHAPITRE IV - ARTICLE 1

Haptic discrimination of object shape in humans: two-dimensional angle discrimination

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4.1 ABSTRACT

The human ability to recognize objects on the basis of their shape, as defined by active exploratory movements, is dependent on sensory feedback from mechanoreceptors located both in the skin and in deep structures (haptic feedback). Surprisingly, we have little information about the mechanisms for integrating these different signals into a single sensory percept. With the eventual aim of studying the underlying central neural mechanisms, we developed a shape discrimination test that required active exploration of objects, but was restricted to one component of shape, two-dimensional (2D) angles. The angles were machined from 1-cm-thick Plexiglas, and consisted of two 8-cm-long arms that met to form an angle of 90° (standard) or 91° to 103° (comparison angles). Subjects scanned pairs of angles with the index finger of the outstretched arm and identified the larger angle of each pair explored. Discrimination threshold (75% correct) was 4.7° (range 0.7° to 12.1°), giving a precision of 5.2% (0.8–13.4%: difference/standard). Repeated blocks of trials, either in the same session or on different days, had no effect on discrimination threshold. In contrast, the motor strategy was partly modified: scanning speed increased but dwell-time at the intersection did not change. Finally, 2D angle discrimination was not significantly modified by rotating the orientation of one of the angles in the pair (0°, 4° or 8° rotation towards the midline, in the vertical plane), providing evidence that subjects evaluated each angle independently in each trial. Subject reports indicated that they relied on cutaneous feedback from the exploring digit (amount of compression of the finger at the angle) and mental images of the angles, most likely arising from proprioceptive information (from the shoulder) generated during the to-and-fro scans over the angle. In terms of shoulder angles, the mean discrimination threshold here was 0.54° (range 0.08° to 1.36°). These values are lower than previous estimates of position sense at the shoulder. In light of the subjects' strategies, it therefore seems likely that both cutaneous and proprioceptive (including both dynamic and static position-related signals) feedback contributed to the haptic discrimination of 2D angles.

Keywords : Tactile shape discrimination · Two-dimensional angles · Active touch · Cutaneous · Proprioceptive

4.2 INTRODUCTION

The human capacity to recognize objects on the basis of their shape as defined by active exploratory movements of the hand is a complex ability. Sensory feedback critical to object identification is generated by receptors located in the skin and in deep structures. Together we refer to this as haptic feedback (Gibson 1966). Haptic signals provide information about the surface properties of the object (texture, consistency, local contours and edges) and the whole-object properties (shape, size, weight). The challenge is to understand how the central nervous system translates and integrates the various sensory signals generated during touch into a single perception of an object, so allowing one to distinguish between an apple and an orange on the basis of the specific attributes of each (e.g. shape, texture, consistency, etc.). Whereas we now have considerable information about the primary input-output properties of the somatic sensory system (encoding capacities of the peripheral receptors and perceptual abilities, respectively), we have relatively little information about the intervening central neural mechanisms for integrating the different signals into a single sensory impression. With the eventual aim of determining the underlying central neural mechanisms that contribute to shape discrimination, we chose to approach this question by developing a new shape discrimination test that we expected would be dependent on both cutaneous and proprioceptive inputs. A simple definition (Oxford English Dictionary) states that shape is the external form or contour of an object. However, as noted by Goodwin et al. (1991), defining shape is not simple because it is multidimensional. For example, a series of small spheres of different sizes that can be enclosed in the hand can potentially be discriminated using cues about the relative position of the various joints involved in grasping different sized objects and/or by changes in the surface area of skin in contact with the grasped objects. Conceivably, both sources of information contribute to defining the human ability to discriminate object shape. To allow a controlled study of shape, we used a restricted working definition of shape that can be applied to any object with angles: namely, that shape can be specified as a series of edges or surfaces and the spatial relations between them (Ullman 1995). In this study, we have chosen specifically to examine the human ability to discriminate differences in two-dimensional (2D) angles. In addition to limiting the experimental problem, this approach had the added advantage of allowing a direct comparison between our results with those of studies aimed at characterizing position sense in humans. The interest here was that the latter studies evaluated position sense alone, independent of cutaneous feedback generated during active exploration of object shape. We further chose to require that subjects explore the 2D angles using active touch as this corresponds to the strategy used in everyday life. This same approach was previously taken by Roland and Mortensen (1987) in an earlier study that evaluated the human ability to discriminate differences in the shape of 3D macrogeometric forms (spherical ellipses and rectangular parallelepipeds). Lederman and Klatzky (1987) characterized the types of hand movements used in haptic exploration of objects. In particular they reported that subjects use static enclosures to obtain information about small object shape (see also Roland and Mortensen 1987). In contrast, contour-following movements are used to obtain information about the shape of larger objects. This latter movement strategy was employed in the present experiments. The task was designed so that both cutaneous feedback (from the glabrous skin of the index finger) and proprioceptive feedback (from the shoulder, as the exploratory movement was performed with the outstretched arm) could contribute to performance. The results indicate that humans can discriminate 2D angle differences of an average of 4.7° using a contourfollowing movement of the index finger. We suggest that 2D angle discrimination is an integrative task, using both cutaneous and proprioceptive feedback, consistent with the cognitive strategies of the subjects and our observation that discrimination was better than could be predicted from a consideration of shoulder position sense. This hypothesis is addressed in the companion paper (Voisin et al. 2002). Preliminary reports of the results have appeared (Voisin and Chapman 2000, 2001).

4.3 MATERIALS AND METHODS

4.3.1 Subjects

Nine naive, paid subjects (four women and five men, 21–27 years of age), all but one right handed for writing, volunteered to participate in experiment 1. A further six right-handed subjects (four women and two men, including one of the experimenters, aged 19–25 years) volunteered for experiment 2. The experimental protocol was approved by the institutional ethics committee, and all subjects gave their informed consent prior to the experiments. Subjects participated in one (n=8), two (n=1) or three (n=6) experimental sessions. Each session lasted 3–4 h, and consisted of two or three blocks of trials (see also the companion paper).

4.3.2 Angles

As shown in Fig. 4.3.2, the discriminanda consisted of a standard angle of 90° and seven comparison angles spanning a range from 91° to 103° (increments of 2°). The 90° standard angle was chosen for its familiarity in everyday life. We chose to concentrate our studies on comparison angles greater than 90° for two reasons. First, we were concerned that physical factors (e.g. finger circumference) might limit the ability of some subjects to collect relevant information about the angle if we used angles less than 90°. Second, this approach allowed us to maximize the number of trials collected for each difference presented. This was an important concern because the trials were long (up to 33 s). The angles were machined from a solid sheet of Plexiglas (1 cm thick), with an accuracy of ~0.1°.

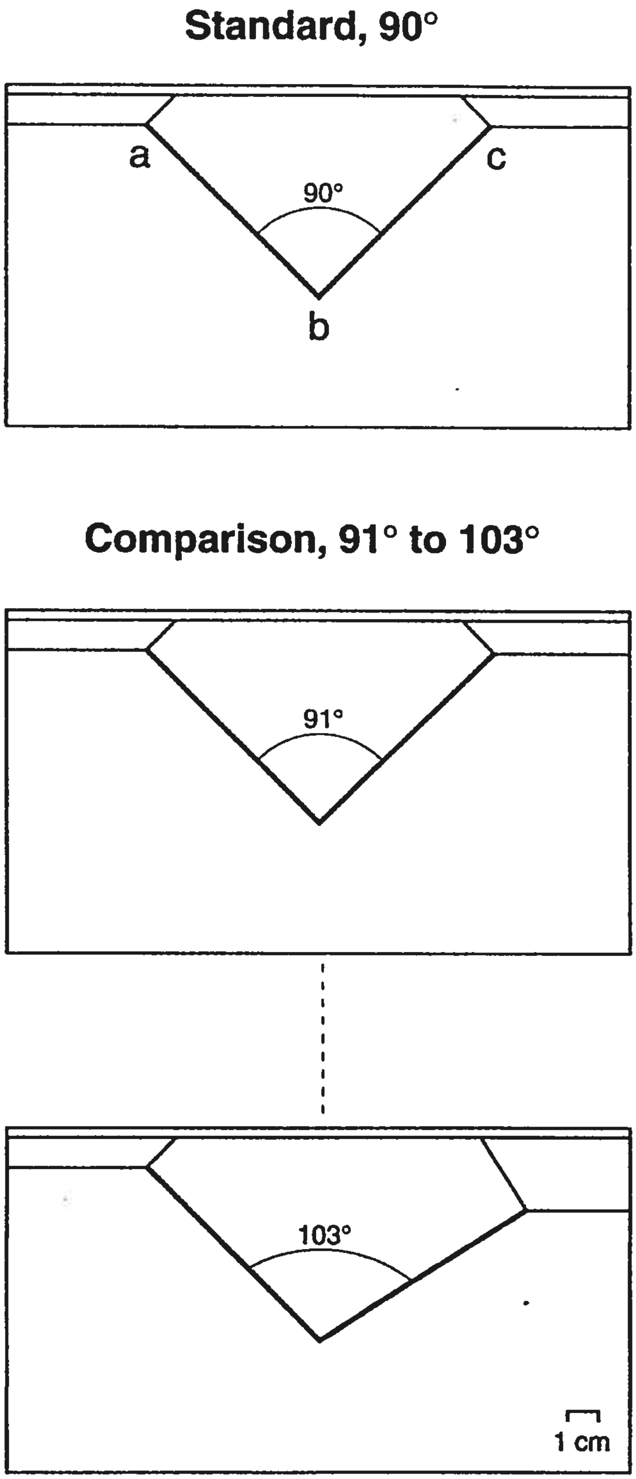

Fig. 4.3.2 Schematic depiction of the 2D angles, as seen from the point of view of the subject. All objects were identical over the portion scanned initially by the subjects (segment ab). The second scanned segment, bc, formed an angle of 90° at the intersection (b) for the standard angle; the angle at the intersection was incremented in 2° steps for the comparison angles (range 91° to 103°). The surface explored by the subject is indicated in bold. All scans began with the index finger placed at position a.

Each arm of the angle was 8 cm long. The two extremities of the arms ended in a 90° angle for all of the experimental objects (positions a and c in Fig. 4.3.2, top). The change in orientation was restricted to one arm of the angle, corresponding to the second arm explored during the scan (right side of the view shown in Fig. 4.3.2). The planar surfaces of the angles were polished and checked with a microscope to ensure that there were no microscopic cues upon which subjects could base their performance. In the same vein, we employed four replicates of the standard 90° angle in all experiments.

4.3.3 Apparatus

The angles were clamped upright in an apparatus instrumented with six strain gauges along with three pairs of light emitting diodes (LEDs) and optical sensors (Fig. 4.3.3 A). Pilot testing indicated that some subjects based their response on an estimate of the orientation of the second arm of the angle relative to the horizontal rather than the whole angle. In order to discourage the subjects from using this strategy, the orientation of the apparatus in the vertical plane, and so the orientation of the angle, was randomly shifted for one angle of the pair presented in each trial (4° rotation towards the midline in experiment 1; 4° or 8° in experiment 2; see below). The axis of rotation for the shift is shown in Fig. 4.3.3 B.

4.3.4 Two-dimensional angle discrimination task

As shown in Fig. 4.3.3C, the subjects were seated in a chair with the apparatus positioned at arm's length from the subject at the level of the shoulder, 30° to the right. To prevent any visual or auditory cues, vision of the apparatus was occluded, and white noise was delivered through headphones. Each subject received written and verbal instructions at the beginning of the session, indicating that they were going to explore pairs of objects consisting of two arms (or edges) that joined to form an angle, and that their task was to indicate which of the two objects had a larger angle. The subjects were instructed to scan each angle using the glabrous skin of the middle phalanx of the right index finger, keeping the upper limb straight throughout so that angular changes occurred only at the shoulder. Although the combination of shoulder/finger might appear artificial and contrived, haptic exploration of larger objects often uses a combination of proximal rotation at the shoulder and distal cutaneous feedback. We did not immobilize the other joints at which rotation could have occurred during the task (elbow, wrist, metacarpophalangeal, proximal interphalangeal joints) because we were concerned that a splinting device might generate systematic additional cues on which the subjects might base their decisions. Concerns about subject fatigue and comfort also contributed to our approach. Nevertheless, the positioning of the subject with respect to the apparatus ensured that trials with such extraneous movements were rejected at acquisition. With this posture, we also eliminated cues (e.g. contact of the arm with clothing or the trunk) that might have contributed to angle discrimination. The experimenter guided the subject to place their finger at the initial position (Fig. 4.3.3C, nail up). This corresponds to position a in Fig. 4.3.2, the beginning of the first arm of the angle. Subjects slid their finger over the angle using a to-and-fro scanning movement, so that the digit was moved successively over each arm of the angle, and this with two directions of movement. Subjects kept the upper limb rigid throughout, and so the skin area

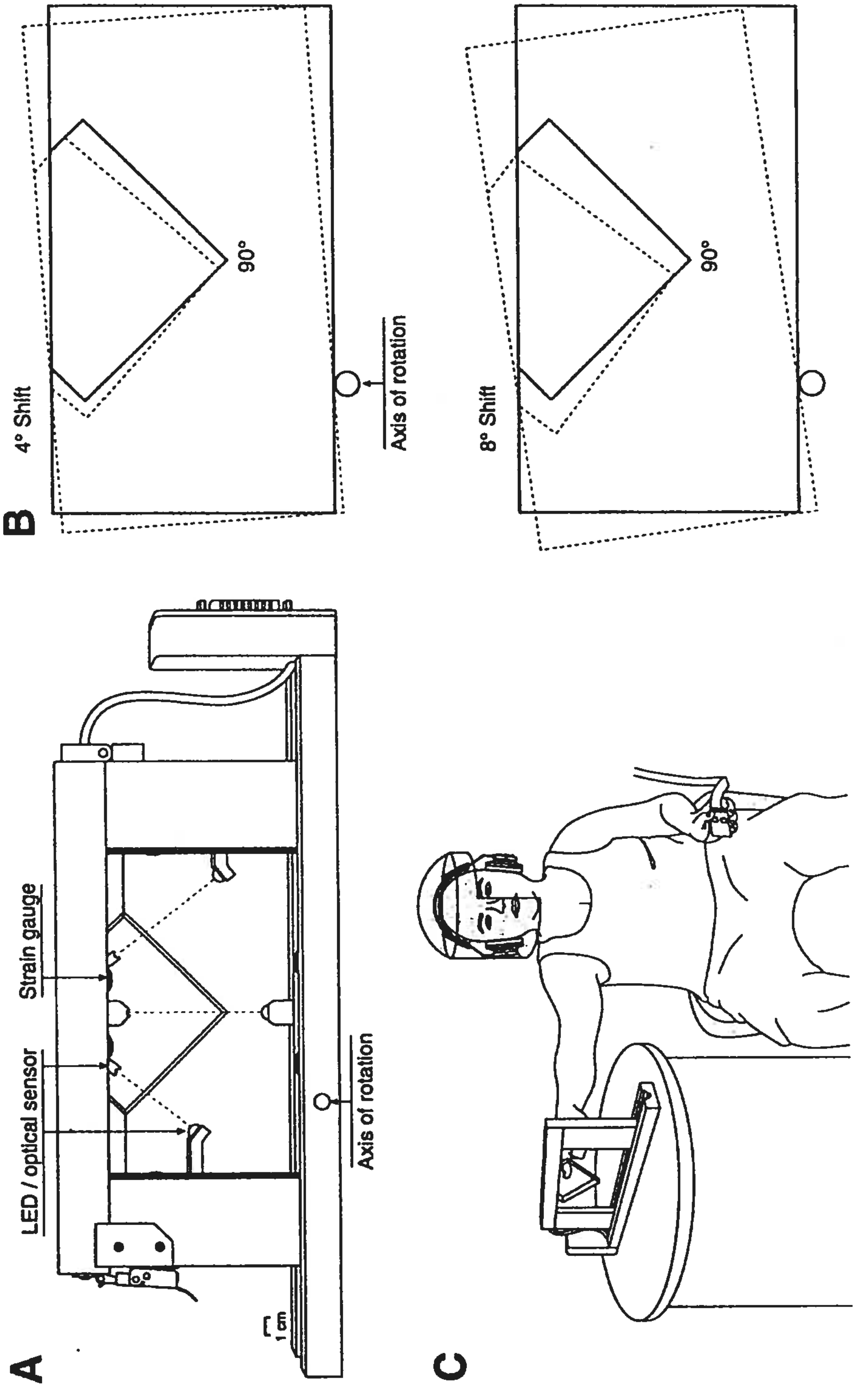

Fig. 4.3.3 A Experimental apparatus into which the angle was clamped for exploration. Shown here is the placement of the three pairs of LEDs and optical sensors that monitored digit position during the scans (dotted lines), along with the location of the strain gauges. B Standard angle (90°), as presented to the subject, in the 'no-shift' position (solid outlines) and in the shifted orientation (4° or 8°, dotted outlines). One angle in each pair was presented in the no-shift position; the other was shifted. C Subject's position relative to the apparatus at the beginning of the trial (index finger at the start position)

in contact with the object varied as a function of the arm explored (radial side for ab; ulnar side for bc). The sequence of movement was a-b-c-b-a, with b corresponding to the intersection between the two arms of the angle, and c the end of the second arm of the angle. By using the middle phalanx for exploration, the position of the digit relative to the angle was monitored with the LEDs positioned at each of positions a, b and c. The latter were interrupted by the protruding distal phalanx of the index finger. This arrangement ensured that the angular displacement was confined to the shoulder: the arm had to be fully extended throughout the movement; otherwise the distal phalanx did not interrupt the LEDs. When the latter happened, the trial was aborted and repeated later in the session. Two angles were successively scanned in each trial, one standard angle (90°) and one of the comparison angles (91° to 103°). There were no restrictions on the motor strategy (contact force, scanning speed, dwell-time at the intersection). The order of presentation of the standard (S) and the comparison or modified (M) angle followed the MSSM strategy of Johnson (1980), i.e. the standard angle was either the first or the second angle of each pair presented to the subject. Subjects were asked to identify the larger angle of each pair (two-alternative forced-choice) using a keypad operated with the left hand (1 = first angle larger, 2 = second angle larger). No feedback on performance was provided, and subjects were not informed about the existence of the shift. The sequence of events in a trial was as follows: (1) the first angle was clamped in the apparatus; (2) the experimenter positioned the digit of the subject; (3) data acquisition was initiated by the experimenter; (4) a tone cued the subject to commence the scan; (5) the subject scanned the index finger over the angle (sequence, a-b-c-b-a); (6) after completing the scan, the subject withdrew the finger from the angle; (7) the second angle was installed in the apparatus; (8) steps 2–6 were repeated; and (9) the subject entered his/her response in the keypad. The intertrial interval was ~30 s. Trial duration, including the time to change the angle and the subject's response time, varied from 12 to 33 s (mean 21 s). The average delay between the end of the first scan and the beginning of the second one was 14 s (range 7.6–25 s).

4.3.5 Experimental design

In experiment 1, the standard angle (90°) and seven comparison angles (91°, 93°, 95°, 97°, 99°, 101° and 103°) were presented 8 times in a pseudorandom order for a total of 56 trials (method of constant stimuli). A shift of 4° was applied to one-half of the angles. In experiment 2, there were three blocks of 32 trials (eight replications for each of four comparison angles, 91°, 95°, 99° and 103° along with the standard angle); the amplitude of the shift was varied across the three blocks of trials (0°, 4° or 8°). The order of testing was counterbalanced for all relevant factors (shift on the first or second angle; standard angle presented as the first or second angle; amplitude of the shift, with the exception of the 0° shift that was always tested in the final block of trials in experiment 2). Before each block of trials, subjects first practised the scanning movement on a standard angle of 90° (up to four movements). To familiarize the subjects with the perceptual task, they then scanned two pairs of angles, starting with an easy discrimination (90° vs 100°). After two correctly discriminated presentations (two to three trials), a more difficult comparison was presented (90° vs 95°). Six to seven trials were performed until two correct responses were given. Thereafter, data collection commenced.

4.3.6 Data acquisition and analysis

The task and data acquisition were controlled by a microcomputer. The force signals were digitized at 200 Hz. The times that the digit arrived at and left position a, b and c were also recorded (output of optical sensors). For each scan, acquisition started 300 ms before the tone that instructed the subject to begin the scan, and ended when the scan was completed (return to position a). For each trial, the subject's response was stored along with information about the trial type, including the value of the comparison angle, the order of presentation of the standard and comparison angles, and the order of presentation of the shift. For each subject in each block of trials, the proportion of correct responses (PC) for each comparison angle was computed. The results were fitted to the following logistic function (adapted from Weder et al. 1998; see also Fasse et al. 2000): In this equation d is the unique degree of freedom of the logistic curve that was adjusted to fit the raw data. The discrimination threshold (T=75% correct) was computed from the logistic function as follows: For each scan, the average scanning speed was calculated using the outputs of the optical sensors. For contact force, we first inspected each individual trace to exclude trials with artefacts. Mean contact force during the scans was estimated from trials with a constant baseline. Differences in discrimination threshold or scanning speed with three repeated sessions or three imposed shifts (0°, 4° or 8°) were analysed using repeated measures analyses of variance (ANOVA). The level of significance significance was fixed at $P<0.05$ for all analyses. Additional analyses are detailed in the “Results”.

4.4 RESULTS

4.4.1 Performance of the 2D angle discrimination task (experiment 1)

Discrimination performance was evaluated as seven pairs of standard (90°), and comparison angles (91° to 103°) were presented in a quasi-random order, spanning a range of angular differences of 1° to 13°. The results of one subject (first session) are shown in Fig. 4.4.1 A. When a small difference was presented (1°), performance (proportion of correct discriminations) was at the chance level for this two-alternative forced-choice paradigm (~50%); performance improved as the angular difference was increased, reaching 100% when the difference was ≥9°. The data were fitted to a logistic function, and from this the discrimination threshold (75% correct) was estimated to be 4.2°. We considered the possibility that the presence of three consecutive bins with 100% correct performance biased the results obtained from fitting the data to a logistic function. When these data were reanalysed after omitting the data obtained with angular differences greater than 9°, the logistic function was very similar (see dotted line in Fig. 4.4.1 A) and the estimated discrimination threshold was little changed, 4.4°. Similar results were obtained in all cases with two or more consecutive bins of 100% correct performance (7 out of 22 blocks of trials): estimated threshold was not significantly changed when the data were truncated to remove therepeated bins (paired t-test, P=0.128). This observation suggested that our estimate of discrimination threshold was not unduly biased by fitting the logistic function to all of the data collected.

Figure 4.4.1 B shows the results obtained from nine subjects during their first experimental session. In this case, only the logistic curves are shown.

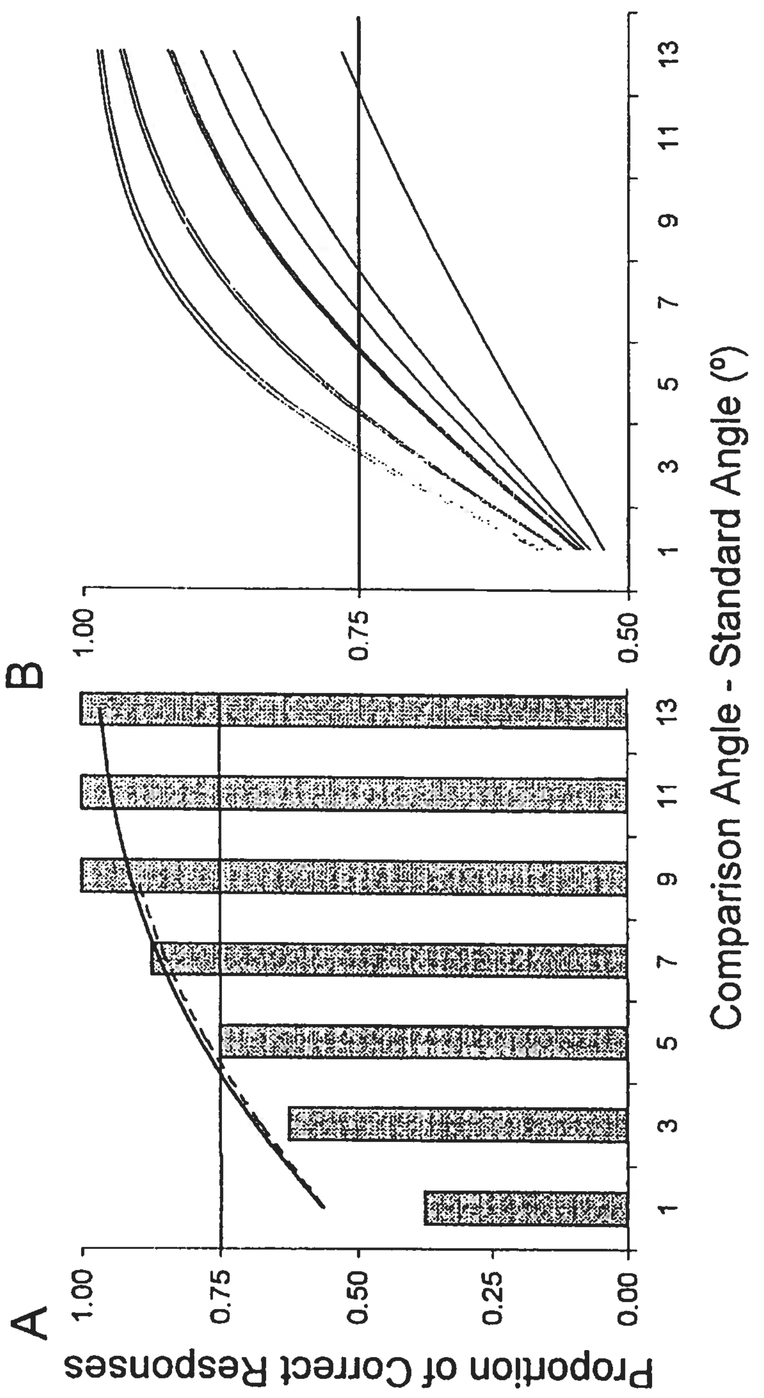

Fig. 4.4.1 A Performance of subject 2 in the 2D angle discrimination task (experiment 1, first experimental session). The proportion of correct responses is plotted as a function of the angular difference between the comparison angle (91°–103°) and the standard angle (90°). Two logistic curves were fitted to the data: one used the entire data set (solid line) while the other (dashed line) excluded the data from the two largest comparison angles as performance had reached 100% correct for a difference of 9°. B Individual logistic functions showing the performance of nine subjects in the 2D angle discrimination task (experiment 1, first session). Discrimination threshold (75% correct) ranged from 3.3° to 12.1°

Inspection of the results indicates that, for all subjects, performance improved as the angular difference was increased. The mean discrimination threshold was 5.9° (range 3.3° to 12.1°; see Table 4.4.2). Several factors could have contributed to the intersubject variability, including anthropometric factors, sex, and strategy (motor and cognitive). These factors are addressed below using the pooled data from experiments 1 and 2.

4.4.2 Effects of practice on 2D angle discrimination

In this study, the number of replications of each standard/comparison pair of angles was relatively low (eight trials) in order to minimize subject fatigue, and so optimize the quality of the data collected. This approach was adopted because all experimental sessions included two or more blocks of trials, and each trial was relatively long (time to secure each angle in the apparatus and to position the subject's digit in the initial position). The possibility that practice might improve performance on the 2D angle discrimination task was evaluated by having six subjects repeat the task on three separate days. The results are shown in Fig. 4.4.2 and Table 4.4.2. Mean discrimination threshold showed a modest decline with repetition: session 1, 5.0°; session 2, 4.1°; session 3, 3.6°. A repeated measures ANOVA indicated that discrimination threshold was not significantly different across the three sessions (F(2,10)=1.196, P=0.34) because not all subjects showed improved performance with repetition (e.g. subjects 6 and 7). The results suggested that the number of replications per pair was adequate to measure performance in the 2D angle discrimination task, and that practice did not significantly improve performance.

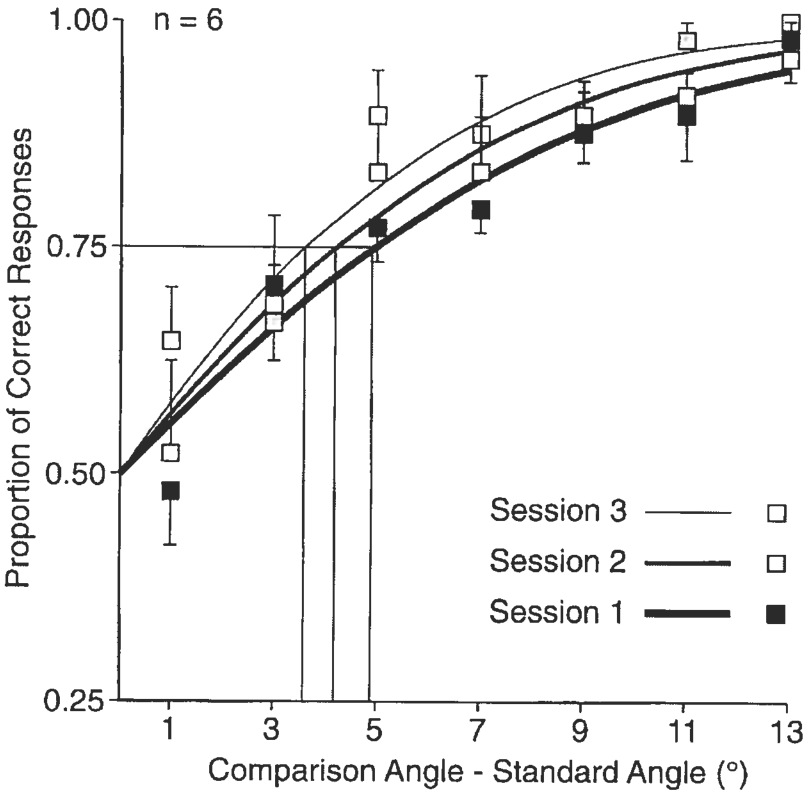

Fig. 4.4.2 Effects of practice on performance of the 2D angle discrimination task (experiment 1) in six subjects who repeated the task on three separate occasions. Shown here are the logistic functions fitted to the pooled data along with the mean proportion of correct responses (± SEM) for each comparison angle

Subject	Session 1	Session 2	Session 3	Sex	Strategy
1	5.7	4.5	2.1	m	*WI*
2	4.2	3.9	2.6	m	*WI*
3	5.7	0.7	2.6	m	*W*
4	6.7	5.3	3.6	f	*MI*
5	12.1	5.1		f	I
6	3.3	5.8	4.4	f	*WI*
7	4.3	4.4	6.2	m	*W*
8	7.8			f	*WI*
9	3.3			m	*WI*
Mean	5.9	4.2	3.6		

Table 4.4.2 Discrimination thresholds (°) in nine subjects (experiment 1) as a function of the session (first, second or third), sex (female or male) and cognitive strategy (W mental image of whole angle, I intersection, M movement)

4.4.3 Motor strategies employed in 2D angle discrimination

The motor strategy employed in scanning the angles was evaluated by measuring the contact force employed in the task, the dwell-time at the angle of intersection, and the speed of the scanning movements. In general, subjects used very light contact forces during their scanning movements. Indeed, in many trials, contact force could not be reliably estimated since the contact force was too low (<0.2 N). For trials in which the contact force could be estimated, and so an overestimate of the actual value, contact force was an average of 0.95 N (range 0.34–2.42 N across different subjects). These values are comparable to the contact forces used by subjects in evaluating surface roughness (Meftah et al. 2000). Contact force showed no consistent change with repetition: one subject decreased the contact force across three repeated sessions, one subject increased the contact force, and two subjects showed no change (incomplete data for two subjects). The length of time that the digit was in contact with the angle (dwell-time) was measured in all trials. Figure 4.4.3 A plots the mean dwell-time for six subjects that participated in three repeated sessions (2,016 scans) as a function of the value of the explored angle. Inspection of the results indicates that dwell-time did not covary with the absolute value of the angle explored. Linear regression analyses indicated that the slopes of the relations calculated for each session, dwell-time versus angle, were not different from 0 ($P>0.5$). Figure 4.4.3A also shows that there was a trend for dwell-time to decrease with repetition, but this was not significant (repeated measures ANOVA, $F(2,10)=1.053$, $P=0.38$). Dwell-time also did not vary with the direction of the scan (respectively, a-b-c and c-b-a, as in Fig. 4.3.2), consistent with subjects collecting relevant sensory information during both passes over the

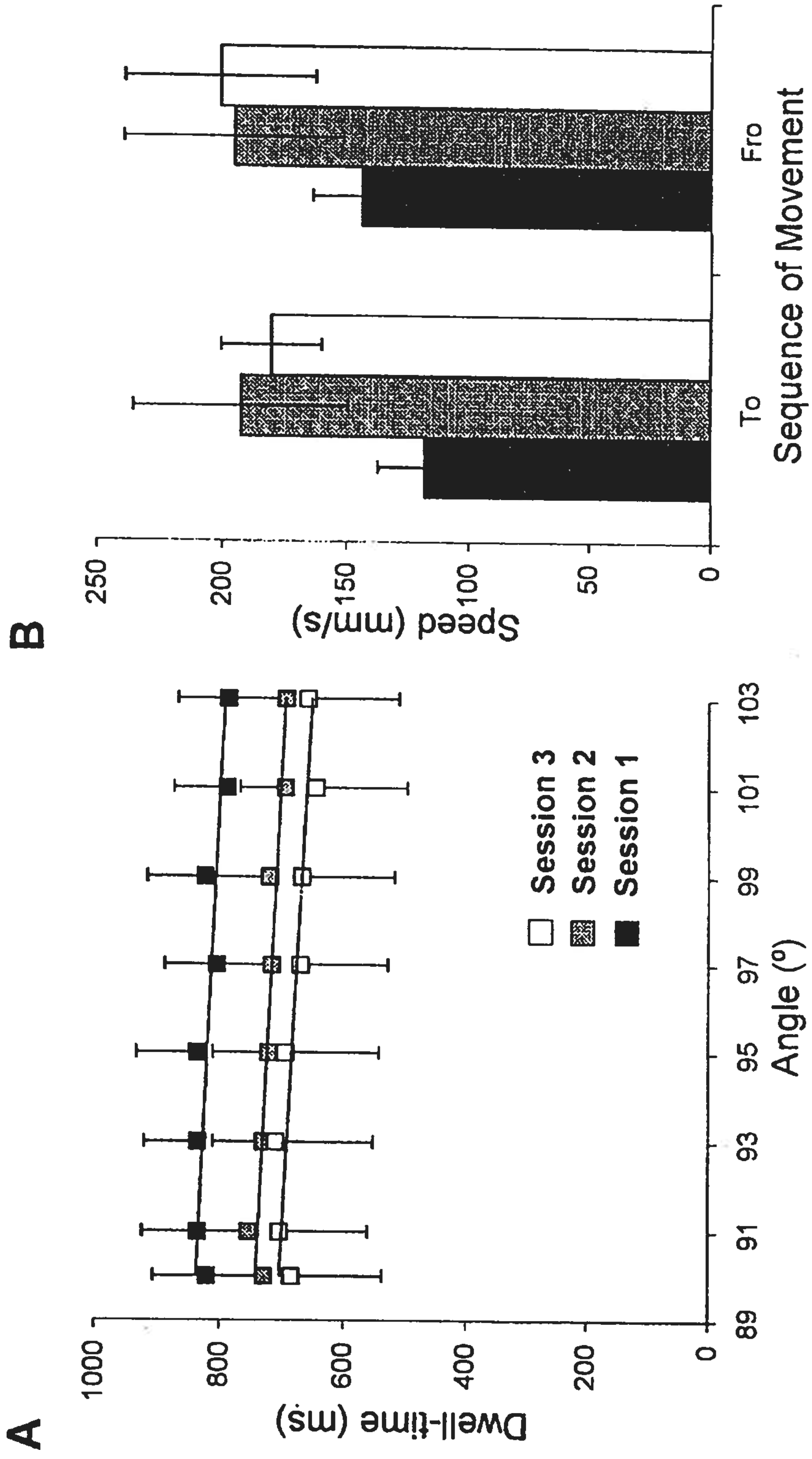

Fig. 4.4.3 A Mean dwell-time (±SEM) at the intersection, b, as a function of the angle presented (n=6, experiment 1). Data from three repeated sessions are shown along with the linear regressions. B Mean scanning speed (± SEM) as a function of the direction of the scanning movement over the angle (to: ab, bc; fro: cb, ba) and the session (three repetitions in six subjects)

angle of intersection (F(1,5)=0.021, P=0.89). Finally, there was considerable variability in dwell-time between subjects, ranging from a low of 208 ms for subject 5 (session 1) to 1,286 ms for subject 7 (session 3). Similar analyses were applied to measures of scanning speed (n=6). As in Fig. 4.4.3 A, speed did not vary as a function of the angle explored (P>0.7). Practice, on the other hand, led to a significant increase in speed (F(2,10)=7.804, P=0.009), from 135 mm/s in session 1 to 156 mm/s in session 2 and 220 mm/s in session 3. Inspection of Fig. 4.4.3 B shows that the latter effect was evident when the data were resorted according to the direction of the to-and-fro movement. As found with dwelltime, speed did not vary with the direction of the scanning movement (F(1,5)=2.22, P=0.13). Thus, subjects likely collected relevant sensory information during both passes over the 2D shape. Individual subjects were free to choose their own scanning speed; consequently there were large variations between subjects, from a low of 87 mm/s for subject 1 (session 1) to a high of 392 mm/s subject 6 (session 3). Nevertheless, there seemed to be no speed-accuracy trade-off because performance did not change significantly across the three repeated sessions (above). Indeed, performance was marginally improved with practice. Finally, we used linear regression analyses to determine whether dwell-time and speed covaried (18 sessions in six subjects). Only one of six subjects showed a significant and consistent relationship between dwelltime and scanning speed across all three sessions, suggesting that the two parameters were controlled independently.

4.4.4 Cognitive strategies employed in 2D angle discrimination

All but two subjects reported creating mental images of the angles (Table 4.4.2, W for whole angle), and using these to compare the two angles of each pair. One subject specifically reported creating a mental image of the scanning movements themselves (M in Table 4.4.2). The majority of subjects (seven of nine) also reported using the pattern of cutaneous feedback from the intersection (I for intersection in Table 4.4.2), with one subject describing this as her sole strategy. Interestingly, the dwell-time at the intersection did not vary as a function of the strategy used by the subjects, i.e. subjects that used the pattern of cutaneous feedback from the intersection did not spend more time at the intersection than those relying only on mental images of the angles (respectively, 650 ms and 810 ms; t-test, P=0.51; see also the previous section). Finally, when asked to estimate the values of the angles presented, subjects over estimated the range of differences presented by an average of 32° (12° to 77°).

4.4.5 Two-dimensional angle discrimination is independent of angle rotation (experiment 2)

The results of experiment 1 indicated that the mean discrimination threshold across all subjects and all sessions was 4.7°±0.5° (SEM). This value was close to the 4° shift that was imposed on one of the angles presented in each trial, leading us to question what the contribution of the arbitrary choice of a 4° shift was to the results. In order to address this issue an additional six subjects were recruited to participate in a second experiment in which the value of the shift applied to one of

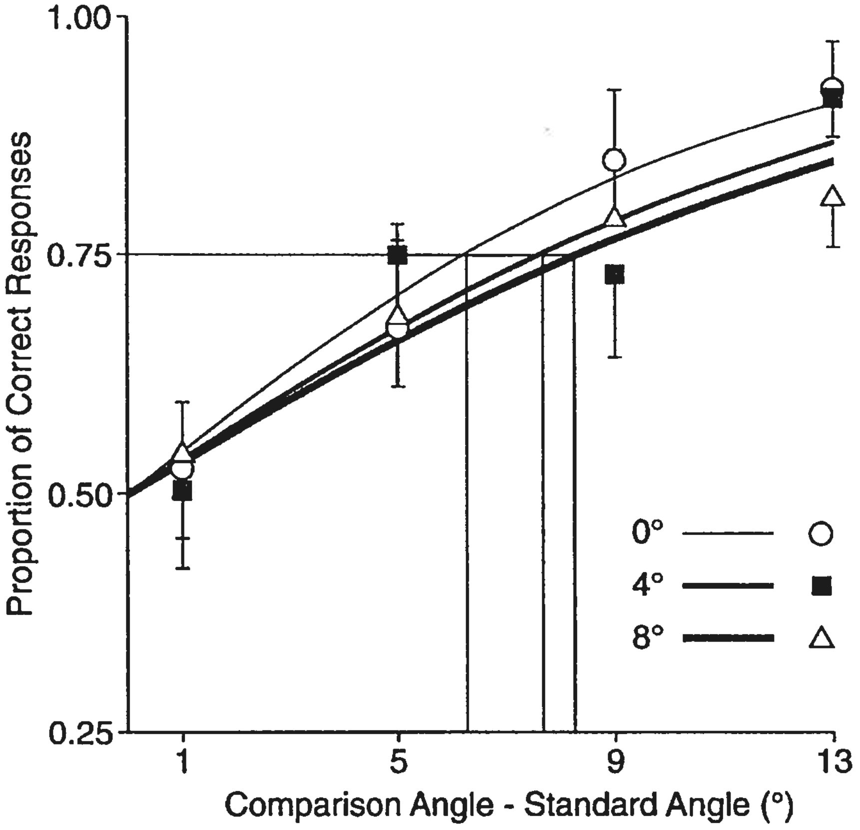

Fig. 4.4.5 Effects of modifying the shift that was imposed on one angle in each pair, 4°, 8° and 0° (no shift), on the ability of six subjects to discriminate 2D angles (experiment 2). Note that only five subjects participated in the no shift condition. Data plotted as in Fig. 4.4.2

Subject	0° Shift	4° Shift	8° Shift	Sex	Strategy
10	–	5.3	**6.6**[a]	m	–[b]
11	6.0	8.7	**>13**	f	*WI*
12	3.0	**5.7**	8.6	f	*WI*
13	7.8	**3.7**	4.2	m	*WI*
14	5.2	>13	**>13**	m	*WI*
15	3.7	**12.2**	5.5	f	*W*
Mean	5.1	8.1	8.5		

[a] First block in the session indicated in bold; the 0° shift was tested in the third and final block of trials

[b] Subject not naive

Table 4.4.5 Discrimination thresholds (°) in six subjects (experiment2) as a function of the magnitude of the shift applied to one of the angles presented in each trial, sex and cognitive strategy the angles was systematically varied across three blocks of trials, 4°, 8° and 0°, all performed within a single experimental session. We did not want to influence the subjects' strategy, and wanted them to adopt the same strategy that was encouraged in experiment 1. Thus, the order of testing in the first two blocks was counterbalanced for the 4° and 8° shifts, with the 0° shift being tested as the final block of the session. As in experiment 1, the subjects were not informed about the existence of the shift. The pooled results are illustrated in Fig. 4.4.5. In this experiment, only four comparison angles were presented (91°, 95°, 99° and 103°) in order to collect all of the data during a single session. As can be seen in Fig. 4.4.5, the three logistic curves calculated from the pooled data were similar, although there was a small shift to the left, and so a decrease in discrimination threshold, as the shift was decreased from 8° to 0°. The individual discrimination thresholds are given in Table 4.4.5. Mean discrimination threshold increased from 5.1° (no shift) to 8.1° (4° shift) and 8.5° (8° shift). A repeated measures ANOVA, however, indicated that the difference was not significant (F(2,8)=2.0, P=0.197). This observation suggested that our choice of a 4° shift likely did not contribute to the results.There is nevertheless some suggestion that evaluation of the orientation of one arm of the pair of angles, which would have been the optimal strategy in the no shift condition, is better than the ability to discriminate a whole angle since threshold was lowest in the no shift condition. As in experiment 1, neither dwell-time nor scanning speed covaried with the angle scanned. In addition, neither parameter showed a significant change with practice during the same experimental session (dwelltime, F(2,8)=2.3, P=0.16; speed, F=2.94, P=0.11). Subjects reported using the same strategies as those that participated in experiment 1 – a mental image of the angles along with, in all but one subject, cutaneous feedback from the intersection, specifically the amount of compression of the finger at the angle. Interestingly, only one subject (subject 8, experiment 1) noticed the presence of the shift in these experiments.

4.4.6 Intersubject variability

There was considerable variability between subjects in their ability to discriminate changes in 2D angles in experiments 1 and 2 (Fig. 4.4.1 B, Tables 4.4.2, 4.4.5). We considered the contribution of differences in arm length to the results. This was a potentially important factor since the relevant proprioceptive feedback came from the shoulder. If proprioceptive input were critical for the task, then we reasoned that subjects with a longer arm would have a higher discrimination threshold than subjects with a shorter arm because the increased length of the lever arm would require a larger displacement to effect the same angular change at the shoulder. As shown in Fig. 4.4.6, there was a trend for discrimination threshold to increase with arm length, but the linear regression was not significant (n=15, P=0.52), suggesting that some other factor was responsible for the differences between subjects. We also examined the possibility that the difference was related to subject gender, but no difference was observed: threshold was 8.1° for women (n=7) and 5.7° for men (n=8) (P=0.16: t-test on the data used for Fig. 4.4.6). Perceptual performance likewise did not vary with the motor strategy: discrimination threshold did not vary with either scanning speed (n=15, P=0.21) or dwell-time at the intersection (n=15, P=0.32, linear regression analyses). Finally, it did not appear that differences in the cognitive strategy contributed to the results b cause there was no difference in discrimination

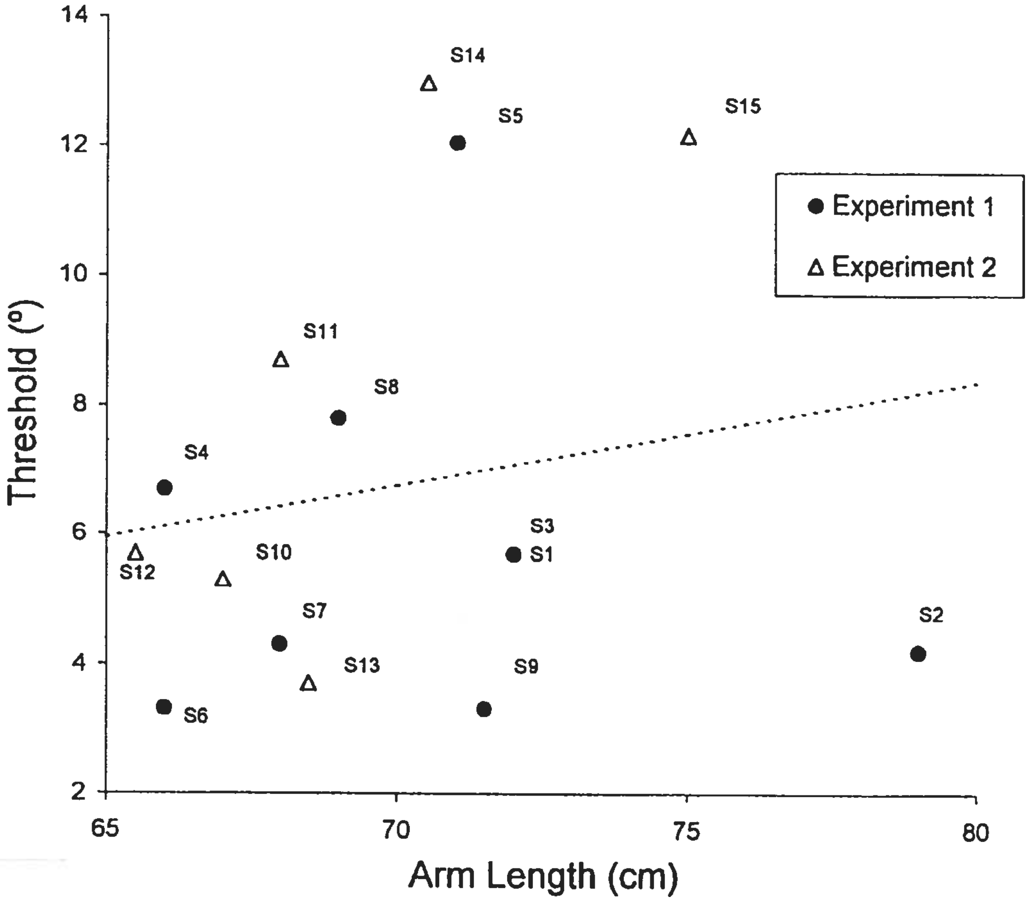

Fig. 4.4.6 Discrimination threshold did not covary with arm length (linear regression, P=0.52). Data from both experiment 1 (nine subjects, session 1) and experiment 2 (six subjects, 4° shift imposed, as in experiment 1) are shown. Arm length was measured from the acromion to the mid-point on the middle phalanx of the index finger

threshold for subjects using the mental image strategy alone (n=3) versus those using the mental image plus cutaneous feedback (n=9) (P=0.99). Together the results suggest that individual differences in sensitivity to 2D angles were likely responsible for the differences across subjects, although we cannot rule out the possibility that other factors (e.g. finger circumference) also contributed.

4.5 DISCUSSION

This controlled study of the human ability to evaluate 2D shape has shown that subjects can discriminate angular changes of 4.7° (range 0.7° to 12.1°), from a standard angle of 90°, when scanning objects using the index finger of the outstretched arm. Although the motor strategy was partly modified with practice, perceptual performance showed no significant change. Finally, 2D angle discrimination was not significantly modified by rotating the orientation of one of the angles in the pair. If subjects had based their decision on either the orientation of one arm of the angle or the movement trajectories themselves, then performance should have been modified by the shift. The negative findings indicate that the subjects based their sensory decision on a central representation of the angle itself.

4.5.1 Methodological considerations

In these experiments, we employed a strategy described by Johnson (1980) to evaluate the ability of subjects to discriminate small changes in 2D angles whereby subject scanned the standard angle (90°) and a modified or comparison angle (91°–103°) on each trial, with the order counterbalanced (MSSM strategy), identifying the larger angle of the pair. This approach gives a bias-free measure of sensory perception, and it was chosen because subjects have to use a paired-comparison strategy, independently evaluating each angle of the pair. We wanted to avoid the situation in which subjects might initially use a paired comparison strategy, and then switch to another strategy. For example, when the standard stimulus is always presented first, subjects often develop an internal model of the standard and use this for comparison, rather than independently evaluating each stimulus. We were also concerned in these experiments that subjects might opt to attend simply to the orientation of the second segment of the angle, rather than generating an independent, internal representation of each of the scanned angles. This possibility was raised in debriefing of laboratory personnel who participated in the pilot experiments. In order to discourage such an approach, we imposed an arbitrary shift of 4° on one angle of each pair presented. This value was chosen so as to produce a minimal change in the initial position of the digit (position a in Fig. 4.3.2) of approximately 5.5 mm towards the midline. The shift could easily be imposed in these experiments because the subject had to withdraw the finger from the apparatus while the angle was changed. The strategy was successful because few subjects reported noticing the shift, even when it was doubled (8°) or removed entirely (0°) in the second experiment. The one exception was subject 8 (experiment 1). More importantly, the results of experiment 2, showing no difference in discrimination threshold across the range of shifts, indicate that the subjects based their sensory decision on a central representation of the angle itself, and not the orientation of one arm of the angle. In other words, they analyzed the shape of the experimental objects according to the instructions given.

4.5.2 Effects of practice

There was no significant improvement in 2D angle discrimination with repetition, possibly because no feedback as given on performance. There was, on the other hand, a change in the motor strategy with practice. Specifically, average scanning speed increased with practice.We attribute this observation to the subjects growing accustomed to scanning, without visual feedback, the fixed length arms of the experimental objects. Interestingly, the movement speeds chosen by the subjects, ranging from 87 to 372 mm/s, were well within the range that Hall and McCloskey (1983) reported as optimal for the detection of imposed joint rotations (from ~20 mm/s up to 500–1,000 mm/s for the elbow and shoulder). This suggests that the minor increases in speed with practice did not substantially influence the quality of the sensory feedback during scanning. One other parameter of interest, the dwell-time at the angle of intersection, showed no change with practice, possibly reflecting the importance for task performance of the cutaneous feedback generated while the finger was in contact with the angle.

4.5.3 Memory demands of the task

This discrimination task called upon working memory to retain a central representation of the first stimulus for subsequent comparison with the second stimulus. There was a substantial delay between stimuli (14 s, range 7.6–25 s), and it is reasonable to expect that there may have been some degradation of performance over time as seen in studies of visual working memory (Alvarez et al.

1994; Petrides 2000; Toni et al. 2002). However, we do not know the exact influence that the delay between the scans of the first and second angles had on our results. Further experiments, systematically varying the delay interval, are needed to address this point.

4.5.4 Cognitive strategies

Our 2D angle discrimination task was designed so that proprioceptive feedback came mainly from the shoulder, while cutaneous feedback arose from cutaneous mechanoreceptors innervating the glabrous skin of the exploring index finger. Thus, both sources of feedback could, potentially, contribute to task performance. The cognitive strategies employed by the subjects to perform the discrimination task provide an indication of the salient sources of information. Subjects frequently reported generating mental images of the scanned angles and using the pattern of feedback from the intersection of the two arms of the angle. The mental image of the scanned angle was likely based mainly on proprioceptive feedback from the shoulder generated as the two arms of the object were explored. Since scanning speed was similar for both directions of movement, it appears that subjects collected relevant sensory information during both passes over the 2D shape. Muscle spindles in the shoulder musculature are the most likely candidate, although we cannot exclude a role for Golgi tendon organ or joint afferents. Central signals, particularly the efference copy, may also have contributed to the mental image. But only one subject reported basing her discrimination, in part, on the movements themselves. It is possible that cutaneous information from the index finger also contributed to this mental image. In these experiments, subjects were instructed to maintain a rigid arm posture throughout the scan, with the result that the area of skin in contact with the object changed as the first and the second arms of the object were scanned (radial first, ulnar second). This change in the pattern of skin contact may have contributed to the mental image. A further cue may have been generated at the second 90° stop, position c, but none of the subjects reported attending this feature. All of the digital mechanoreceptive afferents involved in tactile perception were likely activated during the scans [slowly adapting types I and II (SAI, SAII); rapidly adapting; Pacinian]. While other sources of cutaneous feedback were likely present (e.g. from the shoulder), extraneous sources that might have contributed unwanted cues were eliminated by having the subjects wear a sleeveless shirt during the testing. The "intersection" strategy, on the other hand, depended on the amount of compression when the finger was at the intersection, i.e. during the dwell-time at the angle. Although the latter varied across subjects (~200–1,300 ms), this evidently provided sufficient time to derive a representation of the angle through skin deformation. The relevant feedback was entirely cutaneous in origin, likely signalled by SAI receptors since it is known that they can provide information about the precise pattern of skin contact with local contours (LaMotte and Srinivasan 1987a, 1987b; Wheat et al.1995; Goodwin et al. 1997). Independent of the cognitive strategies and despite the high degree of precision of subjects in the 2D angle discrimination task, we were surprised at the overestimates of the angles explored by the subjects. While most subjects recognized that a 90° angle had been presented, they thought that the range of differences spanned 25° to 90° (mean 45°). This is appreciably greater than the actual range of 13°. One explanation for this observation is that the subjective estimates were based on the angle formed by the most extreme spatial coordinates encountered during the scans (a vs c, Fig. 4.3.2). With the 4° shift, the apparent range may thus have been 21°. Since the estimates given by the subjects exceeded the apparent range, it appears that some other factor was also involved. We speculate that this might be related to the length of the arms of the angle, which were arbitrarily set at 8 cm. The wide separation of the end positions (a and c in Fig. 4.3.2) may have made absolute angle estimation difficult. If this explanation is correct, then reducing the length of the arms should result in estimates closer to the actual angular values presented. To summarize, most subjects used both a mental image of the scanned angles and the pattern of cutaneous feedback from the intersection to perform the discrimination task. The former was likely based on proprioceptive feedback from the shoulder, but we cannot exclude an additional role for cutaneous feedback as well. As shown in the companion paper (Voisin et al. 2002), selective elimination of each of these sources of salient input led to an increase in discrimination threshold. No other source of sensory information contributed because performance fell to chance levels when both inputs were eliminated.

4.5.5 Previous studies of curvature

Previous studies of the human ability to discriminate differences in object shape have mainly concentrated upon the discrimination of curvature, either local curvature (what can be sensed with a fingertip) or larger macro curvatures that require movement and so likely draw upon information signalling joint position as well as local cutaneous feedback. Goodwin and colleagues (Goodwin et al. 1991;

Goodwin and Wheat 1992) reported that subjects can discriminate differences in local curvature on the order of 10–18% depending on the curvature of the standard surface. This ability is, in part, independent of the area of skin contact. In experiments using larger macro curvatures, Gordon and Morison (1982) reported much less precision in discrimination performance: the absolute difference perceived was impressively small (difference in 0.11 mm between the base-to-peak heights of the surfaces), but performance was relatively poor as a proportion of the standard (85% difference discriminated). Using three-dimensional objects, on the other hand, Roland and Mortensen (1987) found that the discrimination threshold for the size of solid spheres was constant, 0.39 mm, for radii ranging from 10 to 25 mm. This translates into an impressive precision of 1.6–3.9%, clearly superior to the results obtained using local curvature (above) and so suggesting that sensory performance is better in tasks that recruit the entire panoply of somatosensory receptors (cutaneous, muscle, tendon and joint receptors). Consistent with this, the present results gave a precision of 5.2% (4.7°/90°) for 2D angle discrimination. Indeed the best subject could discriminate the smallest difference presented, 1°, corresponding to a precision of close to 1%. Previous studies of position and movement How then do our results compare to studies of joint position/movement sense? In other words, can the results be explained entirely on the basis of the known precision of proprioception at the shoulder? This is a difficult question as our task could call upon both dynamic and static position-related signals. Thus both 'movement' (dynamic) and 'position' (static) sense could have contributed. We know that detection of movement can be extremely precise. For example, Hall and McCloskey (1983) reported that subjects could detect movements of only 0.1° applied to the shoulder at angular velocities of 1.25° up to

80°/s. Less is known about movement discrimination, but Jones et al. (1992) reported that discrimination thresholds for movements about the elbow are of the order of 8% (range 4–19%). In the present study, the corresponding Weber fractions (experiment 1) were 5.2% (range 0.8–13.4%), i.e. discrimination thresholds when expressed as a proportion of the standard stimulus were lower than found by Jones et al. The difference may reflect differences in precision for the shoulder as compared to the elbow (e.g. Hall and McCloskey 1983; Clark 1992; Clark et al. 1995), or alternately the use of additional sources of information (cutaneous, static position sense).

The sense of static limb position, which could also have contributed to our results, has been quantified most frequently by measuring accuracy using either a matching paradigm or a pointing task. Direct comparisons with the present results are complicated by several factors. First, there are more sources of measurement errors in matching paradigms than in this study. Second, pointing tasks often involve a transformation, e.g. from an external to an internal coordinate frame, that was not required in this study. Third, subject strategy needs to be explicitly defined: Soechting (1982) showed that if subjects match orientation in space (an external frame of reference) rather than absolute joint angle (an internal frame of reference), then precision is improved (mean errors of 6.7° and 9.6°, respectively) at least under certain testing conditions (see Darling 1991). Finally, differences in the mode of movement (active vs passive) can influence the quality and quantity of sensory feedback. Consequently, we restrict our comparisons to studies that used active movements to assume both the reference and comparison positions. Cohen (1958), using a task in which subjects repositioned their arm at a remembered location (no vision), reported that the mean error for shoulder position sense was approximately 2.7° (range 1.4° to 4.7°). More recently, van Beers et al. (1998) reported much greater precision for finger-pointing tasks, ranging from 0.6° to 1.1°, but in this case the estimate was based on measures of variance and not absolute error. When the present results are expressed in terms of shoulder angles (difference in position at the end-point of the second arm), the mean discrimination threshold for experiment 1 corresponds to a change in shoulder position of 0.54° (range 0.08° to 1.36°). These values are considerably lower than those measured by Cohen and, in part, fall outside the range reported by van Beers et al. At the very least, these observations suggest that static position sense alone cannot account for the results.

Interestingly, our mean threshold estimate of 0.54° of shoulder movement is identical to that predicted by a model developed by Scott and Loeb (1994), based on muscle spindle distribution in the muscles spanning the human shoulder. Nevertheless, the best performance in this study (0.08°) was considerably more precise than their estimate. We suggest that the results can best be explained by the combination of multiple sources of sensory information – dynamic position sense, static position sense and cutaneous feedback. This suggestion is consistent with the reported strategies of the subjects. On the other hand, the importance of cutaneous inputs might be questioned since mean discrimination threshold in this study, 4.7° difference, was actually larger than the 3° difference obtained by Laszlo and Bairstow (1980) using an angle discrimination task that depended only on kinaesthetic feedback from whole-arm movements. Our results are, however, superior when expressed in terms of vertical displacement of the end point. Our best performance, 0.7°, corresponded to a 1-mm change in the end-point; this was more precise than the best performance of 1° or 5.3 mm in Laszlo and Bairstow's study. The higher sensitivity in our study is consistent with our suggestion that cutaneous feedback contributed to 2D angle discrimination, making the 2D discrimination task one that is dependent on haptic feedback, i.e. the combination of proprioceptive and cutaneous inputs. Direct experimental support for this suggestion is provided in the companion paper (Voisin et al. 2002).

4.6 ACKNOWLEDGEMENTS

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CHAPITRE V - ARTICLE 2

Haptic discrimination of object shape in humans: contribution of cutaneous and proprioceptive inputs.

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5.1 ABSTRACT

Using two-dimensional (2D) angles composed of two straight, 8-cm-long arms that formed an angle, we investigated the importance of cutaneous feedback from the exploring index finger, and proprioceptive feedback from the shoulder (scanning movements made with the outstretched arm), to the human ability to discriminate small differences in the angles. Using a two-alternative forced-choice paradigm, subjects identified the larger angle in each pair explored (standard angle, 90°; comparison angles, 91° to 103°). Subjects were tested under four experimental conditions: (1) active touch (reference condition); (2) active touch with digital anaesthesia; (3) passive touch (a computer-controlled device displaced the angle under the subject's immobile digit); and (4) passive touch with digital anaesthesia. When only proprioceptive feedback from the shoulder was available (condition 2), there was a significant increase in discrimination threshold, from 4.0° in the reference condition (condition 1) to 7.2°, indicating that cutaneous feedback from the exploring digit contributed to task performance. When only cutaneous feedback from the finger was available (condition 3), there was also a significant increase in threshold from 4.2° in the active condition to 8.7°. This suggested that proprioceptive feedback from the shoulder, potentially from a variety of deep (muscle and joint) but also cutaneous receptors, contributed to the ability to discriminate small changes in 2D angles. When both sources of feedback were eliminated (condition 4), subjects were unable to discriminate even the largest difference presented (13°). The results suggest that this sensory task is truly an integrative task drawing on sensory information from two different submodalities and so, following the definition of Gibson, is haptic in nature. The results are discussed in relation to the potential neural mechanisms that might underlie a task that requires integration across two anatomically separate body parts and two distinct modalities.

Keywords Tactile shape discrimination · Two-dimensional angles · Active touch · Passive touch

5.2 INTRODUCTION

When you manipulate an object in your hand with a view to identifying the object, sensory feedback is generated from multiple sources, including mechanoreceptors in the skin and also mechanoreceptors in deep structures (muscle, tendon, joint). This complex feedback, which we term haptic feedback here (following Gibson 1966), must be integrated across both space and time in order to define object shape. In the companion paper (Voisin et al. 2002), we reported on the development of a sensory task that allowed us to begin to evaluate, in a rigorous and parametric fashion, the human ability to discriminate simple two-dimensional (2D) shapes composed of two straight arms that formed an angle. The task was specifically designed so that both cutaneous feedback from the exploring index finger and proprioceptive feedback from the shoulder (movements made with the outstretched arm) could potentially contribute to defining the shape of the experimental objects. Two important observations were made. First, performance of the 2D angle discrimination task was not modified by changing the orientation of one of the two angles that were presented in each trial (standard angle of 90° and comparison angles of 91°–103°). This observation indicates that subjects based their sensory decision on a central representation of the angle itself, and not the orientation of one arm of the angle, i.e. they analysed the shape of the experimental objects, as per the instructions given. Second, performance in the task, when expressedin terms of angular changes at the shoulder, was superior to that predicted from previous studies of static position sense at the shoulder, a range of 0.08° to 1.36° versus 1.4° to 4.7° (Cohen 1958a) or 0.6° to 1.1° (van Beers et al. 1998). This result strongly suggests that static position sense alone cannot explain the results. Two other sources of sensory feedback could have contributed. On the one hand, cutaneous feedback, generated when the finger was in contact with the angle of intersection, could have contributed to the high degree of precision found in this task. Such a suggestion is supported by the fact that a majority of subjects reported basing their sensory decision, at least in part, on cutaneous information from the angle of intersection, specifically the amount of compression of the finger at the angle. On the other hand, dynamic position feedback (movement sense) may also have contributed in the form of sensory reafference from the moving limb, possibly interpreted in relation with the motor command (Gandevia et al. 1993). Such a suggestion is consistent with Kelso's (1977) observation that anaesthesia of the hand and fingers, eliminating cutaneous feedback from the hand while preserving muscle spindle feedback from the long flexors of the digits, had no effect on the accuracy of voluntary finger movements. The purpose of this study was to confirm our suggestion that both cutaneous feedback from the exploring digit and proprioceptive feedback from the shoulder contribute to the human ability to discriminate differences in 2D angles by scanning the angles with the index finger of the outstretched arm. This was addressed by measuring performance in the task under four conditions: (1) active touch, with both cutaneous and proprioceptive feedback available; (2) active touch with digital anaesthesia, so that only proprioceptive feedback was available; (3) passive touch, whereby a computer-controlled device displaced the angle under the subject's immobile digit so that only cutaneous feedback was available; and (4) passive touch with digital anaesthesia, so that neither source of feedback was available. The results support our hypothesis that both cutaneous and proprioceptive feedback contribute to 2D angle discrimination, since perceptual performance declined when either source was eliminated. Indeed, subjects were unable to perform the task when both sources of feedback were eliminated. Preliminary reports of the results have been published (Voisin and Chapman 2000, 2001).

5.3 MATERIALS AND METHODS

5.3.1 Subjects

The subjects were eight healthy adults (three women and five men; 21–27 years of age), all right handed for writing. Participation was voluntary, and remunerated. The institutional ethics committee approved the experimental protocol, and all subjects gave their informed consent prior to the experiments. Subjects participated in one (*n*=4), three (*n*=2) or four (*n*=2) experimental sessions. Each session lasted 3–4 h, and consisted of two blocks of 56 trials. The methods are described in Voisin et al. (2002). Below, there is a brief recapitulation of the methods and a description of the salient differences.

5.3.2 Perceptual task

The angles, apparatus and task are described in the companion paper. In brief, subjects scanned pairs of angles, using the glabrous skin of the middle phalanx of the right index finger of the outstretched arm, and identified the larger angle of each pair by pressing one of two response buttons on a keypad with their left hand (first or second angle larger). Each angle was scanned with a single to-and-fro movement (sequence *a-b-c-b-a*, Fig. 5.3.2 A). The angles were machined from 1-cm-thick Plexiglas (see Fig. 5.3.2 A). Each arm was 8 cm long, and the first arm explored was identical for all angles. The angle at the intersection of the arms was 90° for the standard angle (four replicates used). The comparison angles (n=7) spanned a range from 91° to 103° (increments of 2°). The angles were firmly clamped in an apparatus (see Fig. 5.3.2 B) instrumented to record contact force and digit position. The latter was monitored using the outputs of optical sensors, paired with light emitting diodes (LEDs) placed so that they were interrupted when the index finger was at the start position (*a*), the intersection (*b*) or the end position (*c*). The subject was comfortably seated beside the apparatus (vision and hearing occluded), which was placed at arm's length from the subject, at the level of the shoulder, 30° to the right of midline. During a trial, one standard angle and one comparison angle was presented. As in the companion paper, one of the two angles in each pair was slightly rotated towards the midline (4° shift in the vertical plane) to encourage subjects to evaluate the whole angle, and not simply the orientation of the second arm of the angle relative to horizontal. Subjects were not informed of the presence of the shift, or given any feedback on their performance.

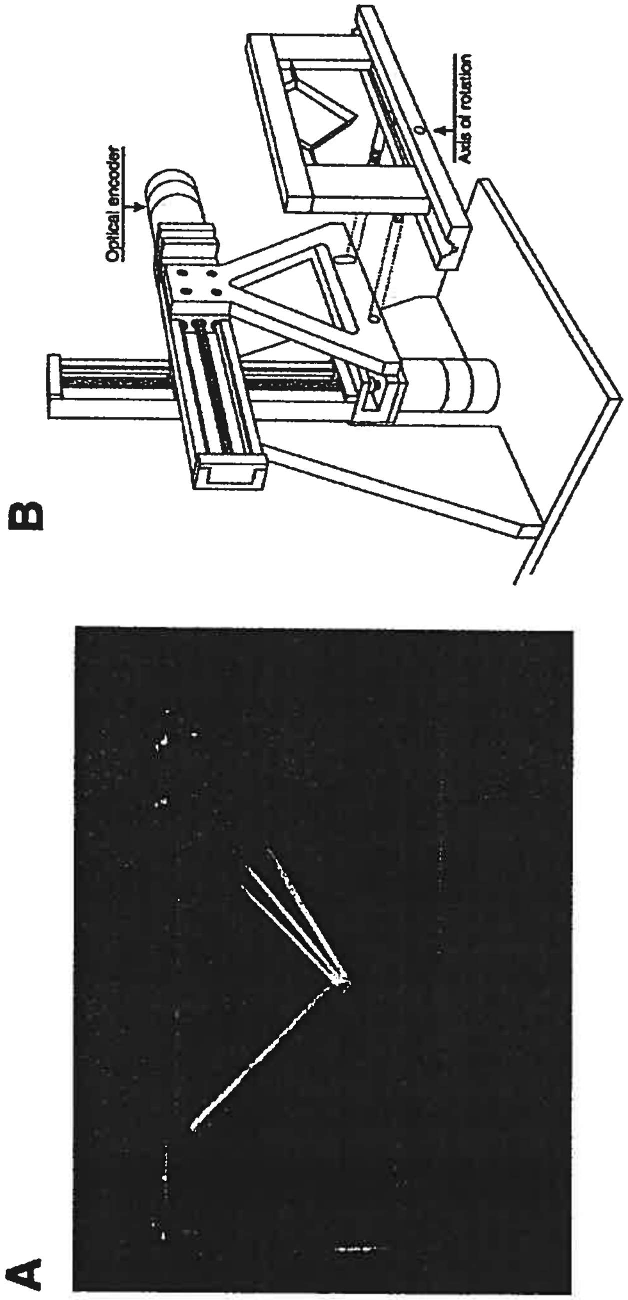

Fig. 5.3.2 A Photograph of the experimental objects showing, from back to front, the standard angle (90°) and two comparison angles (95° and 103°). All scans started with the index finger placed at position a. The sequence of movement was a-b-c-b-a, where b corresponds to the angle at the intersection and c was located at the end of the second of the two arms that formed the angle. B Setup for passive scanning of the angles, showing the x-y stage, optical encoders, and the method for attaching the experimental apparatus, into which the angles were clamped, onto the x-y stage. The apparatus could be rotated on the mounting (see axis of rotation)

Each comparison angle was presented 8 times in a pseudorandom order for a total of 56 trials per block. The order of testing was counterbalanced for all relevant factors (shift on the first or second angle; standard angle presented first or second). The first block of trials in each session was preceded by several practice trials to familiarize the subject with the scanning movement (active or passive, depending on the experiment and the order of testing) and the perceptual task. Practice trials were repeated for the second block of trials in most cases, in order to allow the subjects the time to familiarize themselves with the changed experimental condition (after anaesthesia; passive instead of active scans). An exception was made for three subjects for which the second block was identical to the first (two blocks with local anaesthesia).

5.3.3 Experimental conditions

5.3.3.1 Condition 1: active touch with both cutaneous and proprioceptive feedback

Subjects made an active to-and-fro scanning movement, sliding the index finger over the angle. Subjects were specifically instructed to keep the arm (and digit) straight throughout the scan (nail up), limiting rotation to the shoulder. The sequence of events in a trial was: (1) the first angle was installed in the apparatus; (2) the experimenter guided the subject to position the index finger at the initial position (*a* in Fig. 5.3.2 A); (3) the experimenter started data acquisition with a carriage return; (4) 300 ms later, a tone signalled the subject to begin the first scan; (5) the subject scanned the index finger over the angle (sequence, *a-b-c-b-*

a); (6) after completing the scan, the subject withdrew the finger from the angle; (7) the second angle was installed in the apparatus; (8) steps 2–6 were repeated; and (9) the subject entered his/her response in the keypad. Note that subjects kept the upper limb rigid throughout the scan, so that the skin area in contact with the object varied as a function of the arm explored (radial side of the middle phalanx for *ab*; ulnar side for *bc*).

5.3.3.2 Condition 2: active touch with anaesthesia (no cutaneous feedback)

Performance of the 2D angle discrimination task was tested in the absence of cutaneous feedback from the index finger in order to determine the ability of subjects to perform the discrimination using only proprioceptive feedback. The sequence of events in the trials was identical to that described for condition 1. The right index finger was anaesthetized under medical supervision using a ring block at the level of the proximal phalanx; up to 4 ml 2% lidocaine was injected subcutaneously at multiple sites distributed around the circumference of the proximal phalanx, just distal to the metacarpophalangeal joint. In three subjects, the ring block was repeated after the first block of trials, and a second block of trials with anaesthesia was recorded (pause of ~30 min between blocks). In one subject, 2.5 ml 2% mepivacaine was employed instead of the lidocaine. Light touch was abolished distal to the injection sites within 15–20 min. We verified the state of anaesthesia (abolition of light touch) at 20-min intervals during the session. Subjects reported that the effects of the local anaesthesia lasted for several hours after the end of the session.

5.3.3.3 Condition 3: passive touch (no proprioceptive feedback)

In order to assess the ability of subjects to perform the angle discrimination task using only cutaneous information, the angles were displaced passively, under servo control, over the glabrous skin of the outstretched, immobile index finger. As shown in Fig. 5.3.2 B, the apparatus was mounted on a vertically oriented x-y stage (Thomson microstage, MS33-LXB-L300). Each axis was equipped with a DC servomotor (Aerotech, model 1017) and an optical encoder (Sumtak opticorder, LDA-051-800). The desired movement trajectory was controlled by a microcomputer using a FlexMotion-6C controller to operate a multiaxis linear servo amplifier (Servo Dynamics, SD2-412-45-2F). The trajectory was updated every 125 μs; examples of the up and down trajectories are shown in Fig. 5.4.3 B. The mounting on the x-y stage was adjustable so that the 4° shift in orientation could be imposed as in the active condition (axis of rotation shown in Fig. 5.3.2 B). The sequence of events in a trial was identical to that described for condition 1 with the exception that the subject was now required to remain motionless throughout the angle presentation (position identical to the initial position in condition 1), all the while maintaining contact with the object. The angle was presented using the same movement sequence as in the active condition, *a-b-c-b-a*, with each angle and shift having its own unique point-to-point trajectory. The contact surface on the index finger was identical to that for condition 1, with the skin area in contact varying as a function of the arm presented (radial side for *ab*; ulnar side for *bc*). For each subject, the mean speed was chosen to match the subject's own movement parameters in the active task. This was calculated from the outputs of the optical sensors, using data collected either in the immediately preceding session (subjects 4, 6 and 7) or in the same session (subjects 8 and 9).

5.3.3.4 Condition 4: passive touch with anaesthesia (no cutaneous or proprioceptive feedback)

This control experiment addressed the possibility that subjects used some source of feedback other than cutaneous feedback from the index finger and proprioceptive feedback from the shoulder to perform the 2D angle discrimination. The right index finger was anaesthetized with 2.5 ml 2% mepivacaine (see condition 2 above). After light touch was abolished, performance of the 2D angle discrimination task was evaluated using passive touch, as described for condition 3.

5.3.4 Order of testing

Performance in condition 1 (active touch with cutaneous and proprioceptive feedback) served as the reference for two of the three modified experimental conditions, conditions 2 and 3. The reference data are, in part, a subset of those presented in the companion paper (Voisin et al. 2002). For condition 2 (active touch with anaesthesia), the reference condition was tested before anaesthesia, either in the same session (*n*=2) or in the immediately preceding session (1–3 days earlier; *n*=3). In the latter case, performance during anaesthesia was evaluated in two repeated blocks of 56 trials. For condition 3 (passive touch), the order of testing in the session was counterbalanced (three subjects, condition 1 first; two subjects, condition 3 first). For condition 4 (passive touch with anaesthesia), passive touch (condition 3) served as the "reference" condition; this testing occurred in the same session, immediately preceding the anaesthesia.

5.3.5 Data acquisition and analysis

The following data were recorded with each trial: the subject's response, the value of the angles scanned (including their order of presentation and the presence of the 4° shift), the contact force, and the times that the digit arrived at, and left, positions *a*, *b* and *c* during the course of the to-and-fro movement. For each subject, discrimination performance was characterized by computing the proportion of correct responses for each comparison angle in each block of trials. The results were fitted to a logistic function, and discrimination threshold (75% correct) was computed from the logistic function. To assess the respective contribution of cutaneous and proprioceptive feedback to 2D angle discrimination, the effects of the exploratory condition on discrimination threshold were analysed with paired *t*-tests (condition 1 vs condition 2; condition 1 vs condition 3). The scanning movements were characterized by calculating the scanning speed (output of the optical sensors), the length of time that the digit was in contact with the angle at the intersection (dwell-time) and contact force (output of the strain gauges). Paired *t*-tests were employed to determine whether the exploratory conditions were the same in the reference condition (1) and the modified conditions (2 and 3). Finally, the trajectory of the index finger was recorded in the reference condition at the end of one of the experimental sessions in five subjects, using an Optotrak 3020 motion analysis system. A pair of small infrared light emitting diodes (IREDs) were placed on the proximal phalanx of the index finger. The spatial location of the IREDs was recorded with a precision of 0.5 mm and a sampling frequency of 100 Hz while subjects actively scanned the standard angle (90°) and several comparison angles (95°, 100° and 105°). These data allowed us to examine the active movement trajectories, and to calculate the mean speed profile. In all analyses, the level of significance was fixed at $P<0.05$.

5.4 RESULTS

5.4.1 Scanning movements

In these experiments, the active movement trajectory was constrained by the angles themselves and the 4° shift that was arbitrarily imposed on one angle of each pair presented. In all experiments, the standard angle was 90°, and the comparison angles spanned a range of 91° to 103°. The movements were also constrained by positioning the apparatus at arm's length from the subject, who was instructed to scan the angles using the glabrous skin of the middle phalanx of the index finger. In order to maintain contact between the middle phalanx and the angle, the subject had to limit joint rotation to the shoulder. This was monitored during the experiments by the optical sensors on the apparatus that were located behind the angle (from the subject's point of view), and were interrupted by the protruding distal phalanx of the index finger. At acquisition, trials in which the distal phalanx did not interrupt the LEDs in the pre-determined order, *a-b-c-b-a* (Fig. 5.3.2 A), were aborted and repeated later in the session. These observations suggested that the relevant feedback for task performance was limited to two sources, cutaneous feedback from the glabrous skin of the index finger, and proprioceptive feedback from the shoulder. The relative contribution of each source of feedback to psychophysical performance was therefore assessed by selectively eliminating each source of information, separately and in combination.

5.4.2 Effects of eliminating cutaneous feedback from the finger (condition 1 vs condition 2)

We examined the contribution of cutaneous feedback from the index finger to the performance of the 2D angle discrimination task in five subjects by measuring performance in the reference condition (active touch with both cutaneous and proprioceptive feedback), and then again after anaesthetizing the index finger. Following injection of the local anaesthetic around the base of the index finger, light touch distal to the injection site was abolished throughout the data acquisition period. Thus, sensory feedback during anaesthesia arose principally, if not entirely, from proprioceptors about the shoulder. The pooled results of five subjects are shown in Fig. 5.4.2 A, along with the logistic curves fitted to the pooled data in each condition. When the smallest angular difference was presented (1°), performance was at the chance level for this two-alternative forced-choice paradigm. When larger angular differences were presented, performance improved in both testing conditions. Performance was, however, consistently poorer in the presence of anaesthesia. Consequently, the discrimination threshold (75% correct, shown in Fig. 5.4.2 A) was increased in the presence of anaesthesia. This was consistent with the subject reports to the effect that they generally found the task more difficult during the anaesthetic block.

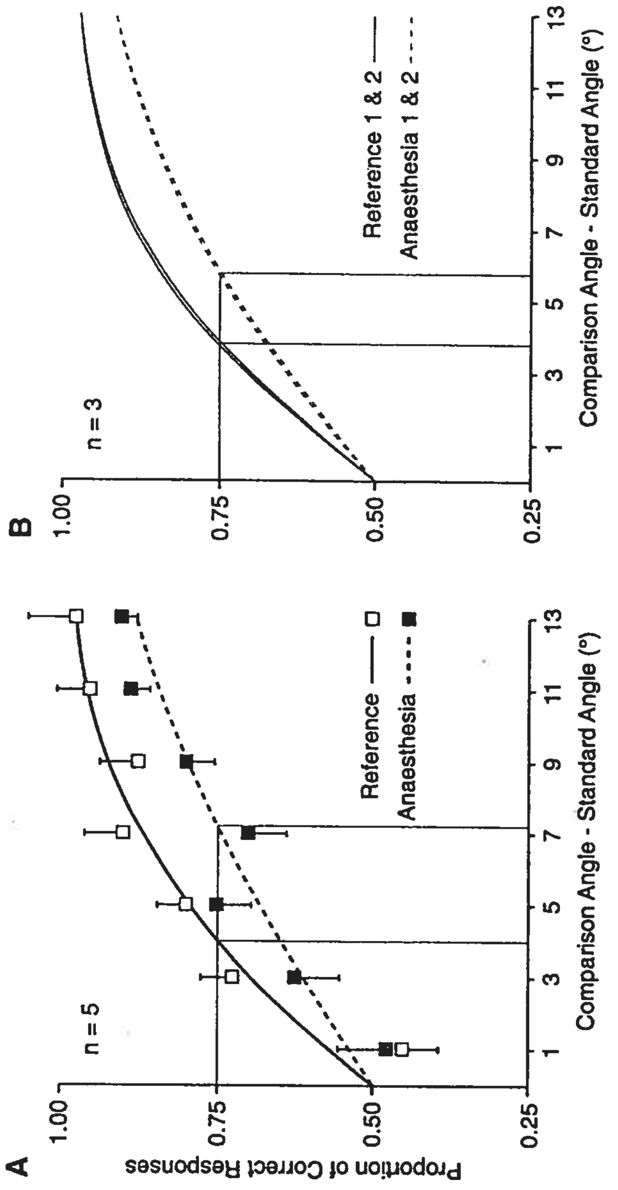

Fig. 5.4.2 A, B Effects of digital anaesthesia on performance of the 2D angle discrimination task. The proportion of correct responses is plotted as a function of the angular difference between the comparison angle (91°–103°) and the standard angle (90°). A Pooled results of five subjects (means ± SEM) during the reference condition 1, active touch with cutaneous and proprioceptive feedback, and condition 2, active touch with no cutaneous feedback (anaesthesia). Logistic curves were fitted to the pooled data. Discrimination threshold (75% correct) is shown. B Results from three of the five subjects shown in A, who performed two repeated blocks of trials with anaesthesia in the same session, along with their performance in the reference conditions in the immediately preceding session and in the subsequent session. Note that the logistic functions for each condition (reference or anaesthesia) were closely similar

Discrimination threshold was calculated from the logistic functions fitted to the data of each subject and the results are presented in Table 5.4.2. All subjects showed an increase in threshold in the absence of cutaneous feedback, but the change was modest (*P*=0.03): mean discrimination threshold increased from 4.0° in the reference condition to 7.2° in the anaesthetized condition. Motor strategy was, in contrast, not significantly changed: there was no significant change in contact force, scanning speed or dwell-time at the intersection across the two testing conditions (see Table 5.4.3 for details). In the companion paper, we reported that subjects generally used a combination of two cognitive strategies to perform the task: mental images of the angles (whole angle strategy), and the pattern of cutaneous feedback from the angle of intersection (intersection strategy). During anaesthesia, most subjects found the discrimination more difficult because they were no longer able to rely on the cutaneous feedback from the angle of intersection. Instead, their decision was now based solely on mental images of the angles or the movement trajectory. One subject (no. 3) reported that the discriminations were easy even during anaesthesia, but this subject reported using only a mental representation of the angles in the reference condition. Nevertheless, this subject's threshold was also increased during anaesthesia, suggesting that the cutaneous input likely contributed to the central representation of the angles. In order to ensure that the observations were robust, we performed two blocks of trials with anaesthesia in the same session for three subjects, after repeating the ring block halfway through the session. Figure 5.4.2 B plots the two logistic functions fitted to the data from each block (dashed lines). The functions were virtually indistinguishable, indicating that the effects of anaesthesia were indeed robust. For these subjects, performance in the reference condition was

Subject	Reference	Anaesthesia	Reference (repeat)[a]	Reference	Passive
1	2.9	5.9	–	–	–
2	3.9	5.0	2.6	–	–
3	0.7	4.9	2.6	–	–
4	6.7	7.9	5.3	3.6	7.9
6	5.8	12.1	–	3.7	6.9
7	–	–	–	2.7	7.6
8	–	–	–	7.8	>13.0
9	–	–	–	3.3	8.0
Mean	4.0	7.2		4.2	8.7

[a] For subject nos. 2, 3 and 4, the reference condition was tested in the preceding session because the effects of anaesthesia were tested in both blocks of trials in the session. Here we give the thresholds from the subsequent session, showing that in all cases discrimination threshold during anaesthesia was higher than the estimates during both reference conditions

Table 5.4.2 Discrimination threshold (°) during the reference condition (condition 1) and the two modified conditions, anaesthesia and passive (respectively, conditions 2 and 3)

	Reference (n=5)	Anaesthesia (n=5)	t-test (P)	Reference (n=5)	Passive (n=5)	t-test (P)
Speed (mm/s)	155±27	169±31	0.09	246±43	162±13	0.13
Dwell time (ms)	754±115	688±82	0.22	560±64	1,115±125	0.01
Force (N)	0.68±0.18	0.69±0.21	0.97	0.88±0.12[a]	0.78±0.10	0.81

[a] Force data available for only four subjects

Table 5.4.3 Comparison of the movement-related parameters (± SEM) during the reference condition (condition 1) and the two modified conditions, anaesthesia (condition 2) and passive touch (condition 3) recorded in the immediately preceding session and in the subsequent session (solid lines). Using the data from a different session as the reference value for these experiments did not bias our estimate of the magnitude of the effect of anaesthesia because performance in the two reference conditions was almost identical.

5.4.3 Effects of eliminating proprioceptive feedback from the shoulder (condition 1 vs condition 3)

The contribution of proprioceptive feedback from the shoulder to 2D angle discrimination was determined by measuring performance in the reference condition, active touch with cutaneous and proprioceptive feedback, and comparing this to performance in a modified condition, passive touch, in which case only cutaneous feedback was available. After subjects positioned their outstretched arm so that the glabrous skin of the middle phalanx of the index finger contacted the angle at the start position (*a* in Fig. 5.3.2 A), the angle was then displaced, under computer control, underneath the immobile digit (glabrous skin of the middle phalanx). The movement sequence was identical to that used in the active condition. The pooled psychophysical results of five subjects are shown in Fig. 5.4.3. Performance was significantly poorer in the absence of proprioceptive feedback: mean discrimination threshold was 4.2° in the reference condition of active touch as compared to 8.7° during passive touch (P<0.0005). Consistent with this, the subjects generally reported the passive condition to be more difficult than the active condition. All subjects reported using the pattern of cutaneous feedback to perform the discrimination, both from the angle of

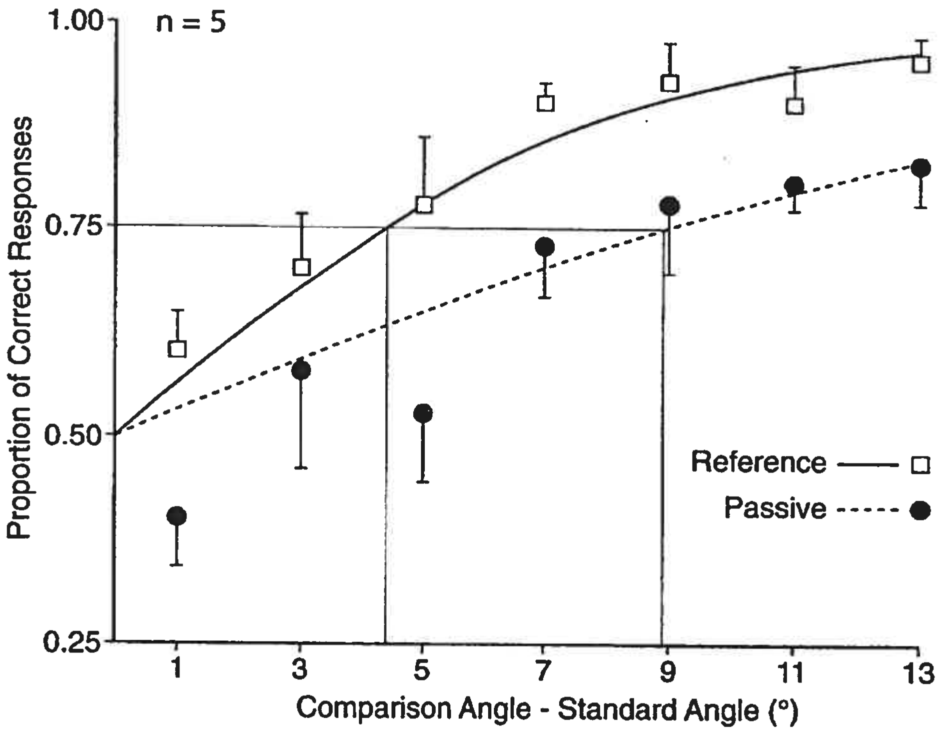

Fig. 5.4.3 A Effects of eliminating proprioceptive feedback on performance of the 2D angle discrimination task. Pooled results of five subjects during the reference condition 1, active touch with cutaneous and proprioceptive feedback, and condition 3, passive touch with only cutaneous feedback. Plotted as in Fig. 5.4.2A

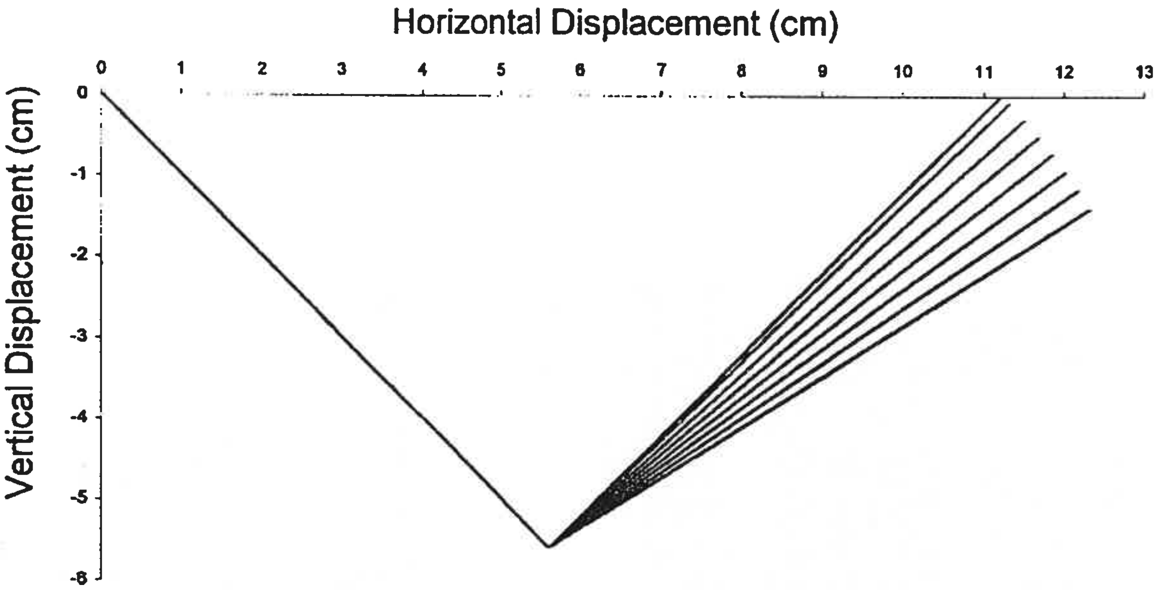

Fig. 5.4.3 B Point-to-point trajectories described by the angles in condition 3, passive touch (no shift applied). Shown here are the trajectories from 56 to-and-fro scans: 28 repetitions of the standard, 90°, and 4 repetitions of each of the seven comparison angles, 91°–103°

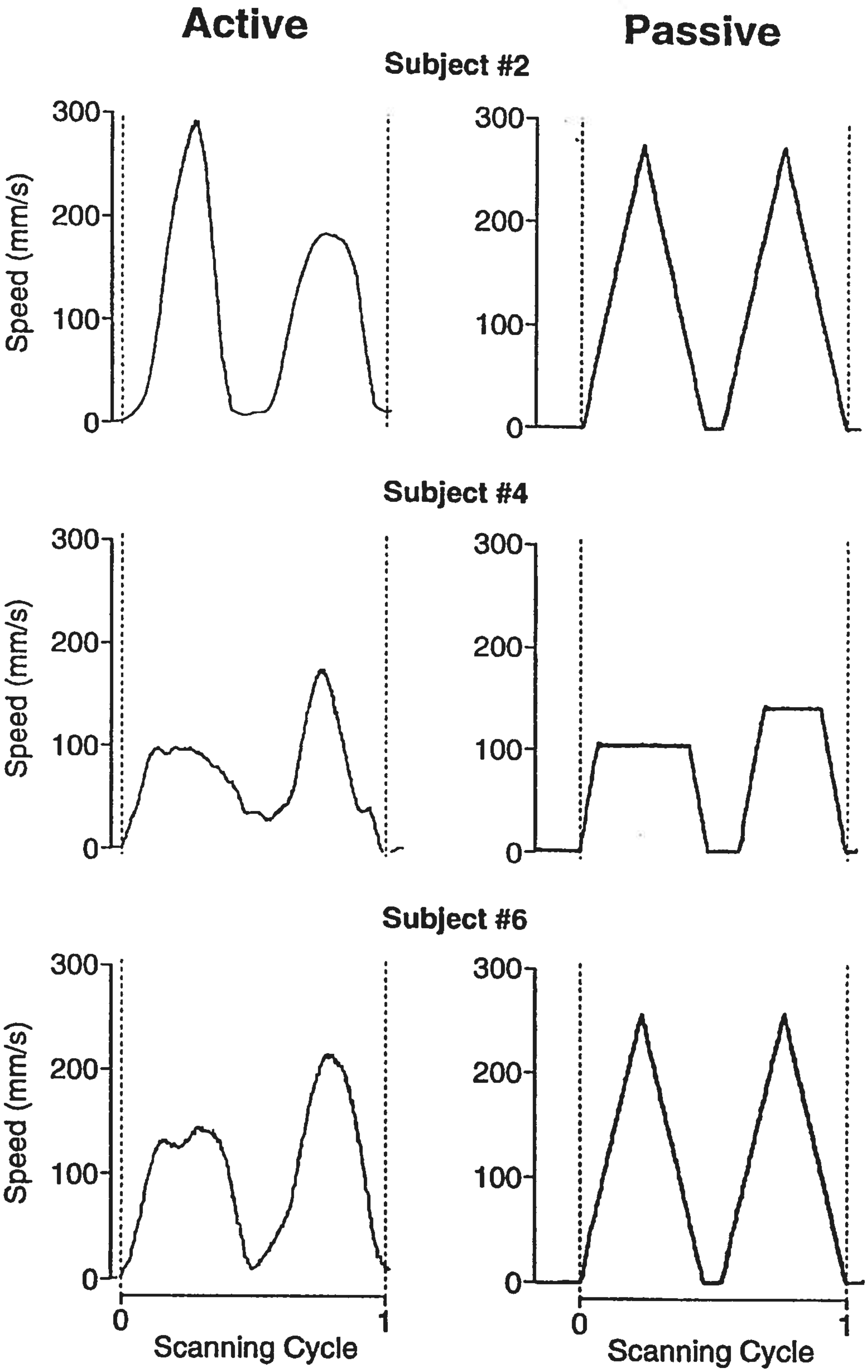

Fig. 5.4.3 C, D Velocity profiles for the active and passive scans of three subjects, normalized to the duration of the scanning cycle (from a, initial position, to c, final position). C Mean velocity profile for four active trials (90°–105°). D Velocity profiles of 56 superimposed trials in the passive condition (90°–103°)

intersection and during the passive scans of the two arms. Interestingly, three of five subjects (nos. 4, 7 and 9) used these inputs to generate mental images of the angles. The passive testing conditions adequately reproduced the active testing conditions. The trajectories described by the angles during the passive scans were closely similar to the trajectories imposed by the angles themselves in the active condition. Figure 5.4.3 B shows the superimposed traces for the to-and-fro passive scans of all eight angles (the standard, 90°, and the seven comparison angles, 91°–103°) in one block of trials. For simplicity, only the ‘no shift’ trials, corresponding to 56 to-and-fro scans, are plotted. The position control system was extremely precise. Inspection shows that each angle had its own unique point-to-point trajectory, with no overlap between angles. The traces for each individual angle are, in contrast, superimposed. Similar results were obtained when the data from the shifted angles (4°) were plotted (not shown). In addition, the mean scanning speed was identical in the two conditions (Table 5.4.3). There were two differences in the testing conditions, but we have no reason to believe that these contributed to the results. First, the speed profiles were not identical during the scans. In the active condition, the movement analyses indicated that all subjects showed an approximately sinusoidally shaped velocity profile as each arm of the angle was explored. Examples from three subjects are shown in Fig. 5.4.3 C. During the passive condition, we approximated this sinusoidal velocity profile in most subjects by imposing a ramp increase and decrease in velocity (subject nos. 2 and 6 in Fig. 5.4.3 D), designed to reproduce the average duration of each segment of the movement. For subjects who used slower active scanning movements (subject no. 4, Fig. 5.4.3 D), however, the ramp increase in velocity was followed by a period of constant velocity scanning before the ramp decrease that preceded the arrival at the end of the first or second arm of the angle. Since mean scanning speed was similar in the two conditions (above), we assume that subjects were able to collect comparable relevant sensory feedback during the angle scanning. Second, in most cases we were unable to match the dwell-time at the angle of intersection due to the weight, and so the inertia, of the apparatus. Thus the digit remained at the intersection significantly longer in the passive condition (mean 1115 ms) as compared to the reference condition (mean 560 ms, Table 5.4.3). Thus, subjects had more time to collect information at the intersection during passive touch as compared to active. This did not appear to confer an advantage to the subjects because their performance was significantly poorer in passive touch. This apparent unimportance of dwell-time to performance of the 2D angle discrimination task is consistent with our previous observation that dwell-time did not covary with the cognitive strategy of the subjects (Voisin et al. 2002).

5.4.4 Effects of eliminating cutaneous and proprioceptive feedback (condition 4)

Two subjects (nos. 2 and 6) participated in a control experiment that aimed to determine whether any other sources of feedback might have potentially contributed to task performance. The right index finger was first anaesthetized. Once all tactile sensation was abolished, performance in the 2D angle discrimination task was tested using passive touch, as for condition 3 (Fig. 5.4.4). In this situation, neither subject was able to discriminate even the largest angular difference presented, 13°. A linear regression analysis applied to the pooled data

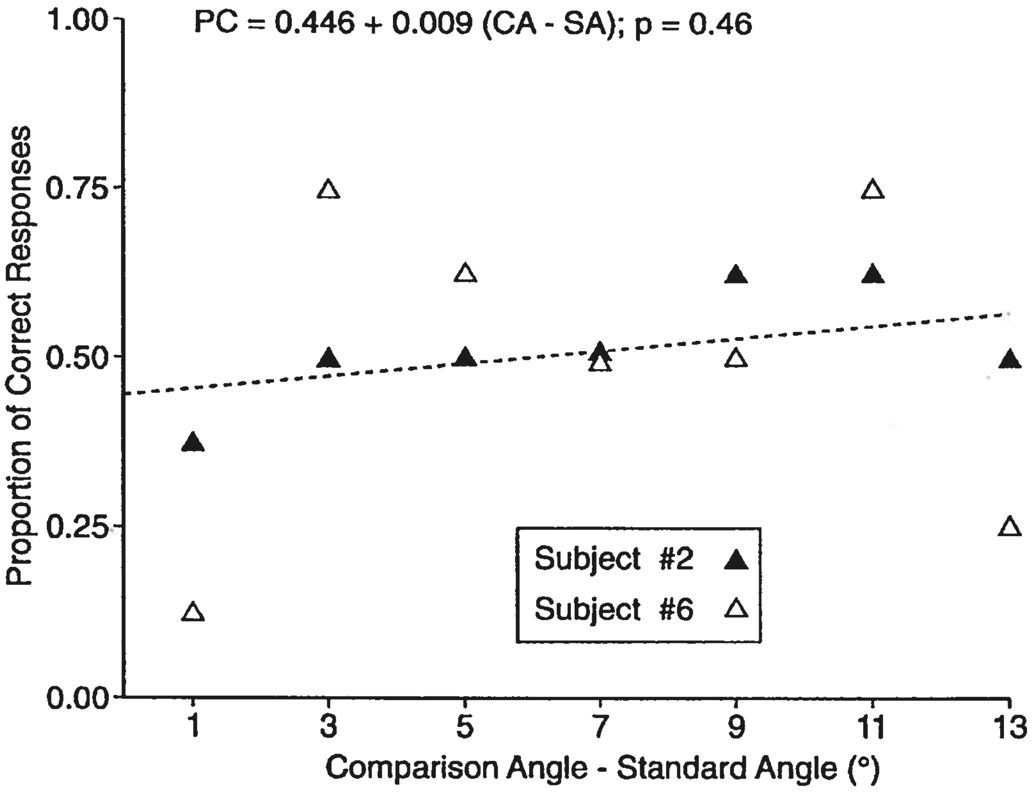

Fig. 5.4.4 Performance of two subjects in the 2D angle discrimination task as the angles were passively scanned under the anaesthetized index finger (condition 4). Subjects were not able to discriminate the angular differences. The constant of the linear regression shown here was close to the level of chance in this two-alternative forced-choice experiment (50% correct) (CA comparison angle, PC proportion correct, SA standard angle)

indicated that the slope was not different from zero (*P*=0.46). Moreover, the constant for the equation, 0.45, was close to the level of chance performance in this task (50% discriminated). The inability of subjects to perform the discrimination under these conditions could not be explained by unfamiliarity with the test condition. Both subjects were able to perform the task in the presence of anaesthesia (Table 5.4.2). They were also able to discriminate angular differences in the passive condition (tested in the same session as condition 4). Together, these results suggest that 2D angle discrimination was entirely based on cutaneous feedback from the scanning digit and proprioceptive feedback from the shoulder.

5.5 DISCUSION

The present study has shown that the sources of salient input for 2D discrimination of macrogeometric angles are twofold: cutaneous input from the exploring index finger and proprioceptive input from the shoulder. No other source of sensory information contributed because performance fell to chance levels for this two-alternative forced choice paradigm when both inputs were eliminated. The results thus suggest that this sensory task is truly an integrative task drawing on sensory information from two different submodalities, and so, following the definition of Gibson (1966), is haptic in nature.

5.5.1 Two-dimensional angle discrimination in the absence of cutaneous feedback

We attribute the decreased performance with digital anaesthesia to the abolition of cutaneous feedback from the finger. It seems likely that all four types of cutaneous mechanoreceptors found in human glabrous skin (slowly adapting type I and II, rapidly adapting and Pacinian afferents; see review by Johnson 2001) were activated during the angle scans. This cutaneous feedback provided information about the pattern of contact between the skin and the experimental objects both while the digit scanned the two arms of the angle (stimulating first the radial and then the ulnar side of the middle phalanx) and also while the digit was at the intersection itself. As suggested in the companion paper (Voisin et al. 2002), it is particularly important role because they can provide information about the precise pattern of skin contact with local contours (LaMotte and Srinivasan 1987a, 1987b; Wheat et al 1995; Goodwin et al. 1997). Is it possible that joint receptors from the digit also contributed to the results, since their afferents would also have been blocked with digital anaesthesia? This seems unlikely for several reasons. First, the apparatus was positioned so that, with the arm outstretched, contact between the index finger and the object was limited to the glabrous skin of the middle phalanx of the index finger, i.e. a cutaneous surface. Second, the subject was required to maintain the distal and proximal interphalangeal joints, and the metacarpophalangeal (MCP) joint in full extension (0°). Careful observation during the experiments indicated that the subjects followed these instructions. In addition, the position of the distal phalanx was monitored throughout with optical sensors positioned behind the angle (see Fig. 4.3.3 in the companion paper). Finally, there is a fairly wide consensus that joint receptors do not contribute greatly to the appreciation of joint angles except at the extremes of the range of motion (reviewed in Matthews 1988; Jones 1994). Interestingly, when we transformed the results from the anaesthetized condition (mean discrimination threshold of 7.2°) into angular changes at the shoulder angles (difference in position at the end-point of the second arm), the mean discrimination threshold was 0.83° (range 0.51°–1.46°). This falls within the range of published values for proprioceptive precision at the shoulder, 0.6° to 1.1° (van Beers et al. 1998). Thus our results provide independent confirmation of their results, and this using a different experimental paradigm (haptic exploration vs a whole-arm pointing task). In addition, this performance is less precise than that obtained when both sources of feedback, cutaneous and proprioceptive, were available (mean 0.54°; range 0.08° to 1.36°), i.e. during haptic exploration.

5.5.2 Two-dimensional angle discrimination in the absence of proprioceptive feedback

We attribute the decreased performance during the passive condition to a loss of proprioceptive feedback from the shoulder, although it is recognized that one other potential kinaesthetic signal was absent in this condition, namely the motor command (reviewed by Gandevia 1996). The importance of the latter is not clear, at least from the subjects' comments, because only one subject (no. 4) reported specifically using the movement trajectory to perform the task. The remaining subjects reported depending on sensations elicited during the scans. The proprioceptive feedback most likely included inputs from muscle receptors (especially primary and secondary endings of muscle spindles, although Golgi tendon organs may also have contributed) and perhaps joint receptors (reviewed in Matthews 1988). In addition, we cannot exclude a potential contribution from cutaneous feedback elicited by skin stretch at the shoulder since Cohen (1958b) found that position sense declined when position-related cutaneous feedback from the shoulder was distorted by applying tape to the skin overlying the joint. Consistent with this, Cohen et al. (1994) have shown that a proportion of cutaneous neurones in primary somatosensory cortex (SI) signal arm position during 2D whole-arm reaching movements. Overall, there was a slightly larger increase in discrimination threshold in the passive condition (4.5°) as compared to the anaesthetized condition (3.2°). On considering the results obtained in the two subjects that were tested in both modified conditions (subject nos. 4 and 6, Table 5.4.2), it seems most likely that this difference was not meaningful. Subject no. 6 showed approximately the same relative increase in threshold in both modified conditions (×2.1 and ×1.9 for anaesthesia and passive, respectively). Subject no. 4 showed a larger increase during the passive condition than with anaesthesia, yet discrimination threshold in the two modified conditions was identical, 7.9°. Taken together, we suggest that cutaneous feedback from the finger and proprioceptive feedback from the shoulder both contributed in equal measure to 2D angle discrimination. This suggestion is consistent with the reported cognitive strategies of the subjects, the majority of whom reported using both sources of information to perform the sensory discrimination.

5.5.3 Two-dimensional angle discrimination is an integrative task

The present results suggest that our 2D angle discrimination task is truly an integrative task drawing on sensory information from two different submodalities, cutaneous and proprioceptive, originating from anatomically separate body parts, the finger and the shoulder. Subject performance was best with both modalities available, and diminished when either of the two sources of information was removed. As discussed in the companion paper (Voisin et al. 2002a), sensory performance in this task was superior to what was expected from previous studies of, for example, position sense in isolation. Mean discrimination threshold was 4.7° (range 0.7° to 12.1°) when scanning objects using the index finger of the outstretched arm (both cutaneous and proprioceptive feedback available). When these results were expressed in terms of shoulder angles (difference in position at the end-point of the second arm), the mean discrimination threshold, 4.7°, corresponds to a change in shoulder position of 0.54° (range 0.08° to 1.36°). These values are lower than previous estimates of static position sense at the shoulder (see "Introduction"). This finding is not an isolated observation since John et al. (1989) reported that the ability to discriminate differences in the thickness of plates using a precision grip (cutaneous + proprioceptive feedback available) is far superior to what could have been expected from previous studies of joint position sense in the fingers (approximately 10°, Ferrell and Smith 1988). John et al. (1989) reported that their subjects could resolve differences in joint angle with a precision of about 0.1° at the proximal interphalangeal joint or about 0.05° at the MCP joint. Taken together, these observations suggest that integrative tasks that can call upon both movement-related reafference (inputs from muscle, joint and skin receptors) and also the motor command reveal that sensory acuity is superior to that found using traditional tests. It is suggested that such integrative tasks, apart from being of more functional relevance, may be much more sensitive than traditional sensory tests to early changes in somaesthetic function that can, for example, herald the development of peripheral neuropathies (e.g. overuse syndromes, diabetic neuropathies).

5.5.4 Central mechanisms underlying 2D angle discrimination

The really intriguing point raised by the present results is to understand how subjects managed to integrate information from two anatomically separate body parts and two distinct modalities, cutaneous and proprioceptive, into a central representation of 2D shape. In the first case, the central representations of the hand and the shoulder within the parietal somatic sensory areas are largely separate. It is only in parietal association regions like the secondary somatosensory cortex (SII) and the posterior parietal cortex (areas 5 and 7b) that one finds large receptive fields that encompass both regions. In the second case, convergence of the two modalities, cutaneous and proprioceptive, is rare in the four areas that together comprise SI cortex, areas 3a, 3b, 1 and 2 (Hyvärinen and Poranen 1978; Chapman and Ageranioti- Bélanger 1991; Ageranioti-Bélanger and Chapman 1992; Iwamura et al. 1993; Salimi et al. 1999) and in several of the parietal association regions, including SII and area 7b (Robinson and Burton 1980). As for area 5 in the posterior parietal cortex, Sakata et al. (1973) reported that about one-third of cells are responsive to bimodal inputs, but these results have not been confirmed in other studies that found only a few area 5 cells responsive to both cutaneous and proprioceptive inputs (Duffy and Burchfiel 1971; Seal et al. 1982). Although substantial convergence between the two modalities may not occur until the signals arrive in regions that are hierarchically superior to those investigated to date (e.g. parietal operculum), other factors also need to be considered. The proportions of haptic cells may have been underestimated in previous studies, given the difficulty in receptive field testing particularly in awake unrestrained animals. Further to this, it is known that SI neurones receive widespread convergent and yet subliminal inputs (Zarzecki and Wiggin 1982; Kang et al. 1985). Such inputs may become liminal in conjunction with other factors. One important factor might be the pattern of stimulation. For example, Iwamura et al. (1985) described neurones in area 2 that did not appear to have a somatic receptive field, and yet discharged when specific shapes were held in the monkey's hand. More recently, these findings have been extended to include posterior parietal cortex (Taira et al. 1990; Gardner et al. 1999). Another factor may be the behavioural context of the testing. Thus, Tremblay et al. (1996) reported that some area 2 neurones, with no identifiable receptive field, signalled differences in texture when tested in a texture discrimination task. Similar results have been obtained in SII (Sinclair and Burton 1993). An alternate suggestion is that, as in the visual system (Engel et al. 1997), coactivation of cutaneous and proprioceptive inputs may elicit some form of temporal binding so that the two inputs are interpreted together to generate a central representation of haptic shape. Such a mechanism is particularly attractive as this could bind together inputs from different modalities and different body regions into the emergent property of shape.

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CHAPITRE VI - ARTICLE 3

Viewpoint dependence of haptic shape discrimination in humans: A window into the haptic frames of reference

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6.1 ABSTRACT

Little is known about factors that can modify the ability to discriminate differences in haptic shape. This study investigated how changes in the physical relations between objects (two-dimensional, 2-D, angles) and the subject, as well as scanning conditions, modified the ability to discriminate small changes in 2-D shape. Subjects scanned pairs of angles (90° standard; 91 - 103° comparison angles) with the index finger of the out-stretched arm, identifying the larger of each pair. In experiment 1 (7 subjects), joint rotation was restricted to the shoulder. Exploratory conditions were modified by changing the "view" of the angles, by changing the angles themselves (inside versus outside), the posture of the subjects (forearm pronated versus supinated) or by modifying the position of the angles relative to the subject (30 versus 60° to the right). All three modifications, involving changes in the quality of either cutaneous or proprioceptive feedback, produced a significant increase in discrimination threshold, consistent with the notion that both sources of feedback are essential for haptic shape. In experiment 2 (11 subjects), exploration was restricted to distal joints (wrist/second metacarpophalangeal joint). The results showed that discrimination threshold was similar for distal, as compared to proximal, articulations. This observation suggests that regional variations in proprioceptive acuity (proximal > distal) may reflect an adaptation to generate an invariant central representation for haptic shape. Insight into the central frames of reference that underlie haptic shape was obtained by modifying the scanning conditions (delay between successive scans, head position in relation to the angles themselves). Discrimination threshold was increased when the delay was decreased from 15 to 5s, but this increase disappeared when the head was turned in the direction of the angles. The results were interpreted as providing evidence for an initial short-lasting, egocentric frame of reference, followed by a second allocentric or object-based frame of reference. Parallels are drawn with the visual system where similar frames of reference have been described.

Keywords Tactile shape discrimination · Two-dimensional angles · Active touch · Passive touch

6.2 INTRODUCTION

Haptic touch, a term coined by Gibson (1966), refers to the ability to extract information about surface or object properties on the basis of combined feedback from cutaneous and proprioceptive mechanoreceptors. Evidence now suggests that haptic sensory abilities are more precise than sensory judgements based upon using signals generated by a single somaesthetic modality. Using a task in which subjects explored pairs of two-dimensional (2-D) angles by scanning the index finger of the out stretched arm over the unseen objects (rotation thus limited to the shoulder), we showed that subjects can discriminate angular differences in the order of 4.7° (0.7 to 12.1°) (Voisin et al. 2002a). The corresponding changes in shoulder angle (mean, 0.54°; range, 0.08 to 1.36°) were much lower than previous estimates of position sense at the shoulder (Cohen 1958; Hall and McCloskey 1983; Clark et al. 1995), suggesting that perception is enhanced with both sources of sensory signals. This latter observation has recently been confirmed by Henriques and Soechting (2003). They estimated that shoulder joint acuity was ~0.2°, using a different task whereby subjects judged curvature and trajectory orientation using a robot arm with added force feedback to generate virtual walls or shapes. Together, these observations suggest that it is the integration of cutaneous and proprioceptive signals that is responsible for the apparently heightened sensitivity to position of the shoulder. This conclusion was supported by our demonstration that suppression of either cutaneous or proprioceptive feedback leads to significant increases in 2-D angle discrimination thresholds, with performance being no better than chance when both sources of feedback are suppressed (Voisin et al. 2002b).

The purpose of this study was to begin to investigate the nature of the representation of haptic shape. At present, relatively little is known about factors that can modify the ability to discriminate differences in haptic shape. There is some evidence suggesting that haptic recognition of shape is viewpoint-dependent, i.e. that object recognition using haptic touch is better when the objects (complex 3-D shapes) are explored in the same orientation as they were originally explored or “viewed” (Newell et al. 2001). While this suggests that subjects do not create a central omnidirectional representation of object shape, the results may have been, as pointed out by the authors, constrained both by the nature of the stimuli used and by the biomechanics of the hands which led subjects to concentrate their exploration on the back surface of the objects. The results of Kappers and colleagues (Kappers and Koenderink 1999; Kappers 1999, 2002), on the other hand, suggest that the accuracy of the central representation of bar orientation, one component of object shape, is modified by a number of factors, including the spatial location of the objects (increased horizontal but not vertical distance) and the exploration strategy (serial, unimanual versus simultaneous, bimanual). Interestingly, they subsequently showed that the large distortions in matching the parallelity of reference and test bars using simultaneous bimanual explorations were decreased by adding a 10 s delay between the exploration and matching (Zuidhoek et al. 2003). This led the authors to suggest that the delay allowed subjects to switch from an initial *egocentric* (subject-centred) frame of reference to an *allocentric* (external) frame of reference. While this is an interesting suggestion, other factors could have contributed to the results, including biomechanical contraints of the limb(s), and systematic changes in the skin area in contact with the objects across the relatively large workspaces used. Changes in limb configuration at different parts of the workspace may also have contributed to the results.

In the present experiments, we determined how changes in the physical relations between the explored angles and the subject, as well as scanning conditions, modified their ability to discriminate small differences in 2-D shape. In all experiments, subjects were constrained to perform unimanual, serial explorations of 2-D angles (91 to 103°) using identical trajectories.

In the first series of experiments, explorations were made with the index finger of the outstretched arm, and joint rotation was restricted to the shoulder. Exploratory conditions were modified by changing the “view” of the angle: by changing the angles themselves (exploring inside and outside angles), by modifying the subject's posture in relation to the angles, or by modifying the position of the angles relative to the subject. In the second series of experiments, the exploratory strategy was changed by limiting rotation to distal articulations (wrist and second metacarpophalangeal, mcp, joint). This allowed us to determine the contribution of changes in receptor sensitivity to the results of the first experiments. We also compared 2-D angle discrimination performance at proximal and distal joints in order to determine whether known variations in position sense, proximal joints being more sensitive than distal joints (Hall and McCloskey 1983), lead to systematic changes in haptic shape discrimination. Finally, some insight into the frame(s) of reference used to represent haptic shape was obtained. We tested Zuidhoek et al.'s (2003) suggestion that the frame of reference changes when a delay is introduced, but in this case using a design in which delay was the only experimental variable to change. As our results suggested that there is indeed a switch from one frame of reference to another with added delay, presumably ego- to allocentric, one final experiment addressed the nature of the initial egocentric reference frame.

Preliminary reports of the results have appeared (Voisin and Chapman 2003a,b).

6.3 MATERIALS AND METHODS

6.3.1 Subjects

Four women and three men (ages 21-27 yr) volunteered to participate in experiment 1 (two or three experimental sessions per subject). Eleven volunteers (5 women, 6 men; 22-50 yr) participated in experiment 2 (one to four sessions each). Two subjects participated in both experiments (see Tables 6.4 A and B). All but two subjects were right-handed for writing. The experimental protocol was approved by the institutional ethics committee, and all subjects gave their informed, written consent before participating in the experiments. The duration of each experimental session was approximately two hr for experiment 1, and one hr for experiment 2.

6.3.2 Angles

Two sets of angles, *inside* (Fig. 6.3.2 B) and *outside* (Fig. 6.3.2 C), were machined from 1 cm thick Plexiglass. Each angle was formed by the intersection of two 8 cm long arms. The first arm explored (*ab* in Fig. 6.3.2 B) was identical for all angles; the second arm (*bc*) was modified to form a standard angle of 90°, or a comparison angle, 91 - 103° (as measured from within). The angles were clamped upright into an apparatus instrumented with three pairs of light-emitting diodes and optical sensors to record digit position at the start position, *a*, the intersection, *b*, and opposite extremity, *c* (see Fig. 4.3.3 A in Voisin et al. 2002a).

6.3.3 Two-dimensional angle discrimination task.

For all sessions, the subjects were seated in a chair with the apparatus positioned at arm's length and at the height of the shoulder (Fig. 6.3.2 A). Vision was occluded, and white noise delivered through headphones. A two-alternative forced-choice task was used, and the methods are described in detail in Voisin et

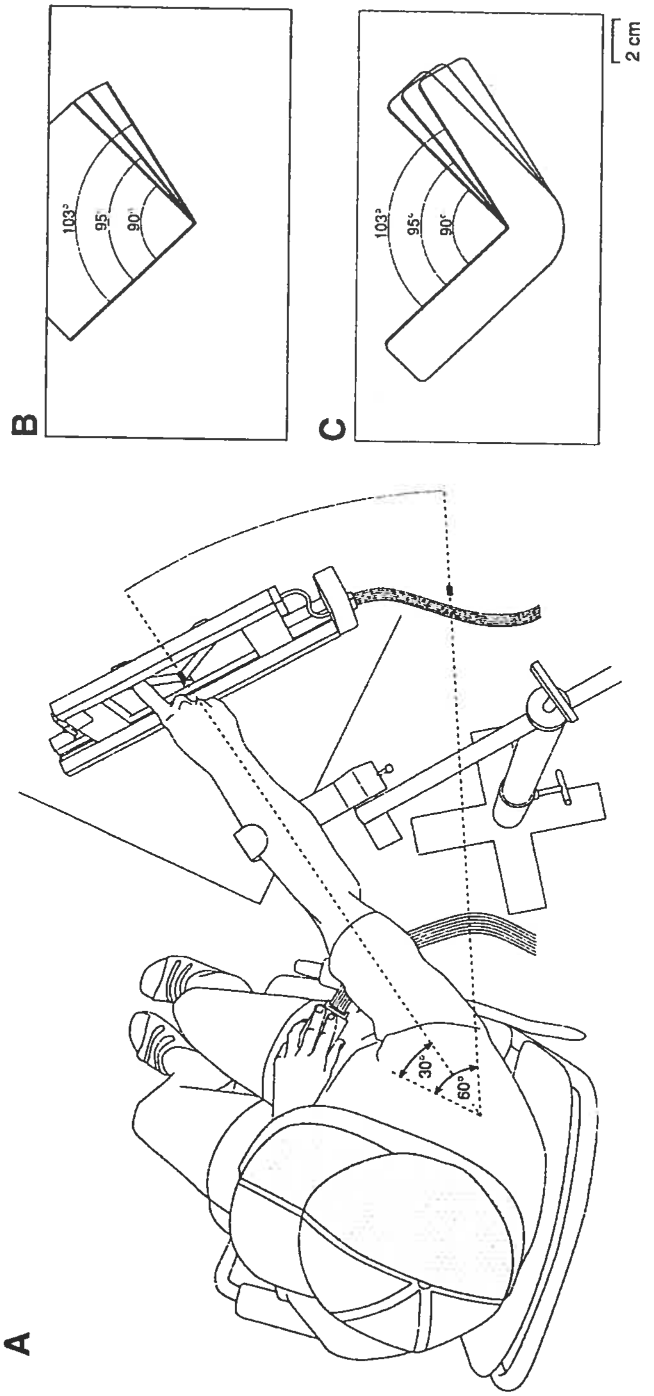

Fig. 6.3.2 A. Subject position with the angle placed at 30 degrees to the right and the index finger at the start position. The dotted line at 60° shows the corresponding position for tests in the eccentric position. Vision of the objects was precluded by a mask over the right-hand side of the head (shaded region). The forearm support was removed for experiment 1 (shoulder movements). B and C. Inside and outside angles. The standard angle in both cases was 90°; the modified angles ranged from 91 to 103° (measured from the inside. The surface scanned by the finger is shown with a thick line.

al. 2002a. Briefly, the experimenter guided the subject's finger to the start position (Fig. 6.3.2 A). Subjects scanned the right index finger (D2) over first one angle and then a second angle (90° and a comparison angle) using a single to-and-fro movement (*abcba*). The delay between the successive scans was ~14 s for experiment 1; for experiment 2, the delay was either ~5 s or ~15s. After scanning the two angles, subjects were asked to identify the *larger angle* by pressing one of two response buttons on a keypad with the left hand (first or second angle larger). No feedback on performance was given. One angle in each pair was slightly rotated towards the midline (4° shift in the vertical plane) to ensure that subjects evaluated the whole angle and not just the orientation of the second arm relative to horizontal (Voisin et al. 2002a). The order of testing was counterbalanced for all factors (shift on the first or second angle, standard angle presented first or second, value of the comparison angle).

6.3.4 Experiment 1

In the *reference condition*, the apparatus was placed 30° to the right of midline as shown in Fig. 6.3.2 A (note that the forearm support used in experiment 2 was removed). The position of the apparatus was adjusted so that the glabrous skin of the middle phalanx of D2 contacted the angle at the intersection (dotted line). The inside series of angles were employed (Fig. 6.3.2 B). Subjects scanned the angles with the glabrous skin of the middle phalanx of D2, forearm pronated and arm out-stretched, so that movement was restricted to the shoulder. Three *modified conditions* were tested, all characterized by having the same movement trajectory. In the *first modification*, performance was tested on the outside series of angles (Fig. 6.3.2 C). The angles were placed at the same position relative to midline (30° to the right) as in the reference condition, and arm posture was identical. Thus subjects "viewed" the same angles (as measured on the inside) from either above (inside, glabrous D2) or below (outside, hairy dorsum D2). For the *second modification*, the inside angles were employed (same position as the reference condition). Arm posture was modified so that the forearm was supinated. Consequently, the subjects scanned the angles using the hairy dorsum of the middle phalanx (D2). For the *third modification*, the position of the angles (inside series) relative to the midline of the subject was modified: the apparatus was positioned 60° to the right of the midline (see Fig. 6.3.2 A). In order to ensure that the cutaneous contact (glabrous skin of D2) was identical to the reference condition, the orientation of the apparatus was adjusted so that it was perpendicular to the arm at the intersection (*b*, and see Fig. 6.3.2 A). For all testing, the average delay between the end of the first scan and the start of the second scan was 14 s. During this interval, the first angle was removed from the apparatus, the second angle was clamped into place, and the subject's finger was repositioned at the start position (*a*, Fig. 6.3.2 B).

6.3.5 Experiment 2

This series of experiments evaluated 2-D angle discrimination when the scanning movements were restricted to the distal articulations (wrist and 2nd mcp joint). Subject position is shown in Fig. 6.3.2 A. During the scans, the forearm rested on a support to ensure that the movements were restricted to the distal articulations. As D2 scanned over the angles, the skin in contact shifted distally at the two extremities of the scan, extending to the distal phalanx for subjects with smaller hands. As a consequence, the tip of D2 did not reliably interrupt the LED/optical sensors at positions *a* and *c* (Fig. 6.3.2 B), and so we were unable to monitor movement kinematics (below). All experiments employed the inside series of angles. Four comparisons were made. *First,* we repeated the final experiment described for experiment 1 (apparatus positioned at 30° or 60° to the right of midline), but the angles were now explored using movements of the distal articulations. This modification sought to dissociate the effects related to the location of the explored angles from potential changes in receptor sensitivity at the moving joint. *Second,* we repeated the latter experiment, decreasing the delay between the end of the first scan and the start of the second from ~15s to ~5 s (silent count), with the aim of determining whether the delay between the successive scans contributed to the results. *Third,* we compared 2-D angle discrimination performance when the angles were explored with either proximal or distal articulations. In this case the position of the angles was as for the reference condition in experiment 1 (apparatus positioned at 30° to the right of midline, delay of 15 s). *Finally,* with the apparatus located at 60° to the right of midline, we evaluated the influence of the orientation of the head on 2-D angle discrimination. Performance with the head pointing forward (e.g. Fig. 6.3.2 A) was compared to that obtained when the subject was instructed to turn their head and eyes in the direction of the apparatus. In both situations, vision of the angles was blocked and the interscan delay was 5 s.

6.3.6 Experimental design.

In each experimental session, one block of trials was the reference condition, and the other was the modified condition (order counterbalanced across subjects). In experiment 1, each block contained 56 trials (eight replications of seven comparison angles, 91, 93, 95, 97, 99, 101 and 103°); this was reduced to 32 trials/block in experiment 2 (eight replications of four comparison angles, 91, 95, 99 and 103°). Each block was preceded by several practice trials to familiarize the subject with the experimental condition.

6.3.7 Data acquisition and analysis.

Discrimination performance was characterized for each subject, in each block of trials, by computing the proportion of correct responses for each comparison angle. The results were then fitted to a logistic function, from which the discrimination threshold (75% correct) was computed (Voisin et al. 2002a). When the estimated threshold was greater than the largest comparison angle presented, 13° (see Tables 6.4 A and B), then discrimination threshold was arbitrarily set at 13°. Paired t-tests were applied to the group data for each comparison made (reference versus modified condition). For experiment 1, the outputs of the optical sensors were used to characterize the scanning movements in terms of average speed and the length of time that the digit was in contact with the intersection (dwell-time at point b, Fig. 6.3.2 B). For experiment 2, these data

Table 6.4 A Discrimination thresholds (°) during the reference and modified conditions of experiment 1 (shoulder): 1, Inside vs Outside (14 s delay; angles 30°); 2, Pronated vs Supinated (14 s delay; angles 30°); 3, Angles 30° vs 60° (14 s delay)

Condition	1 Reference/Modified Inside/Outside		2 Reference/Modified Pronated/Supinated		3 Reference/Modified 30°/ 60°	
Subject #						
1	5.7	6.7	2.1	8.3	4.5	5.5
2	3.9	8.2	2.6	5.3	4.2	5.7
3	5.7	>13.0	5.7	4.5	0.7	2.6
4	-	-	5.3	6.2	6.7	7.6
5	12.1	>13.0	5.4	10.8	5.1	7.2
6	3.3	7.9	4.4	>13.0	-	-
7	4.4	7.9	4.3	7.2	6.2	10.4
Mean	5.9	9.5	4.3	7.9	4.6	6.5

Table 6.4 B Discrimination thresholds (°) during the reference and modified conditions of experiment 2 (wrist/2^{nd} mcp): 1, Angles 30° vs 60° (15 s delay); 2, Angles 30° vs 60° (5 s delay); 3, Wrist vs Shoulder (15 s delay; angles 30°); 4, Head forward vs Head turned (5 s delay; angles 60°).

Condition	1 Reference/Modified 30° /60° (15s)		2 Reference/Modified 30° /60° (5s)		3 Reference/Modified Wrist/Shoulder		4 Reference/ Modified Forward/Turned	
Subject #								
1	-	-	3.2	9.6	-	-	-	-
4	5.1	4.2	4.8	7.8	3.2	1.7	4.2	2.7
10	-	-	-	-	3.7	1.0	-	-
16	-	-	4.5	4.8	-	-	>13	4.6
17	3.4	5.7	4.6	12.6	-	-	6.0	3.9
18	5.6	5.3	4.0	7.8	-	-	7.5	7.2
19	3.4	1.0	5.4	11.4	5.1	4.0	6.2	6.1
20	5.3	7.2	2.6	3.7	3.0	4.1	3.1	1.8
21	4.0	3.3	1.0	3.4	-	-	4.6	1.0
22	-	-	-	-	8.4	2.1	-	-
25	-	-	-	-	1.1	5.7	-	-
Mean	4.4	4.5	3.8	7.6	4.1	3.1	6.3	3.9

were not available (above). The level of significance for all analyses was set at $P < 0.05$.

6.4 RESULTS

6.4.1 Experiment 1

6.4.1.1 Performance of the 2-D angle discrimination task.

Data were collected from 19 sessions in seven subjects. In this series of experiments, the angles were explored with D2, and movement was restricted to the shoulder by instructing the subjects to keep their out-stretched arm rigid throughout the to-and-fro scans. The movement trajectories themselves were defined by the angles (90 to 103°), and were identical across all testing conditions.

The data from the reference condition (forearm pronated, inside angles explored with the glabrous skin of D2, angles positioned 30° to the right of midline) have been described elsewhere (Voisin et al. 2002a). In brief, a wide range of discrimination thresholds was found (0.7 to 12.1°; Table 6.4 A). Practice did not significantly improve 2-D angle discrimination. The only factor to change with practice was scanning speed: subjects were faster when testing was repeated. There was considerable variation in scanning speed and the length of time that the digit was in contact with the intersection (dwell-time) across subjects, but there was no evidence that either factor was systematically modified as a function of the value of the angle explored (Voisin et al. 2002a).

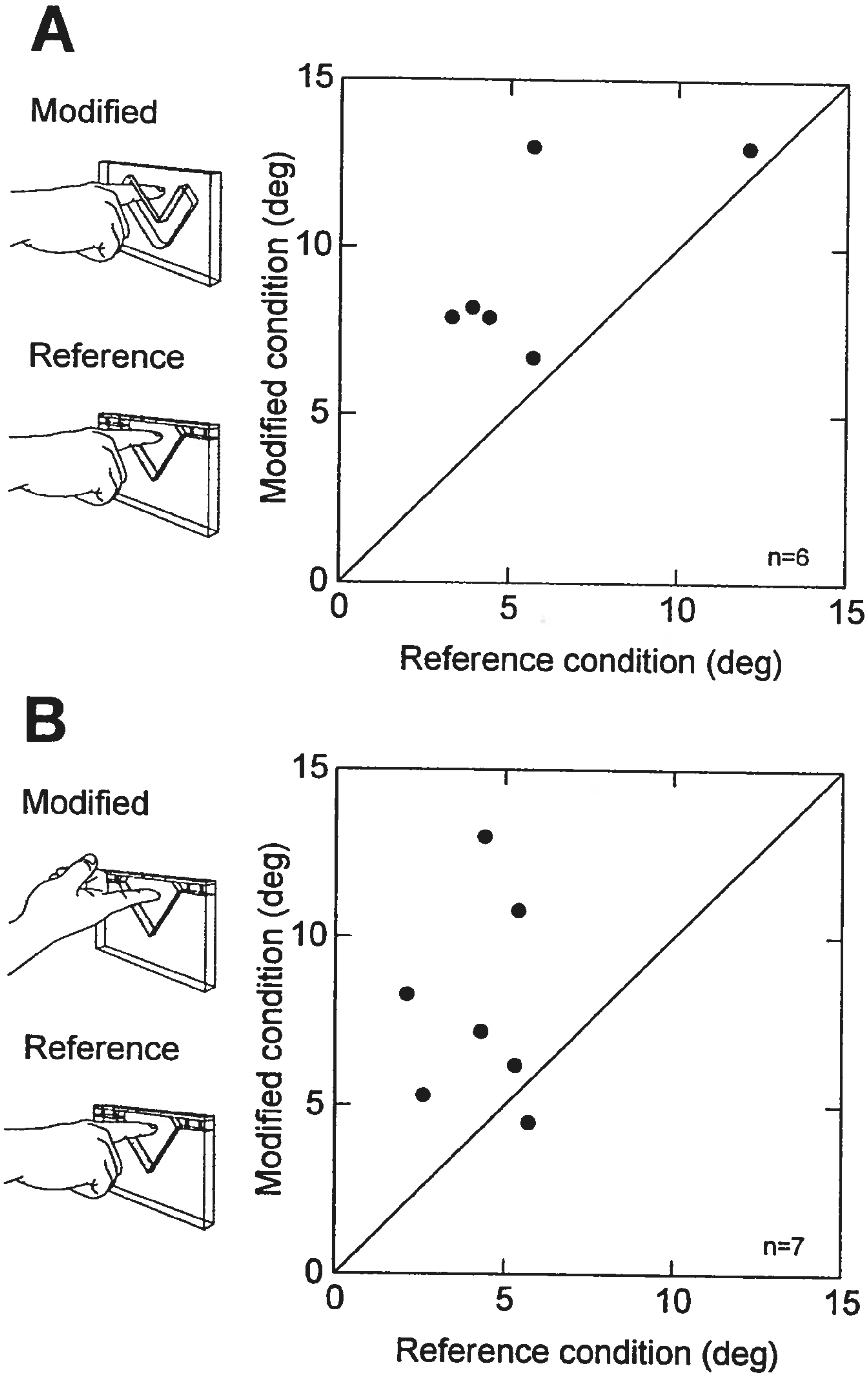

Fig. 6.4.1 A. Outside versus inside (experiment 1). Discrimination threshold in the modified condition (outside) is plotted as a function of threshold in the reference condition (inside) for six subjects. The diagonal line corresponds to identical performance in both conditions. B. Supination (modified) versus pronation (reference) in seven subjects. In both cases, rotation was limited to the shoulder. The cartoons on the left depict the position of the index finger, D2, at the initial position relative to the angles. In both cases, A and B, threshold was increased in the modified condition.

6.4.1.2 Outside versus inside.

This comparison required subjects (n=6) to explore angles from below (outside, force up) and above (inside, force down). Arm posture was identical in both conditions, as were the spatial trajectories. The nominal angles ranged from 90° to 103° for the inside angles, and 270° to 257° for the outside angles. In the reference condition, the glabrous surface of D2 was in contact with the angles (force down); in contrast, the angles were contacted by the hairy dorsum of D2 in the modified condition. The results are shown in Fig. 6.4.1A. All subjects showed an increased discrimination threshold in the modified as compared to the reference condition (9.5° versus 5.9°, respectively, P=0.015). Several subjects reported that the task was more difficult for the outside angles, consistent with their increased threshold in this condition, but others (#2 and #5) reported task difficulty as being similar for both conditions. There was a significant decrease in scanning speed in the modified condition (reference, 157 mm/s; modified, 85 mm/s, P=0.037) accompanied by a decrease in dwell-time at the intersection, b (468 ms and 770 ms respectively, P=0.018). Two factors likely contributed to the decreased performance in the modified condition. The quality of the cutaneous feedback was reduced by using a less sensitive part of the digit to scan the angles, the hairy skin on the dorsum of the phalanx. In addition, the quality of the proprioceptive feedback may have been modified as a result of the changed pattern of muscle activity, working with gravity in the force-down condition, and against gravity in the force-up condition. It is conceivable that alpha-gamma coactivation (reviewed in Prochazka 1989) modified the muscle spindle signals.

6.4.1.3 Supination versus pronation.

The inside angles were explored with either the hairy skin (supination, modified condition) or the glabrous of D2 in contact (pronation, i.e. the reference condition). In contrast to the inside/outside comparison, the pattern of muscle activity was probably similar, as force was directed down in both blocks of trials, thus minimizing any potential changes in the quality of the proprioceptive feedback during the explorations. The modified exploratory condition was rated as either more difficult than the reference condition or similar in difficulty (subjects #3, 4 and 5). Discrimination threshold was, for all but one subject (#3, Table 6.4 A), increased in the supinated position (Fig. 6.4.1B). Overall, there was a significant increase in threshold in the modified condition (pronated, 4.3°; supinated, 7.9°, P=0.028). The motor strategy was similar in both conditions, as regards both mean scanning speed (respectively, 249 mm/s and 225 mm/s, P=0.374) and dwell-time (582 ms and 620 ms, P=0.163). Thus, reduced cutaneous feedback – generated by using a less sensitive cutaneous surface for the angle exploration – produced a significant increase in discrimination threshold. The mean increase in threshold (3.6°) was identical to the increase observed in the force-up condition that combined this same manipulation with a change in the pattern of muscle activity, suggesting that the increase in both cases was related to the reduced cutaneous feedback. This suggestion was supported by the results of a repeated measures analysis of variance, applied to the results of the six subjects that participated in both experiments (inside/outside, pronated/supinated). This showed that there was a significant difference between the reference and modified conditions (P=0.001) but not between the experiments (P=0.242).

6.4.1.4 60° versus 30°.

In this comparison, we tested the effect of changing the position of the angles (inside) relative to the subject (n=7). Angles were scanned at either 60° to the right of midline, or 30° (taking the sagittal plane passing through the right acromion of the subjects as 0°). In both cases, the angles were scanned with the glabrous skin of D2, so that the cutaneous feedback was identical in both blocks of trials. The majority of subjects found that the modified condition was similar in difficulty to the reference condition (subjects #2-5). Nevertheless, there was a systematic and significant increase in discrimination threshold in the more eccentric position, 60° (mean, 6.5°), as compared to the reference condition, 30° (4.6°, P=0.011; Fig. 6.4.2.1 A and Table 6.4 A). The parameters of movement were also systematically changed in the eccentric position: mean scanning speed was faster (reference, 178 mm/s; modified, 190 mm/s, P=0.032), and there was a parallel decrease in dwell-time at the intersection (respectively, 825 ms and 767 ms, P=0.036). Two factors may have contributed to the higher thresholds in the 60° position. On the one hand, the quality of the proprioceptive feedback may have been modified as the pattern of muscle activity may have been subtly altered with the change in location of the angles relative to midline. It seems more likely that the higher thresholds might be explained by cognitive factors, in particular the ability of subjects to interpret signals from a more familiar part of the workspace, closer to midline, as compared to the more eccentric location used in the modified condition.

6.4.2 Experiment 2

Data were collected in 27 sessions from 11 subjects.

6.4.2.1 60° versus 30°.

In order to rule out the possibility that changes in proprioceptive feedback, specifically recruiting muscle spindles in different parts of the musculature controlling the shoulder movements, may have contributed to the results obtained in experiment 1 (60° versus 30°), the experiment was repeated in 14 subjects, but this time the exploratory movements were restricted to the distal articulations (wrist/2nd mcp). For six subjects, all other conditions were identical. For a further eight subjects, the delay between the successive scans was reduced from ~15 s to ~5 s. The results are shown in Fig. 6.4.2.1B and Table 6.4 A. When the delay conditions were similar (14 versus 15 s), there was no change in discrimination threshold across the two test positions (30°, 4.4°; 60°, 4.5°, P=0.983), suggesting that peripheral factors alone were responsible for the increased threshold seen when the exploratory movements were restricted to the shoulder joint. On the other hand, when the delay between successive scans was decreased to 5 s (Fig. 6.4.2.1 B, open symbols), there was now a significant increase in threshold in the more eccentric position (30°, 3.8°; 60°, 7.6°; P=0.005). Interestingly, for the six

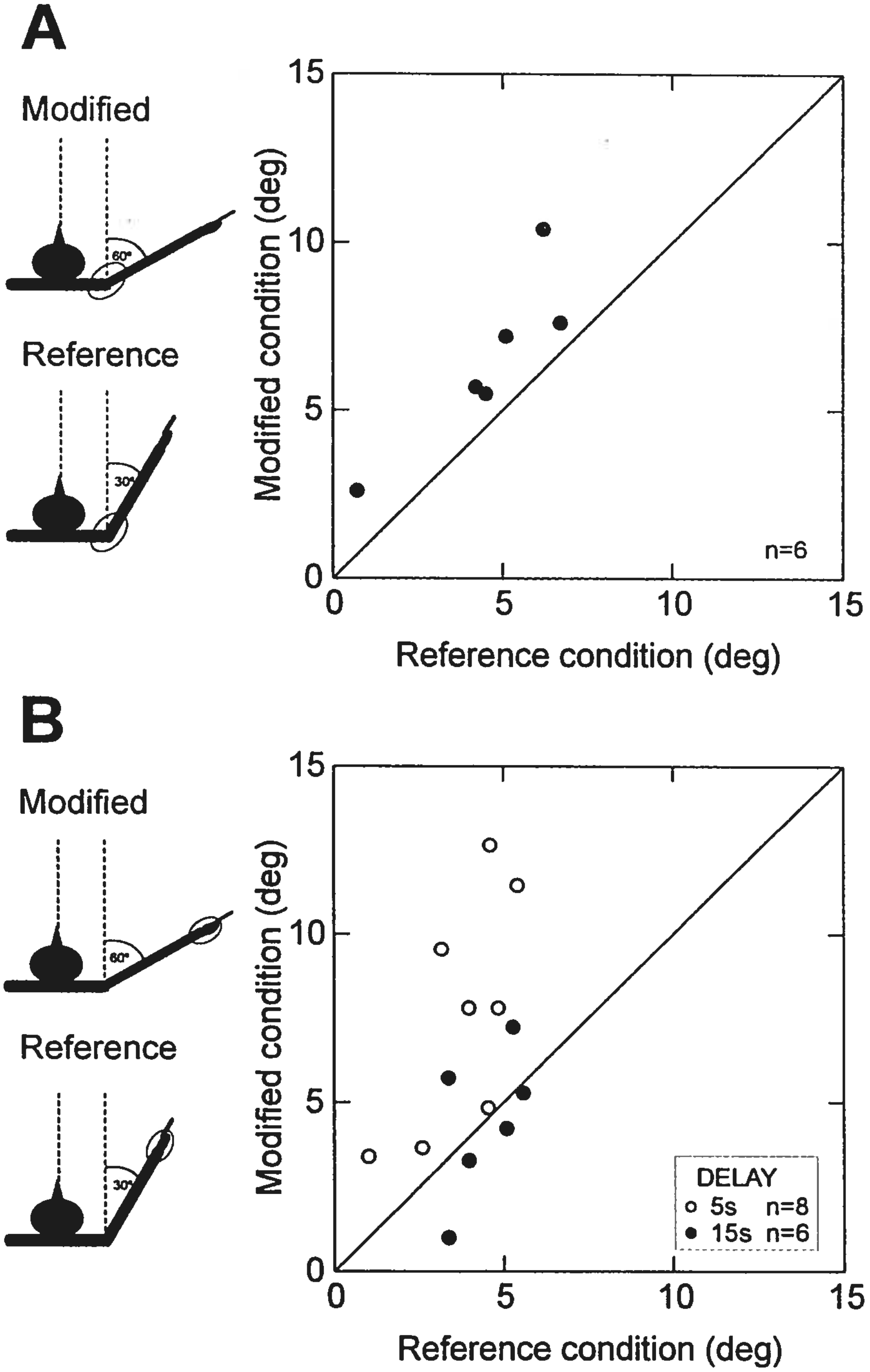

Fig. 6.4.2.1 A and B. 60° (modified) versus 30° (reference) during scans made with either proximal (A) or distal (B) joint movements. The joint at which rotation occurred is encircled on the cartoons (left). For proximal movements (interscan delay, ~14 s), discrimination threshold was increased in the eccentric position (A). For distal movements, discrimination threshold was similar in both positions when the delay was long (filled symbols, B). When the delay was decreased (open symbols, B), threshold was higher at the eccentric position (60°). Data plotted as in Fig. 6.4.1

subjects that were tested in both delay conditions, the delay had no apparent effect on discrimination threshold when the angles were located closer to the midline (5 s versus 15 s delay, P=0.442). These observations suggest that factors, possibly related to the spatial frame of reference, contributed to the results.

6.4.2.2 Proximal versus distal.

We compared the ability of six subjects to discriminate 2-D angles using either proximal or distal (wrist/2nd mcp) joints. The angles themselves were placed at 30° to the right of midline, and the delay between scanning the pairs of angles was set at ~15 s, i.e. comparable to the delay used in experiment 1 and in our previous studies (Voisin et al. 2002a, b). The results are presented in Fig. 6.4.2.2 (see also Table 6.4 B). There was no significant difference in the mean discrimination threshold for the distal explorations, 4.1°, as compared to the proximal explorations, 3.1° (P=0.532). The lack of any difference was confirmed by pooling the data from all of the reference conditions performed with the angles located 30° to the right of midline: mean threshold was 4.9° (n=19) for the shoulder explorations, and 4.1° (n=20) for the wrist/2nd mcp explorations (independent t-test, P=0.222).

6.4.2.3 Effects of head orientation.

We suspected that the increased thresholds in the more eccentric position (short delay), as compared to the position closer to midline, might be related to the

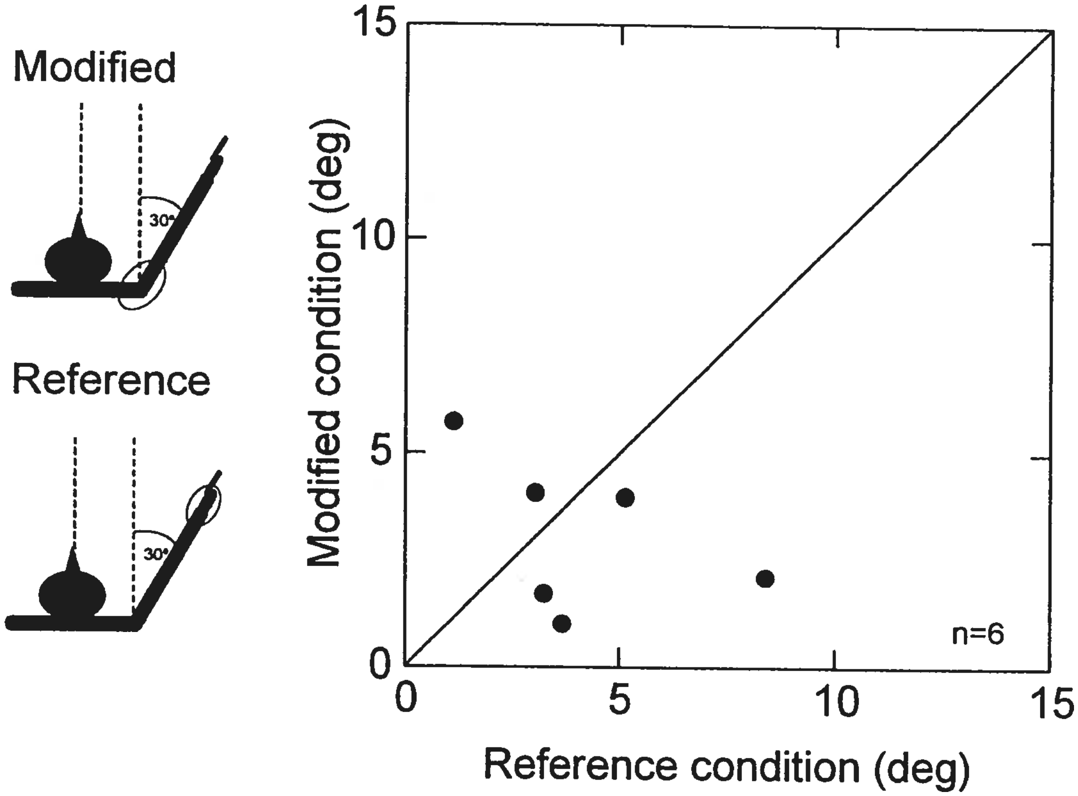

Fig. 6.4.2.2 Proximal (modified) versus distal (reference). Angles placed at 30° to the right; interscan delay 15s. Discrimination threshold was not modified by the change in the joint at which movement occurred. Plotted as in Fig. 6.4.1.

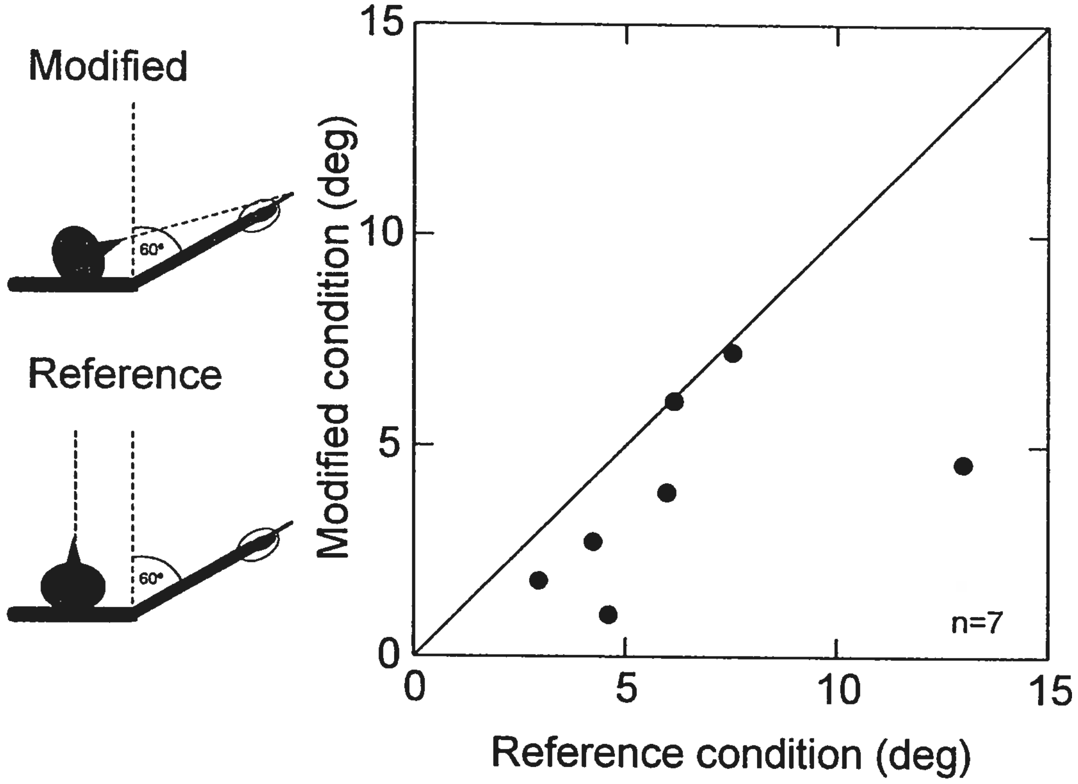

Fig. 6.4.2.3 Effect of changing head orientation on discrimination threshold: head forward (reference) versus head turned toward the location of the angle (modified). The angles were placed 60° to the right; interscan delay 5 s. Exploration was restricted to the distal joints. Discrimination threshold was reduced when the head was turned. Plotted as in Fig. 6.4.1.

central frame of reference used to interpret haptic signals. To further explore this aspect, we tested performance in the eccentric position, 60° (short delay so that threshold was high), under two conditions – with the head pointing straight ahead (as in all other experiments), and then with the head turned in the direction of the apparatus. Vision of the angles was, as in all testing, occluded. As shown in Fig. 6.4.2.3 (see also Table 6.4 B), threshold was *decreased* in the head turned position (head forward, 6.3°; head turned, 3.9°). The effect was nonsignificant when considering the results from all seven subjects (P=0.066), but became significant when the results of subject #16 were omitted (P=0.041). In the latter case, we were not able to estimate threshold in the reference condition (head forward), i.e. the subject could not discriminate the largest angle difference presented (13°). The result indicated that the distance from the midline was not the key factor in modifying 2-D angle discrimination. Instead, it appeared that the angular distance between the head and the object was the determining factor.

6.4.2.4 Subject reports.

Overall, subjects reported no systematic changes in difficulty across the different conditions tested in experiment 2. Interestingly, the two subjects who showed the smallest change in the head orientation experiment (#18 and #19) were the only subjects to report that the task was more difficult in the head turned position. Subject #18 also reported that the head turned position was uncomfortable, suggesting that discomfort may have contributed to reduce the difference in threshold across the two conditions. Most subjects estimated the range of angles explored as ranging from 90° to 120-125°. Thus, subjects correctly identified the use of a 90° angle, but they tended to overestimate the actual range of angles explored (90 - 103°).

6.5 DISCUSSION

In this study, we demonstrated that haptic discrimination of 2-D angles is relatively independent of the spatial location of the objects when conditions were constrained so as to eliminate potential changes in peripheral mechanoreceptive sensitivity, specifically proprioceptive feedback from the moving joint. Changes in the quality of peripheral feedback, cutaneous or proprioceptive, on the other hand, were accompanied by significant changes in 2-D angle discrimination, consistent with both sources of feedback contributing to the haptic appreciation of shape. We also demonstrated that haptic sensitivity is invariant for explorations involving distal and proximal joint movements. Finally, the results provide insight into the central mechanisms that contribute to shape discrimination, particularly as regards the frames of reference used to represent object shape.

6.5.1 View-point and haptic angle discrimination.

These experiments sought to gain insight into how the "viewpoint" of contour following movements - the type of movement that provides essential information for describing the exact shape of objects (Lederman and Klatzky 1987) - modifies the ability to discriminate small differences in 2-D angles. There is considerable evidence in the visual field that object recognition is viewpoint-specific (reviewed in James et al. 2002a,b), i.e. that visual recognition of complex objects is better when the objects are presented in the same view as they were explored. As pointed out in the Introduction, Newell et al. (2001) recently suggested that haptic recognition of complex 3-D objects is also viewpoint-dependent. They found that haptic object recognition was decreased when the object was rotated 180°, as compared to no change in view. In this study, subjects explored an identical range of angles either from the inside or the outside. In contrast to Newell et al., the motor strategy was constrained, and so the spatial trajectories of the movements were identical. Although 2-D angle discrimination thresholds were significantly higher for the outside angles, additional experiments demonstrated that the decline in performance could be explained by the change in the quality of the cutaneous feedback since the outside angles were explored using a less sensitive skin area (hairy dorsum of D2). Although our results suggest that haptic shape discrimination is not viewpoint dependent, it should be pointed out that the conclusion is limited to a consideration of 2-D angle discrimination. Haptic object recognition, of the type studied by Newell et al., may well involve different central representations than serial discriminations of small differences in 2-D angles. In favour of this interpretation, our preliminary evidence using a angle categorization, which more closely resembles an object recognition task, has provided evidence of viewpoint dependence: angle categorization is systematically modified as a function of the initial frame of reference in which angles are explored (Voisin and Chapman 2002).

6.5.2 Spatial location and haptic angle discrimination.

When the angles were explored in a more eccentric position (60° versus 30° to the right of a mid-sagittal plane running through the shoulder), 2-D angle discrimination threshold was significantly increased for explorations made using shoulder joint rotation. We initially interpreted this observation as suggesting that haptic discrimination is better in spatial locations closer to the midline, where most explorations in daily life are carried out (Graziano et al. 2004). Subsequently, however, we showed that spatial location had no effect on 2-D angle discrimination when the explorations were restricted to distal joints (wrist/2nd mcp joint). The latter observation made it likely that changes in proprioceptive sensitivity at the shoulder in the two test positions were responsible for the effects seen when exploration was restricted to the proximal joint. Our finding that haptic angle discrimination is independent of spatial location, within the tested range (30 to 60°), is consistent with Henriques and Soechting's (2003) recent report of no change in haptic appreciation of geometric shapes within a relatively constrained horizontal workspace located directly in front of the subject. As reviewed in the Introduction, on the other hand, Kappers and colleagues (Kappers and Koenderink 1999; Kappers 1999) found that haptic judgments of parallelity (orientation of bars placed on a large horizontally disposed workspace) are less precise as the horizontal, but not the vertical, distance from midline is increased. Our results are nevertheless consistent with their observations since our experimental manipulation, with the angles placed at arm's length from the subject, generated relatively large changes in the "vertical" location of the angles (within a horizontal plane relative to the subject's midline and running through the shoulder) and minimal changes in the horizontal location (relative to midline).

6.5.3 Proximal versus distal articulations.

Previous studies of position sense at proximal and distal articulations have shown that proprioception is better at proximal joints than distal joints (reviewed in Clark and Horch 1986). When, however, position sense is measured within the context of more natural tasks, proprioceptive acuity is generally greater than found in studies of joint position sense in isolation. For example, Hall and McCloskey (1983) found that, under optimal conditions (i.e. sufficiently fast movements), the best performance for the terminal joint of the middle finger was ~1° (detection threshold for joint rotation). In contrast, John et al. (1989) found that subjects could resolve digit joint angles with a precision of ~0.1° at the proximal interphalangeal joint, or 0.05° at the mcp joint, using a task in which subjects discriminated the thickness of metal plates explored with a precision grip. Similar disparities have also been reported for measures of shoulder proprioception (Van Beers et al. 1998; Voisin et al. 2002a; Henriques and Soechting 2003).

The present finding of similar performances with proximal and distal explorations argues in favour of an invariant central representation of object shape independent of the joints involved in the exploration, a conclusion that is necessarily limited to the 2-D angles investigated here. The acuity of the underlying proprioceptive signals, on the other hand, must logically follow the proximal-distal gradient previously described. Explorations with the distal joints necessarily required larger angular excursions than did explorations with the shoulder joint, given the difference in the length of the lever arm. This leads to the suggestion that regional variations in proprioceptive acuity may reflect an adaptation to generate an invariant central representation of haptic shape. Why? One suggestion is that the central representation is based on an object-based, or allocentric, frame of reference. This subject is considered further below.

6.5.4 Frame(s) of reference.

Much of our knowledge about spatial frames of reference comes from studies of visuomotor control. Such studies have provided evidence that multiple reference frames are used, depending upon task conditions. As recently reviewed by Cohen and Andersen (2002), these can be related to the subject or they can be related to external world coordinates. A variety of egocentric reference frames have been identified, including eye-centred, head-centred, limb-centred and hand-centred reference frames. Intermediate combinations have also been described (Flanders and Soechting, 1995; Soechting and Flanders 1993).

Studies in the visual system, particularly aimed at understanding visuomotor processing, suggest that the initial processing of the spatial location of visual stimuli is relatively rapid and precise, and is based upon an egocentric frame(s) of reference, presumably facilitating interactions with the motor systems (oculo- or somatomotor). This representation, however, degrades over time, and is replaced by a second, slower system, presumed to be more involved in perceptual functions, that represents stimuli in an allocentric frame of reference (Milner and Goodale 1995). Thus, when a delay is introduced between the end of a visual stimulus and the initiation of movement towards the stimulus, subjects generally show increased errors (Bridgeman et al. 1997; Rossetti 1998), reflecting a degradation of the initial egocentric representation. Subjects with “blindsight” (preservation of the dorsal processing stream for action, with loss of the ventral stream for perception) show greater accuracy when the delay between the stimulus and the motor response is short (Rossetti 1998). Lesions that damage the dorsal processing stream have the opposite effect: Milner et al. (1999) described a patient with bilateral parietal lobe damage who showed improved pointing accuracy to a visual target with long as compared to short delays, i.e. opposite to the findings in normal subjects.

What then are the reference frame(s) for haptic shape? As described in the Introduction, Zuidhoek et al. (2003) proposed that haptic bar orientation is initially represented in an egocentric frame of reference, and that this switches to an allocentric reference frame when a delay (10 s) is added between the exploration and the subsequent matching. Further to this, Kappers (2002) proposed that the egocentric representation was based on an intermediate reference frame derived from a hand-centred and an allocentric (fixed in space) representation of bar orientation. Our results are consistent with the existence of at least two frames of reference, an initial short-lasting one and a second reference frame evident with the longer delay, and provide some insight into the nature of these representations. When considering all of the data collected with the short delay (Table 3), we suggest that these can best be explained by a single egocentric

Table 6.5.4 Mean discrimination thresholds as a function of the joint at which rotation occurred (wrist/2nd mcp, shoulder), the delay between successive scans of each pair of angles, and the nominal angular difference between the spatial location of the hand and the direction in which the head was pointing.

	Wrist		**Shoulder**
	Delay 5 s	Delay 15 s	Delay 14 s
Arm/Hand – Head			
0°	3.9°	-	-
30°	3.8°	4.4°, 4.1°	4.6°, 3.1°
60°	7.6°, 6.3°	4.5°	6.5°

frame of reference, based on the difference between the position of the arm/hand and the direction in which the head was pointing. Note that "gaze" was directed in the same direction as the head, but vision was occluded. When the difference was small (0° or 30°), discrimination threshold was low, an effect that was independent of the position of the arm/hand (30 or 60° to the right). When the difference was large (60°) then discrimination threshold was high. This initial reference frame was not, on the other hand, evident when the time between successive scans was increased: for explorations performed using the distal joints, performance was as accurate for large (60°) as for small (30°) angles between the arm/hand and head. Given the results from studies in the visuomotor system, it seems most likely that a coordinate transformation occurred during the longer delay interval, as the haptic representation changed from an ego- to an allocentric or object-based frame of reference.

The suggestion that the initial, short-lasting representation is egocentric, while the delayed representation is allocentric is consistent with current thinking of the central representation of visual space (above). Interestingly however, and different from the visual system, our results suggest that both representations of haptic stimuli are highly accurate, i.e. low discrimination thresholds were obtained both with short and long delays. A direct comparison is likely not warranted as the studies in the visual system concentrated mostly upon visuomotor performance, and so reflected errors in both sensory processing and motor planning/execution. In contrast, the present study focused only on sensory performance. The results are, on the other hand, pertinent for the interpretation of the effects of delay seen by Zuidhoek et al. (2003) (above). They found that adding a delay (bimanual task) improved matching, and the effect was more pronounced as the horizontal distance between the bars and the subject's midline increased. In our experiments, in contrast, horizontal distance was constant because all angles were explored at arm's length, and yet delay significantly modified the results. Can these different results be reconciled? One possibility is that the observed distortions in the perception of bar orientation may have reflected the pattern of asymmetric stimulation of the glabrous skin of the hand and fingers at different locations in the workspace. It should be noted that these distortions arose particularly in the bimanual explorations, in which case subjects had to transpose one pattern of stimulation into its mirror image on the opposite hand (Kappers 1999). Moreover, it was in the bimanual condition that delay was found to reduce the errors. We suggest that the improved performance with an added delay in the study by Zuidhoek et al. (2003) provided time to remap the pattern of sensory stimulation. Consistent with this interpretation, there was little evidence for distortion at different vertical distances from the body (in which case the pattern of stimulation would have been similar at different spatial locations). Likewise, performance was better when the same hand was used for exploring the reference and test bars (Kappers 2002).

The present results cannot determine whether the initial egocentric frame of reference was head-centred or gaze-centred since both changed together in this study. Moreover, the subjects' vision of the angles was blocked at all times. Our suggestion that the initial reference frame is in part dependent on "head" position appears, at first glance, to be counter-intuitive. Why would head orientation modify haptic discrimination of unseen 2-D angles? First of all, vision and haptics are complementary sensory abilities, and both can encode object shape. Indeed, one can argue that vision is the dominant modality for object shape identification, and that touch serves as a back-up system for situations in which vision is inadequate (e.g. searching for an object in the dark). Second, several studies have suggested that visual imagery contributes to haptic object recognition (Zangaladeze et al. 1999; Amedi et al. 2001). Indeed, most subjects in the present experiments reported creating mental images, including visual, of the angles (Voisin et al. 2002a). In support of this idea, the results of imaging studies show that there is a common central representation of object shape, haptic and visual, involving areas in the occipital cortex associated with the ventral visual stream (Amedi et al. 2001; James et al. 2002a). Finally, head orientation relative to the explored angles may help to direct attention towards the haptic stimuli, and so enhance the central neural representation of the objects (e.g. Meftah et al. 2002). Certainly there is considerable evidence that spatial attention can enhance tactile perception, and moreover there are cross-modal links between modalities, including vision and touch (Spence et al. 2000; Meftah et al. 2002). Taken together, it is thus not too surprising that head orientation modified haptic angle discrimination.

6.6 ACKNOWLEDGEMENTS

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CHAPITRE VII - DISCUSSION

Les objectifs de la thèse étaient tout d'abord de définir une tâche haptique simple, conservant le caractère intégratif du toucher de forme macroscopique, ce qui a été montré dans les deux premiers articles de cette thèse. Dans le troisième article, l'effet de diverses manipulations expérimentales sur les conditions d'exploration ont été testés afin: 1) de vérifier la dépendance au point de vue de la stéréognosie haptique (modulation des performances en fonction de la posture ou des conditions motrices) ; et 2) d'en inférer des informations sur la nature des traitements cognitifs liés à la stéréognosie haptique. Après une discussion des évidences et limites de ces études (section 7.1), l'implication de coordonnées centrés sur le regard et la main sera discutée en relation avec deux expériences ultérieures (non publiées) portant sur la catégorisation d'angles (section 7.2). Par la suite, l'interprétation de ces résultats sera discutée (section 7.3), en proposant en particulier deux modèles basés soit sur un cadre de référence unique, soit sur deux cadres égocentrés dont les implications diffèrent à travers le temps. Nous verrons que ce dernier modèle rend compte également de plusieurs résultats expérimentaux au niveau du contrôle moteur d'une part, et de l'imagerie mentale d'autre part, sans que nous puissions apporter de preuve définitives à ce sujet. Nous proposerons alors plusieurs expériences visant le test de ce modèle (section 7.4). Finalement, quelques implications cliniques de ce travail seront abordées dans la section 7.5.

7.1 RESUME DES ETUDES PRESENTEES

7.1.1 Méthodologie

A partir du premier article, on voit l'opérationnalisation d'une tache haptique destinée a tester les performances d'exploration et de perception de formes haptiques, ainsi que leur lien entre elles et l'effet de modifications expérimentales sur la performance humaine de stéréognosie haptique. Les sujets devaient explorer des formes composées de deux barres dont l'intersection formait un angle, la différence entre deux objets pouvant alors se quantifier par une seule valeur entre 1° et 13°. Les sujets devaient examiner les angles par un seul mouvement d'aller et retour de l'index sur chaque forme présentée successivement, sans vision ni feedback sur leurs réponses. Le pourcentage de bonne réponse pour chaque différence d'angle présentée était ensuite calculé et approché par une fonction logistique allant de 0 à 1 (proportion de bonne réponse) en passant à 0.5 (performance obtenue si un sujet répond au hasard) pour une différence d'angle de 0° (pas de différence entre les objets). La perception des sujets était alors caractérisé par un seuil de discrimination correspondant au nombre de degrés de séparation nécessaire entre deux formes à examiner pour obtenir 75% de discriminations correctes. Les mouvements d'exploration étaient contraints au niveau de la trajectoire, mais pas au niveau de la vitesse ni de la force exercée sur les objets lors de l'exploration, qui étaient laissées au libre choix des sujets (des entraînements succincts étaient données au préalable pour stabiliser les performances et les mouvements d'exploration). Les mouvements des sujets étaient en revanche enregistrés, d'une part au niveau de la force d'application (6 jauges de contraintes disposés sur les côtés des formes), et d'autre part de la vitesse d'exécution de chaque mouvement de poursuite de contour (vitesse sur les barres et intervalle du passage d'une barre à l'autre). Chacun de ces paramètres était alors analysé pour observer les effets de répétition ou de modifications des séances expérimentales, de la variabilité inter-sujet, de l'orientation de l'appareil, et la covariance de chacun de ces paramètres entre eux. Finalement, les résultats de la tâche de référence ou de modifications des conditions expérimentales étaient discutés et comparés à ceux de la littérature.

7.1.2 Premier article

Dans le premier article, nous avons tout d'abord vérifié que les performances étaient correctement approchées par une fonction logistique (voir ci-dessus). Nos tests nous indiquaient par ailleurs la stabilité et l'efficacité de cette méthode, puisque des approximations basées sur 4 ou 7 différences d'angles (7 testés) aboutissaient à des résultats très proches. De façon surprenante, les performances individuelles montraient une très forte variabilité, dont la source était obscure. En effet, les performances variaient peu en fonction de la répétition des séances, de la vitesse d'exploration, de la force d'application du doigt sur la surface des formes, ou des caractéristiques des sujets (genre, age, taille). De la même façon, les mouvements d'exploration montraient une grande variabilité, sans que nous ayons pu mettre en évidence la source de cette variabilité, et sans corrélation forte entre les variations des mouvements d'exploration et de la performance. Finalement, la variabilité intra-sujet était également importante de séance en séance, un sujet pouvant présenter un seuil de 5.7° sur une séance, et de 0.7° à une autre. Nous sommes confiant que cette variabilité n'était pas due à notre méthode de calcul du seuil, puisque des seuils similaires étaient retrouvée en utilisant les résultats d'un échantillon de 4/7 différences d'angle. En conséquence, cette variabilité est probablement intrinsèque à la stéréognosie haptique, possiblement liée à l'utilisation d'imagerie mentale telle que rapportée par les sujets. Au niveau pratique, les résultats d'une modification des conditions expérimentales sur la performance de stéréognosie haptique doivent donc être comparés à ceux d'une condition de référence testée chez les mêmes sujets, de préférence au cours d'une même séance. C'est cette stratégie que nous avons employée par la suite. En particulier, nous avons pu montré que les performances de discrimination des angles étaient trop peu affectées par une variation de l'orientation des formes pour se baser uniquement sur l'orientation d'un des deux segments. Cela prouve donc que les sujets ont effectivement construit une représentation de l'angle formé, ainsi que demandé.

7.1.3 Second article

Dans le second article, la double implication des informations cutanées et proprioceptive dans ce type de tâche a été démontrée puisque la suppression sélective de chacune de ces sources amenait à une diminution des performances. D'une part, une condition d'anesthésie cutanée amenait à une augmentation significative du seuil de discrimination sans changement significatif de la vitesse d'exploration (vitesse d'aller et retour su les barres et latence à l'intersection angulaire). D'autre part, les seuils de discrimination étaient moins élevés (meilleurs) dans une condition de référence que dans une condition passive (suppression d'informations proprioceptives). Pour cette condition passive, les objets étaient déplacés mécaniquement sur deux axes x (horizontal) et y (vertical), en reproduisant (utilisation d'un servo-contrôle des positions x et y) les vitesses d'exploration naturelles de chaque sujet (enregistrées dans une condition de référence antérieure). En générale, cette procédure s'est révélée satisfaisante pour reproduire la vitesse des mouvements, mais moins en ce qui concerne la latence entre le passage d'un segment à l'autre des formes –beaucoup plus longue dans la condition passive. Il est donc possible que ce facteur ait diminué la performance des sujets en condition passive indépendamment ou en interaction avec la suppression des informations proprioceptives. Malgré ce problème, nous sommes confiant que la détérioration des performances en condition passive était due en grande partie à la suppression des informations proprioceptives. Premièrement, la vitesse des mouvements n'était pas corrélée à la performance en condition de référence, ce qui plaide pour un faible impact de la vitesse des mouvements sur la performance. Ensuite, les sujets en condition d'anesthésie avaient une performance diminuée mais supérieure à des réponses aléatoires, suggérant que les sujets disposaient d'une autre source d'information que les informations cutanées. Finalement, l'anesthésie du doigt combinée à une condition passive amenaient une suppression de la capacité de stéréognosie (pas de performance supérieure aux performances que les sujets obtiendraient en répondant au hasard), ce qui confirme que seule les sources cutanées et proprioceptives étaient disponibles (pas de vision ni d'indice non contrôlé). En conséquence, cette étude suggère que la discrimination d'angles par le toucher se base effectivement sur une intégration somatosensorielle entre les modalités cutanées et proprioceptives. Bien que la plupart des auteurs s'accordaient sur cette hypothèse, il s'agit à notre connaissance de la première démonstration publiée de cette double implication à la stéréognosie haptique.

7.1.4 Troisième article

Dans l'article 3, nous avons réalisé deux choses. Tout d'abord, il a été de démontré que des variations des conditions d'explorations ont un impact à la fois sur la performance et sur le mouvement d'exploration, suggérant ainsi que la représentation des formes est dépendante du point de vue. De façon intéressante, cette dépendance au point de vue s'explique non seulement par des variations dans la qualité des informations périphériques disponibles, mais aussi par des effets cognitifs liés à la nature des processus sous-jacents. Ensuite, nous avons transformé cet effet de dépendance au point de vue en outil d'exploration des représentations haptiques. En particulier, les informations somesthésiques liées à la forme seraient codées dans un ou plusieurs cadre(s) de référence égocentré(s), au moins en absence de contraintes mémorielles. Ainsi, l'implication d'informations référencées à la main et au regard, amènerait des distorsions proportionnelles aux différences d'alignement entre ces coordonnées lorsque le sujet désaligne son regard de sa main explorant les objets, dans une condition d'exploration de la forme par le toucher sans vision. Ce schéma ne serait toutefois valable que lorsque les contraintes mémorielles sont faibles, puisque cet effet de désalignement des cadres de références liés à la main et au regard ne se retrouve pas lorsque les sujets doivent maintenir en mémoire une des formes à discriminer pendant une durée relativement longue (15s). En conséquence, la nature des cadres de références utilisés varie en fonction des contraintes opérationnelles de la tâche, ce qui permet de faire ressortir l'existence d'un ou plusieurs cadre(s) égocentré(s) sur le regard et la main par de simples manipulations psychophysiques. La nature des cadres de références utilisées lorsque les contraintes mémorielles sont importantes demeure toutefois une question ouverte avec les données présentées jusqu'ici.

7.2 ETUDES DE CATEGORISATION D'ANGLES

Dans les sections suivantes, un court résumé de deux études ultérieures portant sur la catégorisation d'angle sera présenté, ces études suggérant un impact de contraintes mémorielles importantes sur la ou les représentations haptiques de la forme.

7.2.1 Catégorisation, protocole et absence d'effet du regard ou de la main

A la suite des expériences de discrimination, l'implication de référence(s) égocentré(s) a été démontrée lorsque les délais entre les présentations des angles sont courts (i.e. la contrainte mémorielle faible), mais pas lorsque les délais sont longs (i.e. contrainte mémorielle forte). La nature du(es) cadre(s) de référence utilisé dans le dernier cas n'est donc pas claire. Deux expériences complémentaires portant sur la catégorisation d'angle permettent toutefois d'apporter des éléments de discussion (expériences non présentées dans les sections précédentes). Dans les tâches de catégorisation, les sujets devaient explorer un angle unique (84-86-88-92-94-96°), et déterminer s'il s'agissait d'un angle petit (<90°) ou grand (>90°). L'intérêt de cette catégorisation est que les sujets doivent se baser sur une représentation interne du 90°, ce qui induit donc une contrainte mémorielle forte, analogue au cas où les sujets doivent attendre un long délai avant d'examiner le second angle d'une paire à discriminer. Dans une tâche de ce type, il a effectivement été impossible de trouver un effet de l'orientation du regard, de la tête ou des yeux, malgré un protocole incluant 16 sujets[1]. En conséquence, cette tâche ne semble pas mobiliser des cadres de références égocentrés, tout comme les tâches de discrimination d'angles lorsque le délai entre la présentation des angles est important. Une possibilité est donc que des contraintes mémorielles causent ou permettent l'utilisation de cadre(s) allocentré(s), c'est à dire centré(s) sur un cadre de référence externe au sujet, et possiblement sur les objets eux-mêmes. Alternativement, la catégorisation d'angle pourrait effectivement passer par un cadre égocentré sur le regard, mais sans conflit avec un cadre égocentré sur la main.

7.2.2 Evidence pour de la rotation mentale?

Dans une expérience ultérieure de catégorisation d'angle à travers quatre quadrants couvrant les 360° de l'espace de travail (Fig. 7.2.2 A), des performances faibles (haut seuil de catégorisation) ont été observé pour le quadrant orienté en bas à droite (Fig. 7.2.2 B). A première vue, ce résultat

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1- Ces résultats pourraient toutefois être lié à une différence insufisante entre les orientations du bras et du regard. En effet, une prolongation de cette étude utilisant des différences plus importantes semble faire ressortir un effet du regard dans ce type de tâche de catégorisation. En conséquence, ces nouvelles données (Michaud, Voisin et Chapman) pourraient supporter l'idée que la catégorisation d'angle utilise effectivement sur un cadre égocentré sur le regard.

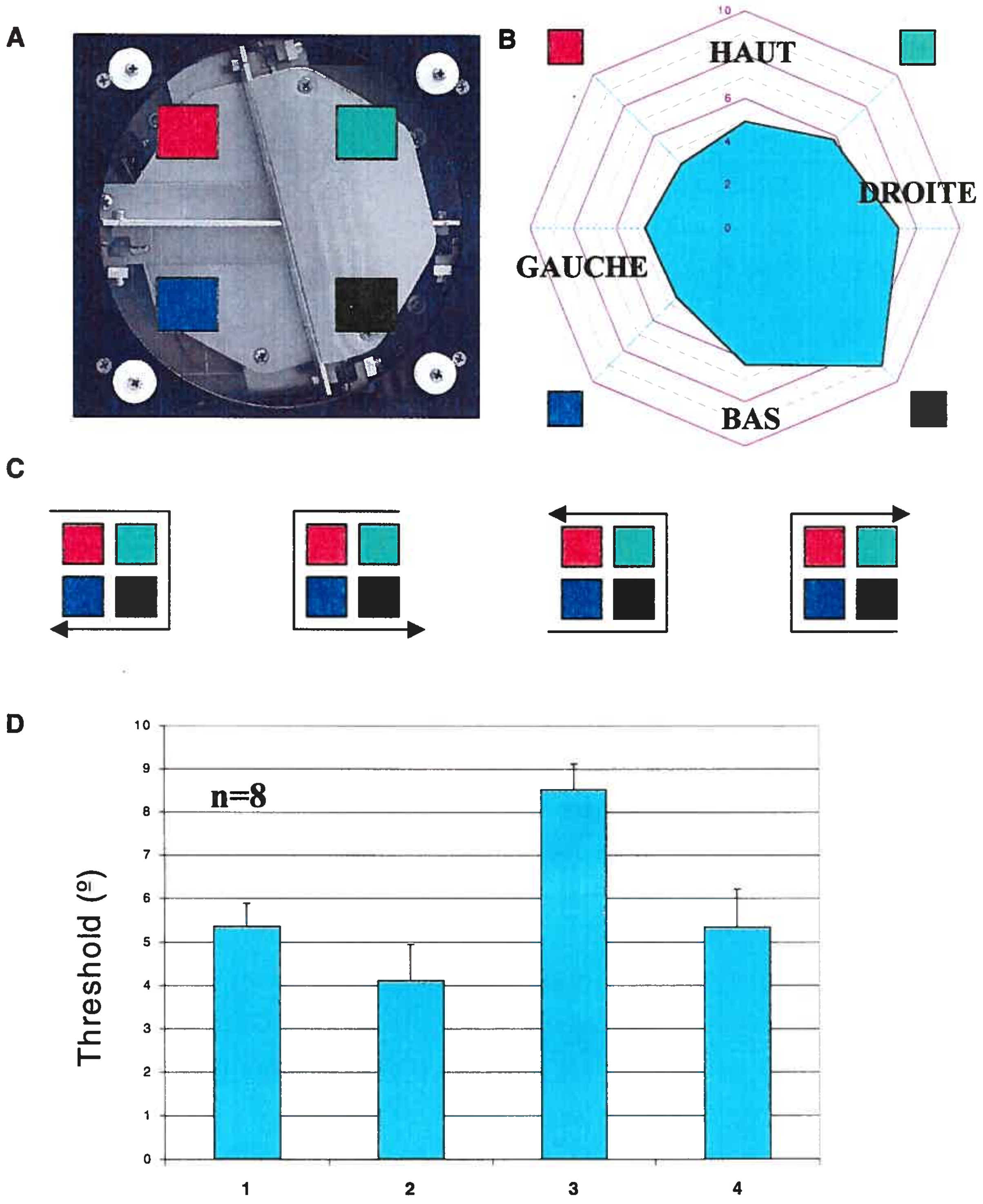

Fig. 7.2.2 A Apparatus B Mean categorisation thresholds across four physical disposition (interpolated data for the four quardinal directions) C The four orders of testing used (n=2/order of testing) D Mean categorization thresholds as a function of the order of testing.

s'explique facilement par une diminution de la sensibilité périphérique, puisque les sujets utilisaient dans ce cas la partie dorsale (peau poilue) du doigt. Cependant, les sujets montraient une performance normale (i.e. identique aux performances retrouvées pour les quadrants du haut) pour le quadrant en bas à gauche, pour lequel les sujets utilisaient également la partie dorsale de leur doigt. Il s'agit donc d'une première indication concernant un effet cognitif, possiblement lié à une orientation préférentielle des angles. De façon intéressante, un effet d'ordre (une augmentation très importante du seuil de catégorisation pour le 3ème quadrant testé) a également été retrouvé dans ces expériences (Fig. 7.2.2 D). Cet effet ne peut s'expliquer par des changements de sensibilité périphérique, puisque chaque disposition physique était contrebalancée pour chaque ordre de test des quadrants (Fig. 7.2.2C). En conséquence, cet effet est vraisemblablement lié à un facteur cognitif, c'est à dire à la nature du(es) cadre(s) de référence utilisé(s) par les sujets dans cette tâche. Dans une tentative pour comprendre l'origine de cet effet, quelqu'un peut remarquer que le troisième quadrant testé était toujours opposé (tourné à 180º) par rapport au premier quadrant testé (Fig. 7.2.2C), alors que les quadrants examinés en deuxième ou en quatrième était tourné de 90º seulement par rapport au premier quadrant testé. En se souvenant que les sujets doivent utiliser un référentiel interne (un 90º séparant les petits angles des grands angles) pour réussir la tâche, alors nous proposons que cette représentation interne soit fabriquée selon une orientation particulière: celle correspondant au premier quadrant testé. Par la suite, une rotation de ce 90º interne serait utilisée dans les quadrants testés ultérieurement. Pour les quadrants testés en 2ème et en dernier (4ème), ce processus nécessiterait une rotation minime (90°) et donc pas ou peu de détérioration de la performance. Pour le quadrant testé en troisième en revanche, le 90° interne devrait être complètement retourné (rotation de 180°), ce qui aboutirait à une diminution de performance (augmentation du seuil de catégorisation). Cette interprétation, bien que nécessitant encore confirmation expérimentale, présente deux caractéristiques intéressantes: l'utilisation de rotation mentale d'une part, et une représentation présentant une orientation préférentielle d'autre part.

7.3 CADRES DE REFERENCE POSSIBLES

En conséquence des résultats du troisième article et des expériences ultérieures de catégorisation, nous proposons que les cadres de références utilisés pour représenter la forme des objets dépendent des contraintes mémorielles. Pour des contraintes mémorielles faibles, les formes seraient perçues via des cadres de références égocentrés sur la main et le regard, ou un seul cadre comportant les deux types d'information. Pour des contraintes mémorielles plus fortes, cette stratégie serait modifiée, sans que la nature des cadres de référence utilisée soit clairement tranchée avec les données présentées jusqu'ici. Un point majeur est l'amélioration paradoxale des performances lorsqu'une contrainte mémorielle est imposée, il faut en déduire que les informations haptiques elles-mêmes ne sont pas directement dégradées. La détérioration des performances en cas de désalignement de la main et du regard doit donc s'expliquer en terme d'un conflit entre deux cadres de référence, ou à l'intérieur d'un même cadre de référence codant les deux coordonnées.

7.3.1 Questionnement

Deux interprétations différentes demeurent possibles pour rendre compte de nos données.

Tout d'abord, un même cadre de référence unique pourrait collecter des informations différentes, représentées en termes centrés sur la main et le regard, et aurait pour fonction de réorganiser ces informations en termes allocentriques, centrés sur les objets et suivant une orientation préférentielle. Cette première interprétation rend compte de nos données psychophysiques, et correspond également à des données préliminaires collectées dans le cortex somatosensoriel primaire (probablement l'aire 2). En effet, une diversité de facteur affecte différentiellement les quelques neurones enregistrés jusqu'ici. Cela est donc compatible avec l'idée d'un cadre de référence unique incluant une multitude d'informations relatives aux différents facteurs expérimentaux.

Une seconde interprétation peut toutefois être fournie, selon laquelle deux cadres de références égocentriques sont utilisés, un premier centré sur la main et de courte durée, un second centré sur le regard et de longue durée. La suppression du premier cadre amènerait à une suppression du conflit (en cas de désalignement entre la main et le regard) sans nécessitée de remapper les informations au sein d'un cadre allocentrique. De manière intéressante, cette interprétation pourrait rendre compte à la fois des données obtenues en contrôle moteur et en stéréognosie haptique.

7.3.2 Généralité du cadre de référence centré sur la main

Dans la troisième article, nous montrons que les performances de discrimination supportent une interaction entre deux cadres de référence pour les informations haptiques, dont l'un serait lié à l'orientation de la tête et de longue durée (voir section suivante), et un serait lié à l'orientation du bras explorant et de courte durée. Ce dernier cadre présente plusieurs caractéristiques similaires au cadre de référence proposé par plusieurs auteurs pour le contrôle du mouvement. Tout d'abord, la plupart des auteurs en contrôle moteur s'entendent pour proposer que la commande motrice soit codée en partie ou en totalité sur des cadres de référence égocentrés, et notamment liés au bras (Millner and Goodale 1995, Glover in press). De plus, les représentations liées au contrôle du mouvement se dégraderaient très rapidement (Elliott et Madalena, 1987, Rossetti, 1998, Westwood et al., 2001). Un dernier support vient de l'observation que les sujets ne semblent pas conscients de la diminution de performance avec l'excentricité des objets, alors que l'augmentation du seuil de discrimination dans ces expériences est du même ordre ou supérieure à plusieurs autres modifications rapportées comme difficiles ou très difficile (condition de suppression des informations proprioceptives rapporté dans le 2nd article, conditions de supination et outside du 3ème article). Hors, cette inaccessibilité à la conscience est un des traits caractéristiques proposés pour le contrôle moteur. En conséquence de tous ces éléments, il est tentant de considérer qu'un même cadre de référence servirait non seulement au contrôle moteur, mais aussi à la perception haptique.

7.3.3 Généralité du cadre de référence centré sur le regard

Finalement, le point le plus original de notre étude est la découverte d'un cadre de référence centré sur le regard. Étant donné que les informations disponibles dans cette tâche sont uniquement d'origine somesthésique, lié aux inputs cutanés ou profonds, on peut se demander pourquoi le système haptique utilise un cadre de référence apparemment visuel. Cependant, cette découverte s'inscrit dans un nombre grandissant d'évidence supportant l'implication du cortex visuel pour la somesthésie, et plus particulièrement l'analyse des formes. En dehors des évidences d'une implication des zones visuelles pendant la lecture du Braille chez les personnes aveugles, possiblement lié à une plasticité des zones visuelles en cause (Cohen et al., 1997, Buchel et al., 1998), il a en effet été démontré (Zangaladze et al., 1999) que l'interruption par TMS d'aires visuelles extra-striées (probablement V6) provoque un déficit spécifique pour l'analyse de la macrogéometrie (orientation), mais pas de la microgéometrie (texture). L'interprétation probable de ce résultat passerait par l'utilisation d'imagerie mentale, qui serait donc basée sur des structures en partie visuelles. Dans cette veine, nous proposons donc que le cadre de référence lié à l'orientation de regard tel que suggéré par nos donnés, soit en fait utilisé pour l'imagerie mentale, une capacité apparemment visuelle dans notre tâche. Une suggestion pourrait être que cette représentation visuelle permet, via un mécanisme de rotation mentale, de transformer la représentation des objets afin de les présenter sous une vue préférentielle (Newel et al., 2001). Cette idée, bien qu'encore hypothétique, expliquerait aussi pourquoi cette représentation est long-lasting, contrairement à la représentation 'motrice' de courte durée.

7.4 MODELE PROPOSE & PREDICTIONS

7.4.1 Modèle proposé

Nous proposons donc que le toucher haptique se base sur deux cadres de référence égocentrés, chacun orientés vers une étape spécifique de processus de collecte et de représentation des informations haptiques. Tout d'abord, un cadre de référence centré sur la main serait responsable de la collecte des informations haptiques, possiblement en relation avec le contrôle moteur du mouvement d'exploration. Au même moment, un cadre de référence centré sur le regard collecterait les informations haptiques et en établirait une image mentale. Lorsque les contraintes mémorielles sont faibles, la coexistence de ces deux représentations aboutirait à une diminution de performance en cas de désalignement de la main et du regard. Lorsque les contraintes mémorielles sont plus fortes, alors le cadre de référence centré sur la main disparaîtrait, et avec lui la diminution de performance en cas de désalignement du regard et de la main. Dans cette proposition, chacun des cadres de référence serait délimité temporellement selon son utilisation. Tout d'abord, le contrôle du mouvement et le recueil des informations proprioceptives s'effectuerais en même temps durant l'exploration, et donc serait basé sur un cadre de référence identique. Ensuite, ces informations seraient recueillies au sein d'une représentation centrée sur le regard permettant l'imagerie mentale, et en particulier la rotation mentale des formes haptiques vers une orientation préférentielle.

7.4.2 Prédictions

Comme souligné précédemment, ce modèle rend compte de nos données, sans que nous puissions exclure d'autres modèles qui pourraient rendre compte aussi bien des résultats. Seul le caractère éventuellement généralisable au contrôle moteur plaide pour considérer particulièrement ce modèle, puisque l'utilisation d'une même stratégie cognitive pour différentes fonctions permettrait d'économiser les ressources disponibles et de simplifier l'organisation du système nerveux. D'autres études seront toutefois nécessaires pour trancher ce débat.

Toutefois, si le modèle retenu n'est pas trop erroné, alors les prédictions suivantes devraient pouvoir être validées dans une tâche de discrimination d'angles avec 1) désalignement du regard et de la main et 2) courte durée entre les angles présentés :

- Au niveau de l'implication d'un cadre de référence à courte latence, centrée sur la main, responsable à la fois de la collecte des informations et du contrôle du mouvement : si on demande aux sujets de dessiner (ou une autre tâche nécessitant un contrôle moteur) durant la période d'attente du deuxième angle, alors l'interférence entre les deux tâches devrait amener à un désengagement du cadre de référence lié au contrôle moteur pour la discrimination d'angle, et donc une amélioration paradoxale de la performance de discrimination. Cette amélioration disparaitrait en ajoutant un délai entre les angles à discriminer.
- Au niveau de l'implication d'un cadre de référence visuel pour l'imagerie mentale : suivant le même principe, demander aux sujets de réaliser

l'imagerie mentale : suivant le même principe, demander aux sujets de réaliser une tâche nécessitant de la rotation mentale (par exemple déterminer si un J est présenté normalement ou inversé selon différentes orientations) permettrait de désengager le cadre de référence « visuel », et donc de supprimer la concurrence entre cadres de références, ce qui mènerait à une augmentation paradoxale de la performance.

Dans ces deux cas, il s'agit d'exploiter l'idée selon laquelle la concurrence entre deux cadres de référence produit une diminution de performance. Supprimer sélectivement un de ces cadres par des tâches requérant spécifiquement l'un ou l'autre de ces cadres devrait donc amener à une amélioration paradoxale de la performance. Afin de contrôler pour les effets aspécifiques liés à l'exécution de deux tâches en même temps, il suffirait d'ajouter une tâche sans concurrence spécifique avec les cadres « moteur » et « imagerie visuelle », comme par exemple un jugement auditif.

7.5 APPLICATION CLINIQUE POTENTIELLE

Il est estimé qu'environ 50% des clients ayant eu un accident vasculaire cérébral présente des déficits sensoriels, en particulier au niveau de la discrimination tactile et proprioceptive. De tels déficits ont un impact négatif sur l'exploration de l'environnement, la sécurité, le mouvement et les résultats de la réadaptation (Patel et al., 2000). De plus, des résultats obtenus chez l'animal suggèrent que des atteintes identifiées comme purement motrices pourraient être attribuables au moins en partie à des déficits sensoriels ou à des perturbations dans l'intégration sensori-motrice (Nudo, 2000). Traditionnelement, l'évaluatioin clinique des capacités sensorielles est basée principalement sur l'évaluation des seuils perceptuels (Bell-Krotoski et al., 1993, 1995). Cette approche met en évidence les déficits sensoriels primaires mais néglige les déficits secondaires comme la capacité du système nerveux central à moduler l'information sensorielle afférente et à intégrer l'information provenant de différentes modalités. La présence de déficits secondaires peut influencer les capacités perceptuelles et sensori-motrices, et ce même si les représentations primaires sont intactes (Staines et al., 2002). Le développement d'un test quantitatif et intégratif tel que celui présenté dans cette thèse pourrait alors permettre une meilleure évaluation de l'origine des atteintes perceptuelles des clients ayant subit un accident vasculaire cérébral. En effet, les tests classiques de stéréognosie nécessitent des processus cognitifs de haut niveau liés à l'identification et à la communication, ce qui interfère avec la mesure de la perception. Finalement, l'utilisation de mouvements d'exploration actifs est certainement plus naturelle qu'un simple examen passif.

CHAPITRE VIII - CONCLUSION

Conformément à nos objectifs, nous avons développée une tâche de discrimination d'angle comme modèle de la stéréognosie haptique. Dans les deux premiers articles, nous avons validé ce modèle, en montrant notamment 1) que des petits changements dans l'orientation des objets n'entraînaient pas de modification majeur des performances, attestant ainsi que les sujets perçoivent effectivement l'angle d'intersection formé par les objets, et non pas simplement l'orientation d'une des barres ; 2) que cette capacité se base effectivement sur une double implication des informations proprioceptives et cutanées, puisque la suppression sélective de chacune de ces sources amène une diminution de performance. Par la suite, nous avons également validé nos hypothèses selon lesquelles la discrimination d'angle est sensible à de simples manipulations psychophysiques n'affectant pas la qualité des informations périphériques disponibles, en montrant en particulier un effet réversible du désalignement du regard et de la main. L'amélioration paradoxale de performance avec l'ajout d'un délai dans ces conditions, amenaient à proposer un modèle de la stéréognosie haptique basée sur deux cadres de références égocentriques. Un premier cadre serait lié à la main et de courte durée, et éventuellement impliqué également dans le contrôle moteur. Un second cadre serait lié au regard, et éventuellement impliqué dans l'imagerie mentale visuelle. Toutefois, si ce modèle rend effectivement compte de nos données, en revanche plusieurs autres modèles seraient possibles. En conséquence, nous avons finalement proposée une série d'expériences qui permettraient d'invalider ou non ce modèle.

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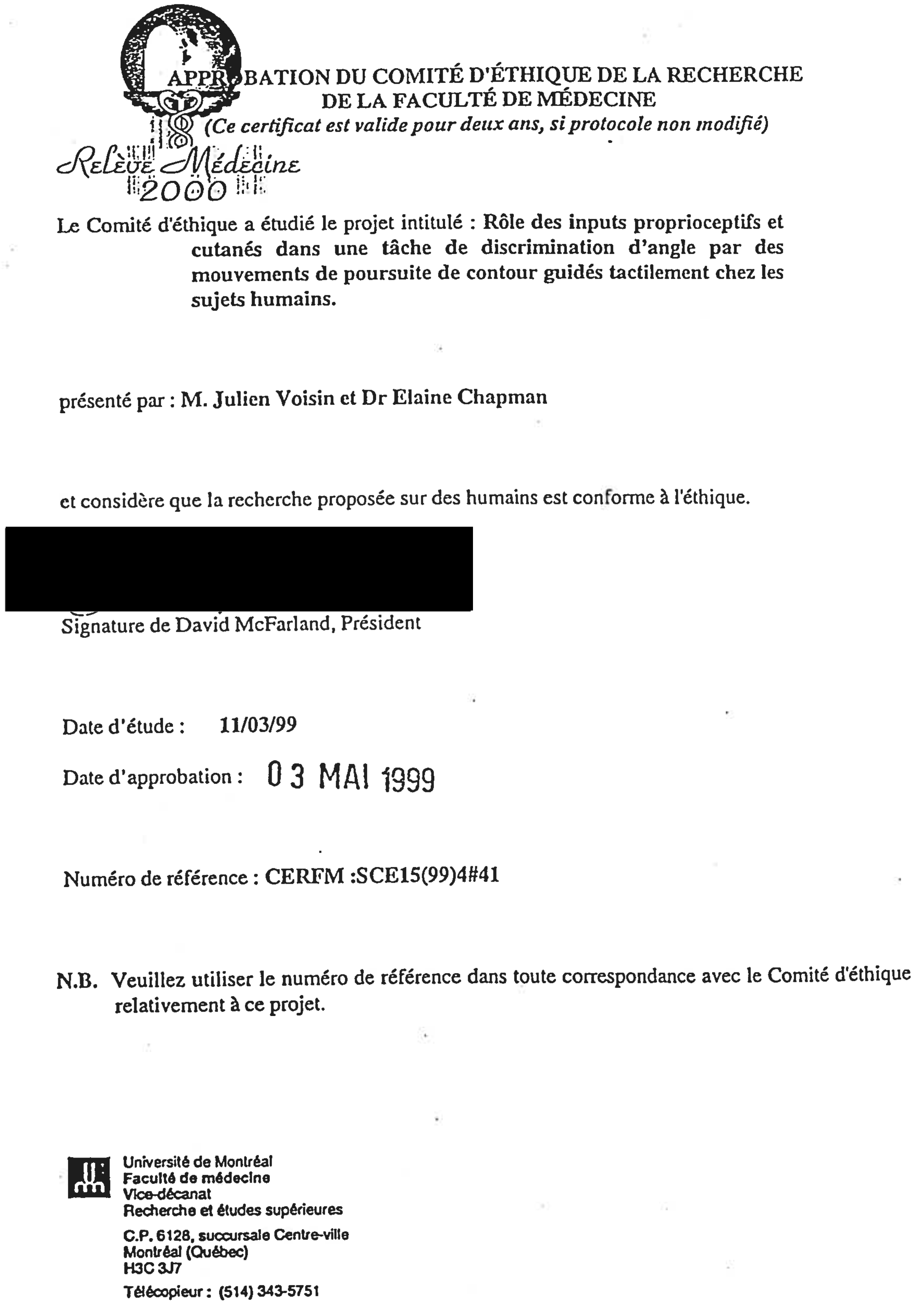
ANNEXE A : CERTIFICAT D'ÉTHIQUE



APPROBATION DU COMITÉ D'ÉTHIQUE DE LA RECHERCHE DE LA FACULTÉ DE MÉDECINE

(Ce certificat est valide pour deux ans, si protocole non modifié)

Relève Médecine
2000

Le Comité d'éthique a étudié le projet intitulé : **Rôle des inputs proprioceptifs et cutanés dans une tâche de discrimination d'angle par des mouvements de poursuite de contour guidés tactilement chez les sujets humains.**

présenté par : **M. Julien Voisin et Dr Elaine Chapman**

et considère que la recherche proposée sur des humains est conforme à l'éthique.

[redacted]

Signature de David McFarland, Président

Date d'étude : **11/03/99**

Date d'approbation : 03 MAI 1999

Numéro de référence : **CERFM :SCE15(99)4#41**

N.B. Veuillez utiliser le numéro de référence dans toute correspondance avec le Comité d'éthique relativement à ce projet.

Université de Montréal
Faculté de médecine
Vice-décanat
Recherche et études supérieures

C.P. 6128, succursale Centre-ville
Montréal (Québec)
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ANNEXE B : CONTRIBUTIONS DES DIFFÉRENTS AUTEURS AUX ARTICLES DE LA THÈSE

Après discussion avec ma directrice de thèse, nous avons fixé les proportions suivantes J Voisin 60%, CE Chapman 35%, autres co-auteurs (G Benoit, Y Lamarre et G Michaud respectivement) 5%, applicables pour les trois articles présentés dans cette thèse.

Les travaux ultérieurs portant sur la catégorisation d'angle (chapitre 7) sont une collaboration entre J Voisin, G Michaud et CE Chapman, sans proportions fixées au moment du dépôt de la thèse (travaux en cours). La contribution de G Michaud est toutefois première pour les expériences variant les orientations du bras et du regard, celle de J Voisin première pour l'expérience variant les orientations des angles.

ANNEXE C : DÉCLARATIONS DES CO-AUTEURS

ACCORD DES COAUTEURS

Déclaration des coauteurs d'un article

Lorsqu'un étudiant n'est pas le seul auteur d'un article qu'il veut inclure dans son mémoire ou dans sa thèse, il doit obtenir l'accord de tous les coauteurs à cet effet et joindre la déclaration signée à l'article en question. Une déclaration distincte doit accompagner chacun des articles inclus dans le mémoire ou la thèse.

1. Identification de l'étudiant et du programme

Julien Voisin
PhD Sciences Neurologiques

2. Description de l'article

Julien Voisin, Geneviève Benoit and C. Elaine Chapman (2002) Haptic discrimination of object shape in humans: two-dimensional angle discrimination. Publié dans Experimental Brain Research 145:239-250.

3. Déclaration de tous les coauteurs autres que l'étudiant

À titre de coauteur de l'article identifié ci-dessus, je suis d'accord pour que Julien Voisin inclue cet article dans sa thèse de doctorat qui a pour titre "L'encodage de la forme par le toucher haptique".

GENEVIÈVE BENOIT	[redacted]	22-5-2003.
Coauteur	Signature	Date
C E Chapman	[redacted]	21-5-2003
Coauteur	Signature	Date

ACCORD DES COAUTEURS

Déclaration des coauteurs d'un article

Lorsqu'un étudiant n'est pas le seul auteur d'un article qu'il veut inclure dans son mémoire ou dans sa thèse, il doit obtenir l'accord de tous les coauteurs à cet effet et joindre la déclaration signée à l'article en question. Une déclaration distincte doit accompagner chacun des articles inclus dans le mémoire ou la thèse.

1. Identification de l'étudiant et du programme

Julien Voisin
PhD Sciences Neurologiques

2. Description de l'article

Julien Voisin, Yves Lamarre and C. Elaine Chapman (2002) Haptic discrimination of object shape in humans: contribution of cutaneous and proprioceptive inputs. Publié dans Experimental Brain Research (Vol. 145: 251-260).

3. Déclaration de tous les coauteurs autres que l'étudiant

À titre de coauteur de l'article identifié ci-dessus, je suis d'accord pour que Julien Voisin inclue cet article dans sa thèse de doctorat qui a pour titre "L'encodage de la forme par le toucher haptique".

Y. LAMARRE	[redacted]	20.05.2003
Coauteur	Signature	Date
C.E Chapman	[redacted]	20-5-2003
Coauteur	Signature	Date

ACCORD DES COAUTEURS

Déclaration des coauteurs d'un article
Lorsqu'un étudiant n'est pas le seul auteur d'un article qu'il veut inclure dans son mémoire ou dans sa thèse, il doit obtenir l'accord de tous les coauteurs à cet effet et joindre la déclaration signée à l'article en question. Une déclaration distincte doit accompagner chacun des articles inclus dans le mémoire ou la thèse.

1. Identification de l'étudiant et du programme

Julien Voisin
PhD Sciences Neurologiques

2. Description de l'article

Julien Voisin, Guillaume Michaud, C. Elaine Chapman (en préparation) Viewpoint dependence of haptic shape discrimination in humans: A window into the haptic frames of reference.

3. Déclaration de tous les coauteurs autres que l'étudiant

À titre de coauteur de l'article identifié ci-dessus, je suis d'accord pour que Julien Voisin inclue cet article dans sa thèse de doctorat qui a pour titre « L'encodage de la forme par le toucher haptique ».

[redacted] Guillaume Michaud 23/04/04
Signature Date

C. Elaine Chapman [redacted] 20/04/04
Coauteur Signature Date