

Université de Montréal

Perception de la vitesse: les bases psychophysiques et neuronales

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Cette thèse intitulée :

Perception de la vitesse: les bases
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RÉSUMÉ

David Katz a fait l'observation que le mouvement entre la peau et l'objet est aussi important pour le sens du toucher que la lumière l'est pour la vision. Un stimulus tactile déplacé sur la peau active toutes les afférences cutanées. Les signaux résultants sont très complexes, covariant avec différents facteurs dont la vitesse, mais aussi la texture, la forme et la force. Cette thèse explore la capacité des humains à estimer la vitesse et la rugosité de surfaces en mouvements. Les bases neuronales de la vitesse tactile sont aussi étudiées en effectuant des enregistrements unitaires dans le cortex somatosensoriel primaire (S1) du singe éveillé.

Dans la première expérience, nous avons montré que les sujets peuvent estimer la vitesse tactile (gamme de vitesses, 30 à 105 mm/s) de surfaces déplacées sous le doigt, et ceci sans indice de durée. Mais la structure des surfaces était essentielle (difficulté à estimer la vitesse d'une surface lisse). Les caractéristiques physiques des surfaces avaient une influence sur l'intensité subjective de la vitesse. La surface plus rugueuse (8 mm d'espacement entre les points en relief) semblait se déplacer 15% plus lentement que les surfaces moins rugueuses (de 2 et 3 mm d'espacement), pour les surfaces périodiques et non périodiques (rangées de points vs disposition aléatoire). L'effet de la texture sur la vitesse peut être réduit en un continuum monotonique quand les estimés sont normalisés avec l'espacement et présentés en fonction de la fréquence temporelle (vitesse/espacement).

L'absence de changement des estimés de vitesse entre les surfaces périodiques et non périodiques suggère que les estimés de rugosité devraient aussi être indépendants

de la disposition des points. Dans la deuxième expérience, et tel que prévu, une équivalence perceptuelle entre les deux séries de surfaces est obtenue quand les estimés de la rugosité sont exprimés en fonction de l'espacement moyen entre les points en relief, dans le sens de l'exploration.

La troisième expérience consistait à rechercher des neurones du S1 qui pourraient expliquer l'intensité subjective de la vitesse tactile. L'hypothèse est que les neurones impliqués devraient être sensibles à la vitesse tactile (40 à 105 mm/s) et à l'espacement des points (2 à 8 mm) mais être indépendants de leur disposition (périodique vs non périodique). De plus, il est attendu que la fonction neurométrique (fréquence de décharge/espacement en fonction de la fréquence temporelle) montre une augmentation monotonique. Une grande proportion des cellules était sensible à la vitesse (76/119), et 82% d'entre elles étaient aussi sensibles à la texture. La sensibilité à la vitesse a été observée dans les trois aires du S1 (3b, 1 et 2). La grande majorité de cellules sensibles à la vitesse, 94%, avait une relation monotonique entre leur décharge et la fréquence temporelle, tel qu'attendu, et ce surtout dans les aires 1 et 2. Ces neurones pourraient donc expliquer la capacité des sujets à estimer la vitesse tactile de surfaces texturées.

Mots clés : vitesse tactile, rugosité tactile, somatosensoriel, humain, primate non-humain, cortex somatosensoriel primaire, main, perception

ABSTRACT

David Katz showed that movement between the skin and an object is as important for touch as light is to vision. Moving tactile stimuli activate all of the cutaneous afferents involved in discriminative touch. The resultant signals are complex, varying with multiple factors including speed and also texture, local shape, and force. This thesis explored the human ability to estimate the speed and roughness of moving tactile stimuli. The neuronal basis underlying tactile speed perception was investigated using single unit recordings from primary somatosensory cortex (S1) in awake monkeys.

In the first psychophysical experiment, we showed that subjects ($n=26$) can scale tactile speed (range, 30-105 mm/s), and this, contrary to previous studies, in a situation in which the duration of each trial was constant across all speeds tested. Surface structure was, in contrast, essential since subjects had difficulty scaling the speed of a smooth surface. Moreover, the physical characteristics of the surfaces influenced tactile speed perception. The roughest surface (8 mm raised-dot spacing) seemed to move 15% slower than the smoother surfaces (2 and 3 mm spacing), and this independently of dot disposition (periodic: rectangular array of raised dots vs non periodic: random dots). The effects of surface texture on speed were reduced to a single continuum when the estimates were normalized by dot spacing and plotted as a function of temporal frequency (speed/dot spacing).

The absence of any difference in speed scaling as a function of dot disposition (periodic vs non periodic) suggested that tactile roughness should also be

independent of dot disposition. A second psychophysical experiment (n=15) confirmed our hypothesis, showing perceptual equivalence for the periodic and non periodic surfaces when these were matched for dot spacing in the direction of the scan.

The third experiment investigated the neuronal mechanisms that underlie subjective tactile speed perception, by recording the responses of cutaneous neurones in the hand representation of S1 cortex to the displacement of textured surfaces under the finger tips of two awake rhesus monkeys. The hypothesis was that neurones implicated in tactile speed perception should be sensitive to tactile speed (similar range to that used in the human experiments) and dot spacing, but be independent of dot disposition (periodic vs non periodic). Furthermore, we predicted that the neurometric function (discharge frequency/dot spacing as a function of temporal frequency) would show a monotonic relation. A large proportion of S1 neurones were sensitive to speed (76/119); 82% of these were also sensitive to texture. Speed sensitivity was widely distributed across the three areas that comprise the cutaneous hand representation, areas 3b, 1, and 2. Of 94 neurons fully tested (periodic and nonperiodic surfaces), the large majority of speed-sensitive cells (60/64) showed a significant monotonic relation with temporal frequency for both surfaces when discharge frequency was normalized by dot spacing. The neurones with the strongest relation to temporal frequency were concentrated in caudal S1, areas 1 and 2, and likely contribute to the human ability to scale tactile speed.

Key words : tactile speed, tactile roughness, somatosensory, human, non-human primate, primary somatosensory cortex, hand, perception

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LISTE DES ABRÉVIATIONS

A	Actif
ANOVA	Analysis of variance
B	Intercept
D3	3 ^e doigt
D4	4 ^e doigt
DIAM	Diamètre
fMRI	Functional magnetic resonance imaging
FT	Fréquence temporelle
G	Glabre
INDENT.	Indentation
K	Constante
M	Mean slope
MDS	Multidimensional scaling
MST	Medial superior temporal
MT	Medial temporal
N/A	Non applicable
N/D	Non disponible
NP	Non périodique
P	Périodique
PA	Passif
PC	Corpuscule de Pacini
PI	Pileuse
PS	Période spatiale
R ²	Coefficient of determination
RA	Adaptation rapide
RECT.	Rectangulaire

RF	Receptive field
RMS	Root mean square
S	Stimuli
S1/SI	Cortex somatosensoriel primaire
S2/SII	Cortex somatosensoriel secondaire
SAI	Adaptation lente de type I
SAII	Adaptation lente de type II
SDS	Sodium dodecyl sulfate
SEM	Standard error of the mean
SEP	Spatial Event Plot
SP	Spatial Period
TEP	Tomographie par émission de positons
TF	Temporal frequency
V1	Cortex visuel primaire
V4	Cortex inférotemporal
V5	Cortex médiotemporal
VPL	Noyau Ventro-postéro-latéral

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INTRODUCTION ET REVUE DE LITTÉRATURE

Les stimuli tactiles se déplaçant sur la peau activent toutes les afférences des mécanorécepteurs impliqués dans le toucher discriminatif. Leur signal est toutefois complexe car il contient l'information non seulement de la vitesse tactile mais aussi celle d'autres attributs physiques des stimuli, incluant la texture, la forme locale, la vibration et la force de contact (normale et tangentielle). L'extraction de l'information est donc tout un défi pour le cerveau. Même si nous avons beaucoup de connaissances sur l'encodage périphérique et central de la rugosité, peu est connu sur les mécanismes centraux impliqués dans la perception de la vitesse tactile.

Cette thèse contient une introduction générale ainsi qu'une revue de la littérature, suivie des résultats de trois études expérimentales différentes et d'une discussion générale brève. La première étude examinait la capacité des sujets humains à estimer la vitesse tactile et les facteurs y contribuant. Puisque nous avons trouvé que l'estimation de la vitesse était dépendante de la texture mais indépendante des détails exacts des surfaces (points en relief disposés de façon périodique vs non périodique), une deuxième étude psychophysique a été faite chez l'humain pour vérifier si la perception de la rugosité tactile est aussi indépendante de la disposition des points en relief sur les surfaces. La dernière étude était basée sur les résultats de la première étude psychophysique sur la perception de la vitesse tactile et vérifiait l'hypothèse développée, qui suggérait que la décharge des neurones corticaux du cortex somatosensoriel primaire ayant un rôle dans l'encodage de la vitesse tactile devrait covarier avec la fréquence temporelle (vitesse/espacement des points) et être

indépendante de la disposition des points (périodique vs non périodique). Des données sur l'encodage de la rugosité tactile ont aussi été obtenues mais elles ne seront pas présentées dans cette thèse.

1. Organisation globale du sens tactile: du bout des doigts au cerveau

La peau est l'organe du toucher. Le bout des doigts a une haute densité d'innervation ainsi qu'une excellente résolution, telle la fovéa de l'œil dans la vision (*Weber, The sense of touch 1978*). Les prochains paragraphes adresseront donc les études, principalement chez le singe, ayant décrites l'innervation de la peau glabre de la main, le trajet des afférences vers le cortex et l'organisation sommaire de ce dernier.

Dans la peau glabre de la main, quatre types de fibres nerveuses ont été identifiés physiologiquement pour avoir des propriétés pouvant leur attribuer un rôle dans le toucher discriminatoire. Elles sont toutes de type A β , donc d'un grand diamètre et myélinisées permettant une vitesse de transmission rapide. Les fibres à adaptation lente de type I (slowly adapting type I : SAI) sont caractérisées par un petit champ récepteur et sont modulées durant toute la période d'indentation de la peau (Knibestol 1975, Talbot et al 1968). Il y a aussi les fibres à adaptation rapide (rapidly adapting : RA) qui sont les plus communes. Elles ont aussi un petit champ récepteur mais sont modulées par les parties dynamiques de l'indentation, par les vitesses d'une gamme de 2-40 mm/s ainsi que par les vibrations de 20 à 40 Hz (Pubols et Pubols 1976, Talbot et al 1968). Le troisième type de fibre, PC,

correspond aux corpuscules de Pacini et sont les moins communes (Johansson et Vallbo 1979). Elles sont aussi à adaptation rapide mais ont un plus grand champ récepteur et ont une fréquence de décharge de 1:1 avec les vibrations de 200-300 Hz (Lamotte et Mountcastle 1975, Mountcastle et al 1972, Talbot et al 1968). Un quatrième type de fibre est retrouvé dans la peau glabre de l'humain, mais aussi dans la peau pileuse des singes. Ce sont les fibres à adaptation lente de type II (slowly adapting type II : SAII), qui ont un grand champ récepteur et sont modulées principalement par l'étirement de la peau (Edin et Abbs 1991, Johansson et Vallbo 1979, Knibestol et Vallbo 1970).

Les terminaisons de ces fibres sont associées à des récepteurs sensoriels spécialisés. Les terminaisons des fibres PC sont en relation avec un large corpuscule (Pacini), tandis que les SAI sont en relation avec les disques de Merkel (Maricich et al 2009). En ce qui concerne les autres afférences, il n'y a pas encore de lien direct qui a été démontré entre leurs propriétés physiologiques et les récepteurs, mais l'hypothèse est que les fibres RA sont associées aux corpuscules de Meissner et les SAII aux corpuscules de Ruffini.

Ces fibres se joignent à la voie des colonnes dorsales du côté ipsilatéral dans la moelle pour faire synapse au niveau des noyaux gracile et cunéiforme du bulbe (Brodal et Pompeiano 1957). Cette voie est aussi composée de cellules post-synaptiques ayant fait synapse au niveau de la corne dorsale (Uddenberg 1968a,b, Petit 1972, Pubols et Pubols 1973). Après synapse au niveau du bulbe, les axones décussent et forment le lemnisque médian pour se rendre au complexe nucléaire ventro-postérieur du thalamus (Berkley 1980, Boivie 1978, Bowsher 1961, Clarke

1936, Tsumoto 1974). Finalement, les neurones thalamiques projettent aux 4 aires du cortex somatosensoriel primaire (S1) (cutané : 3b, 1, 2; proprioceptif : 3a et 2) ainsi qu'au cortex somatosensoriel secondaire, S2 (Friedman et Jones 1981, Friedman et al 1980, Jones et Burton 1976, Jones et al 1978).

Les quatre aires de S1 contiennent chacune une représentation complète mais disproportionnée du corps. De plus, les neurones corticaux sont organisés en colonnes (même champ récepteur et modalité) qui sont l'unité élémentaire composant la carte corticale. La taille du champ récepteur cutané des cellules augmente en se déplaçant caudalement dans le cortex 3b→1→2 (Mountcastle 1957, Nelson et al 1980, Paul et al 1972, Pons et al 1987, Powell et Mountcastle 1959, Werner et Whitsel 1968, Woolsey et al 1942). S1 est la première région corticale où l'information tactile est analysée, mais cette dernière est transmise par un réseau complexe de projections incluant du « feedforward » (ex. 3b→1→2→5/7/S2) et du « feedback » (ex. 1→3b, 2→1...) entre les aires corticales ainsi que le thalamus (Pons et al 1987, 1988, 1992, Zhang et al 1996, 2001a et b).

2. Psychophysiques

2.1. Psychophysiques de la rugosité

Une surface texturée peut être perçue selon différentes dimensions perceptuelles : lisse-rugueux, dure-mou, glissant-collant, plat-raboteux et chaud-froid (Hollins et al 1993). Le continuum lisse-rugueux est abordé dans ce chapitre. Il sera

donc démontré dans les prochains paragraphes que l'être humain est capable d'estimer la rugosité subjective d'une grande variété de surfaces.

Katz (1925) fut un pionnier des expériences psychophysiques autant pour le système tactile que le système visuel. Il a émis de nombreuses hypothèses qui ont été testées par plusieurs au cours du dernier siècle. Pour la plupart, elles se sont avérées véridiques. Dans ses études sur la rugosité, il a utilisé différents matériaux tel le bois, la porcelaine, le métal ainsi que le papier et s'est rendu compte que les sujets étaient capables de les discriminer que ce soit avec les doigts, un crayon ou même un marteau. Hollins et al. 1993 ont élargi la gamme de matériaux avec 17 stimuli différents tels le papier ciré, le velours, le bois, la céramique etc. Les sujets devaient indiquer où ces stimuli se situaient sur les cinq dimensions perceptuelles mentionnées ci-haut. Ce classement a été mis dans l'espace MDS (multidimensional scaling) pour ensuite être analysé par des régressions. Dure-mou et lisse-rugueux étaient des dimensions orthogonales. L'importance de ces dimensions a été confirmée par la suite dans Hollins et al (2000). La rugosité a aussi été étudiée par d'autres auteurs qui utilisent un seul type de matériau pour examiner comment certains changements des caractéristiques physiques affectent sa perception.

LaMotte (1977) a étudié l'intensité subjective de la rugosité en utilisant des tissus contenant des motifs de tissage différents. Les tissus sont perçus comme plus rugueux quand l'espace entre les fils augmente (densité des fils diminue) et quand le diamètre des fils diminue. D'autres ont utilisé du papier abrasif comme stimuli, où le diamètre des grains de sable augmente en même temps que la densité de ses derniers diminue. La rugosité perçue augmente avec une augmentation de diamètre des grains

de sable, mais ceci peut être confondu par une diminution parallèle de la densité ou augmentation de l'espacement (Stevens et Harris 1962, Verillo et al 1999). Toutefois, avec ces types de matériaux (tissus et papier abrasif), plusieurs facteurs varient simultanément sans être contrôlés par l'expérimentateur. C'est pour cette raison que l'élaboration de surfaces manufacturées est devenue la méthode de choix pour étudier un à un les différents facteurs affectant la perception de la rugosité.

Lederman a élaboré des plaques d'aluminium lissé sur lesquelles étaient pratiquées des grillages de grandeur contrôlée. Elle a donc pu évaluer l'effet de la largeur des crêtes et des rainures, la période spatiale (PS : début d'une crête au début de la crête suivante) et le rapport rainure/crête sur la perception de la rugosité. La gamme de largeur pour les crêtes et rainures est de 0.125 à 1 mm (voir détail dans Tableau 1.1), donnant une petite gamme de PS de 0.4 à 1.6 mm. Ce qui a ressorti de ces études est que la rugosité perçue est positivement affectée par la largeur des rainures et négativement par la largeur des crêtes (Lederman 1974, 1981, 1983, Lederman et Taylor 1972 et Taylor et Lederman 1975). Toutefois, l'effet des crêtes est remarqué seulement pour les plus grandes largeurs et il n'y a pas du tout d'effet des crêtes quand les rainures sont larges.

Les études de Lederman ont été poursuivies par Sathian et al (1989) et Yoshioka et al (2000) en utilisant une plus grande gamme de PS (Tableau 1.1, PS de 0.1 à 3 mm). Pour les deux, la rugosité augmente avec une augmentation de la PS. Sathian et al ont, de plus, confirmé l'importance de la largeur des rainures comme facteur important pour la perception de la rugosité. La largeur des crêtes a une certaine influence mais beaucoup moins prononcée.

L'utilisation de points en relief (cônes tronqués) a fait suite pour expliquer les bases du code tactile impliqué dans la forme spatiale, spécifiquement la lecture du Braille. Elle a aussi permis de vérifier la contribution d'autres paramètres des surfaces à l'appréciation de la rugosité, incluant la hauteur et le diamètre des points ainsi que l'espacement transversal et longitudinal (opposé à l'exploration et dans le sens de l'exploration respectivement). Ceci a été rendu possible grâce au développement de surfaces en photopolymère flexible par Darian-Smith et Oke (1980). Connor et al (1990) ont utilisé des patrons de points tétraogonaux dont l'espacement des côtés du carré varie de 1.3 à 6.2 mm (changement d'espacement dans deux dimensions versus une dimension pour les grillages). Ils ont observé avec cette plus grande gamme que les estimés de la rugosité subjective des sujets augmentent jusqu'à un espacement de 3.2 mm et ensuite ils diminuent, pour produire une courbe en U inversé (Fig. 1.1B).

Meftah et al (2000) ont utilisé une matrice rectangulaire de points pour étudier l'effet isolé de l'espacement longitudinal (PS, 1.5 à 8.5 mm). La pente de la relation entre l'espacement et la rugosité perçue est positive sur toute la gamme mais avec toutefois une diminution de pente pour les espacements de plus de 5 mm (Fig. 1.1A). Plusieurs facteurs pourraient expliquer la différence avec les résultats de Connor et al (1990). Premièrement, chez Connor et al, un recalcul des espacements transversaux et longitudinaux donnent des valeurs jusqu'à 8.8 mm, ce qui correspond à la gamme de PS longitudinal de Meftah et al. Toutefois, les changements de PS transversaux sont importants chez Connor et al mais très petits chez Meftah et al (1-2 mm). Connor et Johnson (1992) ont déjà varié indépendamment l'espacement dans

les 2 axes (1.5 à 4 mm) et les sujets ont estimé que la rugosité augmente dans les deux cas, mais plus particulièrement pour l'espacement longitudinal. De plus, il y a une différence dans la hauteur des points (0.35 vs 1.8 mm), qui sera discutée plus tard. Une dernière différence importante est le changement de stratégie d'estimation de la rugosité pour les grands espacements chez les sujets de Connor et al. Il est très probable que les sujets aient utilisé une stratégie pour les petits espacements (courbe à pente positive) et une autre pour les grands espacements (courbe à pente négative), car un même estimé est donné pour deux surfaces complètement différentes (voir Fig. 1.1).

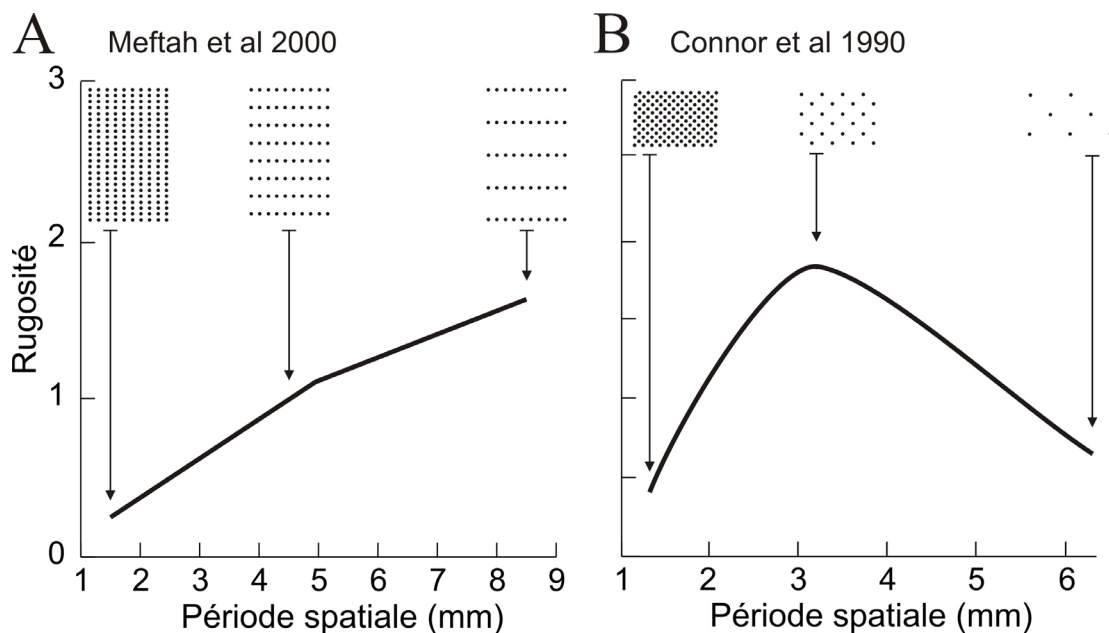


Figure 1. Représentation schématique des courbes psychométriques de la rugosité en fonction de la période spatiale (PS) de deux études antérieures. A) Fonction monotonique positive de Meftah et al (2000). B) Fonction en U inversé de Connor et al (1990).

Pour les autres facteurs intrinsèques à la surface, il y a aussi les caractéristiques physiques des points (diamètre, hauteur). Connor et al (1990) ont

démontré que l'intensité subjective de la rugosité diminue avec une augmentation de diamètre sur une gamme de 0.5 à 1.2 mm. Blake et al (1997a) ont étendu cette observation à une gamme plus large (à 2.5 mm). Ce résultat est comparable à l'effet de la largeur des crêtes des grillages sur la perception de la rugosité, puisque l'augmentation de la taille de ce qui est en relief diminue la rugosité perçue. L'effet du diamètre est toutefois moins important que l'effet de l'espacement. Blake et al (1997a) ont aussi vérifié l'effet de la hauteur des points (280-620 μm) et ont observé une interaction avec leur diamètre. L'intensité subjective de la rugosité augmente avec la hauteur sur une petite gamme de diamètres (les plus petits). Meftah et al (2010) ont étendu la gamme de hauteur investiguée jusqu'à 1.8 mm. Ils ont également démontré que pour les surfaces avec des points moins hauts, la rugosité n'est pas un continuum sur toute la gamme car les fractions de Weber augmentent pour les espacements correspondants à la partie descendante de la courbe psychométrique.

Il y aussi des facteurs extrinsèques aux surfaces, incluant la force de contact, l'hydratation de la peau, et le mode de toucher, qui peuvent avoir un effet sur la perception de la rugosité. Pour commencer, la force de contact peut être divisée en force normale (perpendiculaire) et force tangentielle (parallèle), leur ratio (tangentielle/normale) donne le coefficient de friction. Initialement, il a été démontré qu'une augmentation de la force normale augmentait la perception de la rugosité pour une gamme d'espacements de 0.125 à 1 mm (Lederman et Taylor 1972, Lederman 1974). Taylor et Lederman (1975) ont ensuite démontré qu'une diminution du coefficient de friction par utilisation de lubrifiant n'avait pas d'influence sur la perception de la rugosité. Tandis qu'ils ont suggéré que la friction n'est pas un

déterminant important de la perception de la rugosité, Ekman et al (1965) avaient argumenté du contraire, sur la base de leurs observations avec les papiers abrasifs. Plus récemment, Smith et al. (2002) ont démontré qu'une diminution de friction (en lubrifiant les surfaces) diminue les estimés de rugosité. Dans cette dernière étude, la conclusion était supportée par des mesures de la friction pendant l'exploration. Puisque Taylor et Lederman n'avaient pas mesuré la friction, Smith et al ont soulevé la possibilité que la friction soit restée stable dans leur étude, possiblement puisque la gamme de PS évaluée était trop restreinte (Tableau 1). Smith et al ont également rapporté que le RMS (root mean square) du changement de la force tangentielle expliquait mieux les estimés de rugosité que la friction. Donc, la friction contribue à la rugosité mais est loin d'être le facteur déterminant.

De plus, Verillo et al (1998,1999) ont aussi démontré avec le papier abrasif, que la perception de la rugosité diminue quand le doigt est bien hydraté (trempé dans l'eau) ou asséché par le SDS (sodium dodecyl sulfate). Ceci s'explique par le fait qu'une peau très humide ou très sèche a un coefficient de friction bas (André et al 2010).

Finalement, le mode de toucher peut potentiellement affecter la perception de la rugosité puisque le mouvement diminue la transmission de l'influx somesthésique (Giblin 1964; Chapman 1994). Le mode peut être actif ou passif et direct ou indirecte (discuté dans le prochain paragraphe). Gibson (1962) a défini le toucher actif comme l'action de toucher (avec mouvement) et le toucher passif comme le fait d'être touché (sans mouvement). Malgré l'existence d'une fonction « porte » diminuant la transmission de l'influx tactile pendant les mouvements actif et passif (Chapman et

al. 1988; Williams et Chapman 2002; Chapman et Beauchamp 2006), plusieurs expériences ont démontré que le mode de toucher n'influence pas l'intensité subjective de la rugosité, et ceci pour différents matériaux incluant les papiers abrasifs (Verillo et al 1999), les grillages (Lederman 1981, 1983), et les points en relief (JL Larochelle, E-M Meftah et CE Chapman, observations non publiées), ni la discrimination de la rugosité (Lamb 1983a, Heller 1989). Par exemple, la même courbe en U inversé a été obtenue pour l'estimation de la rugosité en fonction de l'espacement chez Connor et al (1990) en actif et chez Meftah et al (2010) en passif. Donc l'explication pour cette équivalence perceptuelle serait que même si la transmission est diminuée en mode actif, la performance est compensée par la stratégie motrice choisie par le sujet: diminution de la vitesse de mouvement afin d'éviter la gamme de vitesses associées avec une diminution de transmission (Cybulska-Klosowicz et al 2011), et positionnement optimal du doigt (Chapman 1994).

Une surface peut aussi être explorée sans contact direct avec la peau (toucher indirect), soit en utilisant des gants ou un outil (ex. tournevis). En effet, les sujets sont capables d'estimer la rugosité des surfaces par l'intermédiaire d'un instrument rigide (Yoshioka et al 2007), sans différence significative entre les modes passif et actif (Klatzky et Lederman 1999, Lederman et al 1999). La rugosité perçue est toutefois augmentée avec une diminution du diamètre de l'extrémité de la sonde (2 vs 4 mm). Ceci peut être expliqué par le fait que lorsque la sonde est de gros diamètre, elle est seulement en contact avec le dessus des éléments tactiles (ex. crêtes des grillages), produisant des petites vibrations, tandis que la petite sonde entre en contact avec le

fond des surfaces produisant des vibrations plus fortes et plus fréquentes (crêtes plus rainures) (Klatzky et Lederman 1999). Cette suggestion est en accord avec l'hypothèse que Katz (1925) a proposé où les sujets utilisent la vibration pour l'estimation de la rugosité lors du toucher indirect. La vibration se traduit en intensité et en fréquence qui est donc influencée par l'espacement des éléments tactiles ainsi que la vitesse de présentation. Ce phénomène a aussi été observé dans l'exploration de tissus (Yoshioka et al 2007, 2011).

Tableau 1 : Caractéristiques des stimuli utilisés dans les expériences de psychophysique de la rugosité

Référence	Stimulus	PS (mm)	Largeur (mm) points/crêtes	Hauteur (mm) points/crêtes	Vitesse (mm/s)	Force (N)	Mode
Blake et al 1997	Points en relief (patron tétragonal)	3.5	0.25-2.5	0.28-0.62	n/a	1	A
Blake et al 1997	Carrés en relief ou en dépression	n/d	0.2-7	0.28-0.62	n/a	n/a	A
Cascio and Sathian 2001	Grillages	1.5-3*	n/d	n/d	30-70	0.8	Pa
Connor et al 1990	Points en relief (patron tétragonal)	1.3-6.2	0.5-1.2	0.35	n/d	n/a	A
Connor et Johnson 1992	Points en relief (matrice rect.)	1.5-4.0*	1.5-4	0.5	n/d	n/a	A
Kudoh 1988	Grillages	0.5-1.25	n/d	n/d	30-140	0.5-1	Pa
Lederman 1974	Grillages	0.275-1.625*	n/d	n/d	10-250	0.28	A
Lederman 1981	Grillages	0.175-1	n/d	0.175-1	48	0.28-2.24	Pa,A
Lederman et Taylor 1972	Grillages	0.125-1*	n/d	0.125	n/d	0.28-7	A
Lederman 1983	Grillages	0.125-1*	n/d	n/d	17-207	0.28-4.48	Pa,A
Meftah et al 2000	Points en relief (matrice rect.)	1.5-8.5	0.6	1-1.8	51-96	0.8-1.4	Pa
Meftah et al 2010	Points en relief (patron tétragonal)	0.3-6.2	0.7	0.36-1.8	61	n/d	Pa
Phillips et al 1992	Points en relief (patron tétragonal)	0.87-6.4	0.5	0.5	20-90	0.4-1	Pa

Sathian et al 1989	Grillages	0.74-3.09*	n/d	n/d	n/d	n/d	Pa
Smith et al 2001	Points en relief (matrice rect.)	1.5-8.5	n/d	1.8	n/d	n/d	A
Taylor et Lederman 1975	Grillages	0.5-1.25*	n/d	n/d	n/d	1.12	A
Vega-Bermudez et al 1991	Lettres (grandeur : 0.5-7 mm)	n/d	n/d	6	20-80	n/d	Pa,A
Verillo et al 1998	Papier abrasif	n/d	0.14-20	n/d	n/d	n/d	A
Verillo et al 1999	Papier abrasif	n/d	0.16-9	n/d	36	n/d	Pa,A
Yoshioka et al 2001	Grillages	0.1-2*	n/d	n/d	n/d	1	A

* largeur des crêtes et des rainures varient

Abréviations : A: Actif; n/a: non applicable; n/d: non disponible; Pa: passif; PS: Période spatiale

2.2. Psychophysiques de la vitesse tactile

La perception du mouvement tactile est nécessaire pour une variété d'activités dans la vie de tous les jours, telle la détection de glissement durant la manipulation d'objets (Johansson 1998) ou l'interception d'un insecte se déplaçant sur la peau. Surprenamment, peu de connaissances sont disponibles sur la perception de la vitesse tactile. De plus, le mouvement est essentiel pour optimiser la sensation tactile, ce qui suggère qu'on devrait être capable d'extraire un estimé de la vitesse de déplacement d'un stimulus sur la peau. Toutefois, la vitesse pourrait être influencée par des indices de distance et de temps. Donc plus spécifiquement par un code spatial (distance traversée sur la peau) ou par des mesures de durée (temps du début et temps de la fin de la stimulation). La variable temporelle pourrait aussi être influencée par d'autres modalités (ex. indices auditifs du stimulateur). Les études antérieures sont donc confondues car il n'est jamais certain si les sujets estiment la vitesse tactile, la durée du stimulus ou la longueur de stimulation. C'est pour cette raison que les études antérieures ont essayé d'étudier les différents facteurs séparément (longueur et durée) pour ensuite les comparer avec les estimés de vitesse (Tableau 1.2).

Deux approches ont été utilisées et seront décrites plus en détails dans les prochains paragraphes. Premièrement, il y a l'indentation d'une sonde dans la peau à différentes vitesses, mais la durée varie entre les vitesses. Il y a aussi le déplacement transverse d'une brosse sur la peau où soit la durée ou la longueur peut être gardée constante. Tandis que ces deux approches donnent une idée de la capacité des sujets à estimer la vitesse, les deux facteurs ne peuvent pas être gardés constants simultanément.

Franzén et Lindblom (1976) ont démontré que les humains sont capables d'estimer la vitesse d'impulsions mécaniques au niveau de la peau glabre. Ils ont utilisé une sonde de 2mm de diamètre qui pénètre de 600 μm dans la peau à des vitesses d'indentation de 0.07 à 32mm/s. L'exposant de la relation log-log (estimés en fonction de vitesse) est de 0.51. Les vitesses utilisées sont toutefois très lentes. Franzén et al (1984) ont élargi la gamme jusqu'à 64 mm/s, et l'exposant de la relation est resté similaire. Ce type de stimulation implique seulement une indentation dans la peau et non un déplacement parallèle à la peau. Ils ont donc aussi utilisé une brosse en poil de chameau pour vérifier si les sujets humains sont aussi capables d'estimer la vitesse de déplacement transverse sur la peau. Les stimulations (voir Tableau 2) ont été faites au niveau de l'avant-bras et du doigt. La relation entre les estimés et la vitesse tactile est très similaire à celle obtenue avec la sonde (exposant de 0.6 vs 0.51 avec la sonde). De plus, les résultats suggèrent que la densité d'innervation (différente pour les deux régions) n'est pas un facteur important car il n'y a pas de différence entre l'avant-bras et le doigt.

Whitsel et al (1986) ont démontré que l'estimation de l'étendue de peau stimulée est influencée par la vitesse de présentation, donc la longueur et la vitesse semblent être inter reliées. Même si la longueur de peau stimulée est gardée constante (4 cm), elle semble plus courte à grande vitesse et plus longue à faible vitesse. De plus, ce qui est intéressant est que la relation entre les estimés de longueur de peau stimulée et la vitesse est nulle (pente = 0) pour les vitesses de 50 à 250 mm/s, qui correspondent à la gamme utilisée par les humains pour l'exploration des surfaces texturées (Smith et al 2002a). Toutefois, les stimulations ont été faites sur l'avant-

bras où la densité de mécanorécepteurs n'est pas aussi grande que sur le bout du doigt, ceci a pu entraîner un biais dans l'estimation de la distance (point de départ à point d'arrivée de la brosse).

Essick et al (1988) ont ensuite étudié la durée de stimulation pour savoir si elle peut être un facteur influençant la perception de la vitesse tactile. Ils ont effectivement noté qu'elle est reliée à la perception de la vitesse. Pour ce faire ils ont demandé à des sujets d'estimer la durée de stimulation ainsi que la vitesse de déplacement de la brosse sur la peau. Les durées covarient toutefois avec la vitesse (15-8000 ms). Les sujets étaient capables d'estimer la vitesse et la durée, et les deux courbes log-log d'estimation (vitesse et durée) étaient très similaires. Ceci suggère que les sujets pourraient se baser sur la durée pour estimer la vitesse tactile, ou bien que la durée est sur une gamme tellement grande (500x) dans cette expérience, qu'elle ne peut être ignorée.

Essick et al (1991) ont répété pratiquement la même expérience mais en ajoutant aussi l'estimation de la longueur de peau stimulée afin de vérifier si cette dernière a vraiment une influence sur l'intensité subjective de la vitesse. Seulement deux longueurs différentes sont vérifiées, une est de 0.75 cm tandis que l'autre est une stimulation discontinue par une plaque de teflon (deux ouvertures de 0.25 cm séparées par 0.25 cm de plaque de teflon). Donc la gamme de longueur est restreinte, et les points de départ et d'arrêt de la brosse sont les mêmes pour les deux longueurs, impliquant que la durée est la même aussi. Pour la plupart des sujets, il n'y a pas de différence significative entre les courbes des deux longueurs (estimé de distance en fonction de vitesse). Un lien direct est toutefois observé entre les estimés de vitesse et

la réciproque de la durée ($1 / \text{durée}$). Ceci suggère une hypothèse temporelle où les estimés de vitesse tactile dépendent d'indices temporeux (durée de la stimulation). Étant donné la faible gamme de longueur de l'étude précédente, Essick et al (1996) ont élargi la gamme de longueurs de peau stimulée de 0.6 à 4.8 cm et ont aussi confirmé leur hypothèse temporelle. Une autre méthode de stimulation devrait être utilisée pour vérifier que les humains peuvent estimer la vitesse tactile sans indice de durée.

Tableau 2 : Caractéristiques des stimuli utilisés dans les expériences de psychophysique de la vitesse

Référence	Stimulus	Vitesse (mm/s)	Force (N)	Distance (cm)	Durée (s)	Peau
Essick et al 1988	Brosse (poils de chameau)	5-2560	0.05	4	0.015-8	PI
Essick et al 1991	“	5-640	0.05	0.50-0.75	0.01-0.15	PI
Essick et al 1996	“	5-640	0.022-0.257	0.5-8	0.008-16	PI, G
Essick et al 2002	“	7.5-240	variable	0.6-4.8	0.03-6.4	PI
Franzén et Lindblom 1976	Sonde, 2 mm (diam) 0.6 mm (indent.)	0.067-32	n/d	n/a	0.02-9	G
Franzén et al 1984	Brosse (poils de chameau)	5-2560	0.5	0.5-8	0-16	PI
"	Sonde, 2 mm (diam) 0.5 mm (indent.)	?-64	n/d	n/a	0.1-?	G
Whitsel et al 1986	Brosse (poils de chameau)	10- 2560	0.05	4	0.02-4	PI

Abréviations : n/a: non applicable; n/d: non disponible; G: Glabre; PI: Pileuse

2.3. Interaction entre la vitesse et la rugosité

La perception optimale de la texture nécessite un mouvement tangentiel entre la surface et la peau, ce qui introduit une dimension temporelle et donc la possibilité que le facteur temporel soit important. Katz (1925) fut le premier à vérifier l'effet de la vitesse sur la perception de la rugosité en passant des feuilles de différentes rugosités sous les doigts immobiles des sujets (3-60 mm/s). Les sujets trouvaient que les feuilles semblaient moins rugueuses à la vitesse plus élevée. Lederman (1974) a utilisé seulement 3 vitesses d'une grande gamme (10 à 250 mm/s) pour l'exploration de grillages (voir Tableau 1). Les sujets sont capables d'estimer la rugosité à toutes les vitesses. Une diminution de l'intensité subjective de la rugosité est observée à 250 mm/s, mais ce, seulement pour les surfaces ayant des rainures de petite largeur. Ceci est vrai pour les modes d'exploration passif et actif (Lederman 1983). Avec une gamme d'espacements similaire, Kudoh (1988) a démontré que les sujets sont capables d'estimer la rugosité quand la fréquence temporelle est maintenue constante (augmentation de la vitesse en augmentant l'espacement). L'intensité subjective de la rugosité est légèrement plus basse quand la fréquence temporelle est élevée (30 vs 80 Hz), donc à vitesse plus élevée pour un même espacement. L'interprétation des résultats est, par contre, difficile car l'exploration à 30 Hz impliquait un aller tandis qu'à 80 Hz c'était un aller-retour. Cascio et Sathian (2001) ont toutefois confirmé le fait que la largeur des rainures est un facteur beaucoup plus important que la fréquence temporelle sur l'intensité subjective de la rugosité. Finalement, une équivalence perceptuelle est observée avec l'utilisation d'une plus grande gamme d'espacements (1.5 à 8.5 mm) lorsque la vitesse d'exploration est doublée (50 à 95

mm/s) (Meftah et al 2000). Ces vitesses représentent la gamme utilisée dans l'exploration tactile libre (Smith et al 2002a). La vitesse tactile ne semble donc pas avoir d'effet important sur l'intensité subjective de la rugosité. Ce n'est toutefois pas le cas avec l'utilisation d'une sonde, où l'effet est variable selon l'espacement des grillages (Lederman et al 1999). Une augmentation de vitesse fait percevoir les surfaces comme moins rugueuses pour les surfaces avec petit espacement tandis que c'est le contraire pour les surfaces avec plus grand espacement (perçues comme plus rugueuses). Mais tel que discuté précédemment, la source d'information n'est pas la même avec l'exploration indirecte, dépendant surtout de la vibration transmise via la sonde.

3. Électrophysiologie

La perception tactile de la rugosité et de la vitesse provient d'un encodage particulier par le système nerveux. La plupart des informations proviennent d'enregistrements chez le singe, sauf pour les afférences périphériques ou des données chez l'humain sont aussi disponibles grâce à la technique de microneurographie. L'encodage de la rugosité et de la vitesse dans les afférences périphériques, le thalamus, S1 et S2 sera donc discuté dans les paragraphes qui vont suivre.

3.1. Afférences périphériques : Rugosité

Les afférences périphériques contribuent à transmettre le signal de rugosité vers le système nerveux central. Les quatre types d'afférences impliquées dans le

toucher discriminatif (SAI, SAII, RA et PC) sont activées quand une surface texturée est déplacée sous les doigts. Leur patron de décharge est toutefois complexe car le signal reflète non seulement les caractéristiques physiques des surfaces (ex. espacement pour grillages et points en relief) mais également la vitesse de déplacement et la force de contact.

Premièrement, LaMotte (1977) a enregistré des afférences (SAI et RA) chez le singe lors de la stimulation digitale avec quatre tissus différents. Les deux types d'afférences répondent au déplacement de tissus sur la peau glabre. Les RA répondent plus fortement et sont mieux corrélées avec l'intensité perceptuelle de la rugosité, tandis que la fréquence de décharge des SAI est peu augmentée par le passage des stimuli et ne permet pas de différencier entre les quatre tissus. Par la suite, des enregistrements unitaires d'afférences ont été faits lors de la présentation de grillages en mouvement (Darian-Smith et Oke 1980, voir Tableau 3). Ils ont trouvé que les trois types d'afférences (SAI, RA et PC) de la peau glabre sont activés quand les surfaces sont déplacées sur leur champ récepteur. De plus elles joueraient chacun un rôle différent dans l'encodage de la rugosité. La réponse des SAI est à 1:1 quand la fréquence temporelle (vitesse/PS) est sous 60 Hz. Les RA répondent 1:1 pour les fréquences de 100-200 Hz, tandis que c'est au dessus de 150 Hz pour les PC. Goodwin et ses collègues (Goodwin et Morley 1987a,b; Morley et Goodwin 1987) ont aussi utilisé des grillages, mais avec une plus grande gamme de PS (jusqu'à 3 mm). Ces surfaces étaient caractérisées par le fait que le ratio entre la largeur des rainures et des crêtes était constant. Ils ont comparé la fréquence de décharge des afférences avec la PS des grillages (au lieu de la fréquence temporelle) et ont observé

que l'encodage de la rugosité pourrait très bien être expliqué par un code basé sur la fréquence de décharge. Pour les trois types d'afférences (SAI, RA et PC), le nombre de potentiels d'action par crête augmente avec l'espacement entre ces dernières. Les SAI sont toutefois plus sensibles à la PS que les autres types d'afférences (Goodwin et al 1989). Sathian et al (1989) ont confirmé que l'effet sur la fréquence de décharge des afférences est le même quand la largeur des rainures (gamme similaire aux expériences précédentes) est variée indépendamment de la largeur des crêtes.

Darian-Smith et al (1980) et Johnson et Lamb (1981) ont ensuite utilisé les surfaces ayant des points en relief (patrons tétraogonaux et braille respectivement). Ils ont développé une méthode de stimulation pour obtenir des SEP (Spatial Event Plots) pour illustrer et caractériser le patron de décharge des afférences en fonction de différentes surfaces et conditions de stimulation (ex. en changeant la vitesse tactile). Les surfaces sont apposées sur un tambour cylindrique, et le tambour est déplacé latéralement d'une fraction de mm par tour pour ainsi permettre qu'un point sur le doigt soit exposé à l'ensemble de la surface texturée. Ceci permet de générer une représentation graphique de l'image envoyée par les afférences au système nerveux central. En utilisant cette méthode, Darian-Smith et al (1980) ont observé la reproduction des surfaces à travers la réponse des trois types d'afférences, et ont remarqué qu'elles ne donnent pas toutes le même résultat. Ils ont présenté des patrons tétraogonaux de points en relief (changement bidimensionnel; voir Tableau 3), mais pour ceux-ci, l'espacement covarie avec le diamètre des points. Les SAI ont la représentation la plus claire avec une structure spatiale (SEP) préservée à travers les différences de vitesse et de force. Les RA donnent une représentation moins détaillée

que les SAI et les PC encore moins. Lamb (1983b) a étudié l'encodage neuronal de petites différences de rugosité pour expliquer la discrimination de la rugosité de surfaces contenant des points en relief. Pour ce faire, il a utilisé la même gamme d'espacements que Lamb (1983a) mais avec une matrice rectangulaire (voir Tableau 3). Encore une fois, les afférences des trois types sont modulées par la présentation des surfaces (SEP). Les RA représentent très bien les surfaces d'environ 2 mm d'espacement (large espacement) dans leur patron de décharge, tandis que les PC reproduisent mieux les surfaces de 1 mm d'espacement (petit espacement). Il suggère un code neuronal basé sur la fréquence de décharge afin d'expliquer la capacité humaine de discriminer les petites différences de rugosité.

Connor et al (1990) ont ensuite comparé des données psychophysiques avec différents codes neuronaux hypothétiques pour expliquer l'intensité subjective de la rugosité. Pour ce faire, ils ont aussi utilisé des patrons tétraogonaux de points en relief mais avec une gamme d'espacement plus large (jusqu'à 6.2 mm; voir Tableau 3). Ces surfaces ont été présentées aux humains (psychophysique, décrit ci-haut) ainsi qu'aux singes pour enregistrer les trois types d'afférences (SAI, RA et PC) et donc faire une corrélation directe entre les deux. Tel que mentionné précédemment, la relation entre les estimés des sujets et l'espacement entre les points a donné une courbe en U inversé. Tel que discuté précédemment, les sujets auraient utilisé deux stratégies différentes pour les petits et grands espacements. La validité de ces codes neuronaux est toutefois dépendante de la validité des données psychophysiques.

En ce qui concerne les enregistrements, le premier code testé est basé sur la fréquence de décharge moyenne, comme dans les expériences précédentes, mais ce

n'est pas celui qui explique le mieux l'intensité subjective de la rugosité. Il a été rejeté car le sommet de la courbe de fréquence de décharge en fonction de l'espacement n'est pas le même que pour les données psychophysiques. Les codes basés sur les variations dans la fréquence de décharge (variance, écart-type, écart absolu moyen) ont aussi été rejetés. Le code « temporel » qui dépend de la structure temporelle de la décharge des afférences est assez bien corrélé mais pas autant que le code spatial. Ce dernier code est basé sur la variation spatiale qui dépend de la structure spatiale de la fréquence de décharge à deux points différents à travers la population d'afférences. Une corrélation optimale est observée avec les SAI, malgré qu'elle soit aussi très bonne avec les RA. Même si le code spatial semble légèrement mieux corrélé à l'intensité subjective de la rugosité que le code temporel, ils sont tous deux de bonnes hypothèses. Connor et Johnson (1992) ont donc effectué une autre expérience avec des surfaces servant à distinguer le code spatial, le code temporel ainsi que le code basé sur la fréquence de décharge moyenne (voir Tableau 3). Les surfaces contiennent des matrices rectangulaires de points avec des changements d'espacement dans le sens de l'exploration ou dans la direction orthogonale. Ils ont prédit que la variation spatiale augmenterait quand l'espacement entre les points augmente dans les deux directions (horizontale et verticale). Les résultats psychophysiques et électrophysiologiques de cette expérience privilégient effectivement un code spatial, vs temporel ou basé sur la fréquence de décharge, et ce pour les RA mais principalement pour les SAI. Toutefois, les espacements dans les deux directions ne sont pas aussi grands que pour l'expérience précédente (4 mm vs

8.8 mm), donc la partie descendante de la courbe des estimés en fonction de l'espacement n'est pas analysée.

Yoshioka et al (2001) ont ensuite voulu vérifier si le code spatial peut expliquer la perception de la rugosité avec les textures fines ($PS \leq 2$ mm). Un point important de cette expérience est qu'ils ont démontré que les PC ne servent pas à la perception de la rugosité des textures fines. Bien qu'ils soient modulés par le déplacement des surfaces, ils répondent de la même façon pour toutes les surfaces. Ils ont aussi corrélé les résultats psychophysiques avec la réponse des afférences pour vérifier le code neuronal impliqué. Ils ont obtenus une très bonne corrélation pour le code spatial (SAI). La variance est aussi très bien expliquée par les RA à 93%, un peu inférieur aux SAI à 99%. Toutefois, dans cette expérience, un code basé sur la fréquence de décharge ne peut être éliminé car il explique aussi bien l'intensité subjective de la rugosité pour les textures fines que le code spatial (96.4% vs 99%).

Tableau 3 : Caractéristiques des stimuli utilisés dans les expériences d'électrophysiologie de la rugosité*Afférences périphériques*

Référence	Stimulus	PS (mm)	Largeur (mm) points/crêtes	Hauteur (mm) points/crêtes	Vitesse (mm/s)	Force (N)	Mode
Blake et al 1997	Points en relief (patron tétragonal)	3.5	0.25-2.5	0.28-0.62	40	0.3	Pa
Blake et al 1997	Carrés en relief ou en dépression	n/a	0.2-7	0.28-0.62	40	0.3	Pa
Connor et al 1990	Points en relief (patron tétragonal)	1.3-6.2 (1.8-8.8)**	0.5-1.2	0.35	20-50	0.3	Pa
Connor et Johnson 1992	Points en relief (matrice rect.)	1.5-4.0*	0.5	0.5	50	0.3	Pa
Darian-Smith et al 1980	Points en relief (patron tétragonal)	0.55-2.25	0.2-1	n/d	40-150	0.2-0.6	Pa
Darian-Smith et Oke 1980	Grillages	0.5-1	n/d	n/d	20-180	0.2-0.6	Pa
Goodwin et Morley 1987a,b; Morley et Goodwin 1987	Grillages (ratio rainure/crête = 7)	1-3	n/d	n/d	15-480	n/d	Pa
Lamb 1983b	Points en relief (matrice rect.)	1-2 *	1-2	0.65	40-220	0.4	Pa
Phillips et Johnson 1981	Grillages	1-6 P et NP *	0.5-2	2	n/d	n/d	statique
Phillips et Johnson 1981	Sondes	n/a	0.5-1	n/a	n/d	variables	statique
	Barre : 0.5x20	n/a	n/a	n/d	n/d	variables	statique

Phillips et al 1988	Points en relief (patron tétragonal)	0.9-6.2	0.5	0.5	20-80	0.1-1	Pa
Sathian et al 1989	Grillages	0.74-3.09*	0.2-2.75	n/d	n/d	n/d	Pa
Yoshioka et al 2001	Grillages	0.1-2*	0.1-1	n/d	20	0.3	Pa

Thalamus

Référence	Stimulus	PS (mm)	Largeur (mm) points/crêtes	Hauteur (mm) points/crêtes	Vitesse (mm/s)	Force (N)	Mode
Burton et Sinclair 1994	Grillages	0.5-2.9	n/d	n/d	50	0.25	A
Sinclair et al 1991	Grillages	0.75-3.15	0.25	0.5-2.9	> 25	> 0.5	A

Cortex somatosensoriel primaire

Référence	Stimulus	PS (mm)	Largeur (mm) points/crêtes	Hauteur (mm) points/crêtes	Vitesse (mm/s)	Force (N)	Mode
A-Belanger et Chapman 1992	Points en relief (aléatoires)	0-4	0-2	0.5	n/d	n/d	A
Burton et Sinclair 1994	Grillages	0.5-2.9	n/d	n/d	50	0.25	A
Chapman et A-Belanger 1991	Points en relief (aléatoires)	0-4	0-2	0.5	n/d	n/d	A
Darian-Smith et al 1982	Grillages	0.75-3	n/d	n/d	n/d	0.3-0.8	A

DiCarlo et al 1998, DiCarlo et Johnson 2000	Points en relief (aléatoires)	10 dots/cm ²	0.5	0.4	40	0.3	Pa
DiCarlo et Johnson 1999	Points en relief (aléatoires)	10 dots/cm ²	0.5	0.4	20-80	0.3	Pa
Jiang et al 1997	Points en relief (matrice rect.)	2-5	n/d	1	53-67	n/d	Pa
Phillips et al 1988	Points en relief (patron tétrapérial)	0.9-6.2	0.5	0.5	20-80	0.1-1	Pa
Sinclair et Burton 1988	Grillages	0-3	n/d	n/d	n/d	n/d	A
Sinclair et Burton 1991	Grillages	0.5-2.9	n/d	n/d	25-150	0.5-2	A
Sinclair et al 1996	Grillages	0.8-3	n/d	1	25-100	0.25-1	Pa
Sripati et al 2006	Sondes (400)	0.53-?	0.6	n/d	indentation	n/d	Pa
Tremblay et al 1996	Points en relief (matrice rect.)	lisse, 3, 9	1	1	49-89	0.4-3.92	Pa
Warren et al 1986	Roue dentée	0.8-9.6	-	-	30-90	-	Pa

Cortex somatosensoriel secondaire

Référence	Stimulus	PS (mm)	Largeur (mm)	Hauteur (mm)	Vitesse (mm/s)	Force (N)	Mode
Burton et Sinclair 1994	Grillages	0.5-2.9	n/d	n/d	50	0.25	A
Chapman et Meftah 2005	Points en relief (matrice rect.)	2-4.7	2	n/d	50	n/d	Pa
Jiang et al 1997	Points en relief (matrice rect.)	2-5	2	1	53-67	n/d	Pa

Pruett et al 2000	Grillages	0.5-2.9	n/d	0.5	25-100	0.3-0.9	Pa
Pruett et al 2001	Grillages	1.07-2.53	n/d	n/d	40-120	0.3-0.9	Pa
Sinclair et Burton 1993	Grillages	0.5-2.9	n/d	n/d	n/d	n/d	A

* largeur des crêtes et des rainures varient; ** PS dans le sens de l'exploration;

Abréviations : Pa: passif; A: Actif; n/d: non disponible; n/a: non applicable

3.2. *Afférences périphériques : Vitesse*

L'encodage de la vitesse a été adressé en partie dans la section précédente. Les études mentionnées variant la vitesse ont montré que la décharge des quatre types d'afférences (SAI, SAII, RA et PC) est modulée en fonction de la vitesse tactile. Toutefois, ces études étaient plus centrées sur l'encodage de la rugosité que celui de la vitesse. Tel que sera démontré dans les prochains paragraphes, l'encodage de la vitesse tactile au niveau des afférences périphériques a plutôt été étudié en utilisant des stimuli vibratoires (composante de la vitesse), des indentations et des brosses déplacées sur la peau.

L'équipe de Mountcastle a été la première à étudier l'encodage de la fréquence vibratoire. Des enregistrements unitaires ont été faits chez le singe anesthésié lors de la présentation de stimuli vibratoires de 2-300 Hz (voir Tableau 4) au niveau de la peau glabre de la main (Talbot et al 1968). Ils ont démontré que ce sont les RA et les PC qui encodent les vibrations, les SAI n'auraient pas de rôle essentiel. Les RA et les PC ont toutefois une gamme de vibration où elles déchargent de façon périodique avec les vibrations (une impulsion par cycle). Les RA serviraient donc à l'encodage des vibrations autour de 2-40 Hz (sensibilité maximale : 30 Hz), tandis que ce serait de 60-300 Hz (sensibilité maximale : 250 Hz) pour les PC. Mountcastle et al (1972) ont fait une expérience similaire qui a élargi la gamme des PC à 400 Hz. Les deux catégories de réponses ont été attribuées les noms de « flutter » pour les basses fréquences et de « vibration » pour les hautes fréquences, correspondant aux réponses des RA et PC respectivement. Darian-Smith et Oke (1980) ont aussi remarqué que les trois types d'afférences (SAI, RA, PC) ne

répondent pas tous de la même façon aux différentes fréquences temporelles obtenues en présentant des grillages (discuté ci-haut). La vibration reste toutefois une sous-classe des mouvements rencontrés dans la vie de tous les jours.

D'autres ont aussi utilisé la sonde comme stimulus, mais au lieu de la vibration (onde sinusoïdale), c'est la vitesse d'indentation (une seule dépression de la peau) qui est étudiée. Lindblom (1965) a enregistré (au niveau de la 7^e racine lombaire) les afférences à adaptation rapide innervant la peau glabre du pied du singe et a observé qu'elles répondent aux vitesses d'indentation de 1.5 à 80 mm/s. La courbe de fréquence de décharge en fonction de la vitesse est monotonique jusqu'à ce qu'elle atteigne un plateau (à partir de 40 mm/s), alors il semble y avoir une saturation de la fréquence de décharge. Knibestol et Vallbo (1976) ont plutôt démontré chez l'humain une diminution de pente seulement pour les vitesses approchant 100 mm/s pour les RA, tandis qu'il n'y avait pas de diminution pour les PC. Les SAI répondent peu à la vitesse d'indentation mais ils répondent très bien à l'amplitude d'indentation. Gardner et Palmer (1989 a,b) ont démontré que les RA et les PC sont aussi sensibles à la vitesse d'indentation de sondes successives sur une gamme de 30-120 mm/s. En effet, une matrice de rangées de sondes (OPTACON) est utilisée pour produire une simulation de mouvement (vu que ce n'est pas un mouvement transversal sur la peau). Tout comme pour une sonde individuelle, les SAI ne sont pas sensibles.

Franzén et Lindblom (1976) et Franzén et al (1984) ont démontré qu'il y a une corrélation entre la fréquence de décharge des RA et l'intensité subjective de la vitesse chez l'humain (autres types d'afférences moins discutés). Ils ont comparé les

courbes d'estimés des sujets aux courbes de fréquence de décharge pour des vitesses très lentes allant jusqu'à 16 mm/s. Ils ont évalué la fréquence de décharge instantanée et la réciproque de l'intervalle entre les impulsions et ont conclu que cette dernière expliquerait mieux la psychophysique. Toutefois, par des limitations du stimulateur, ils n'ont pu étudier des vitesses plus élevées comme dans les expériences précédentes. De plus, avec l'indentation de la peau, l'amplitude d'indentation est limitée par les contraintes physiques (ex. os sous-jacent). Ceci influence donc la durée de stimulation (partie en mouvement), qui devient très courte quand la vitesse augmente (quelques millisecondes seulement) et donc difficilement perceptible. Ce problème a été résolu par l'utilisation d'une brosse déplacée transversalement sur la peau.

Donc l'utilisation de brosses a permis de pouvoir varier plus grandement la distance de stimulation pour avoir une durée adéquate et de vérifier l'encodage d'un autre type de stimulation, soit le mouvement transversal. Franzén et al (1984) ont été les premiers à étudier l'effet du déplacement de brosses sur la peau à différentes vitesses sur la fréquence de décharge d'afférences périphériques. Ils ont montré qu'au niveau de la peau pileuse du singe, pour la plupart des afférences, il y a une relation linéaire (pente positive) entre la fréquence de décharge de la plupart des SAII et afférences pileuses (type à adaptation rapide) et les vitesses allant jusqu'à 200 cm/s. Donc l'encodage neuronal semble très différent entre les stimulations en un point par sonde et les transversales avec brosse. Il y avait une saturation de la fréquence de décharge vers 40 mm/s pour l'indentation, ce qui n'est pas le cas pour le déplacement de brosses. Toutefois, des vitesses d'indentation plus élevées (couvrant la gamme

avec les brosses) n'ont pas été étudiées. Greenspan (1992) a étendu ces observations aux SAI de la peau pileuse du chat (voir Tableau 4).

Il reste donc à vérifier si la réponse des afférences cutanées de la peau glabre est similaire, puisque c'est plus avec les mains que nous manipulons les objets. Edin et al (1995) ont démontré qu'il n'y a pas de différences entre la sensibilité à la vitesse (stimulation avec des brosses) des afférences de la peau glabre (main) et de la peau pileuse (main et visage) chez l'humain. De plus, la fréquence de décharge moyenne explique bien les expériences psychophysiques d'estimation de la vitesse. Ils ont déplacé les brosses sur une gamme de vitesse assez grande (jusqu'à 32 cm/s). La gamme de vitesses utilisées par l'humain pour l'exploration tactile est toutefois couverte. Le taux de décharge augmente avec la vitesse tactile pour toutes les afférences enregistrées (RA, SAI, SAII), il augmente aussi avec la force de contact. La réponse des différents SAI et SAII est plus uniforme (moins variable) que celle des RA. Malgré ceci, les RA sont quand même les plus sensibles des afférences à la vitesse tactile (Essick et Edin 1995). Elles répondent peu à la plus basse vitesse, comparativement aux SAI. Les PC n'ont pas été étudiés dans ces deux expériences.

LaMotte et Srinivasan (1987a,b) ont déplacé des surfaces lisses contenant une bosse (pente de différents degrés menant d'une partie plus basse à une plus haute de la surface). Ceci implique que toutes les parties du stimulus passent au même endroit sur la peau, contrairement aux brosses et à l'OPTACON qui se déplacent d'un point à un autre. Avec ce protocole, ils ont démontré que les deux types d'afférences étudiées au niveau de la peau glabre (SAI et RA) sont sensibles à la vitesse, et ce surtout quand la bosse passe au niveau du champ récepteur de la cellule.

Donc, les variations de décharge des afférences périphériques peuvent expliquer la capacité humaine à estimer la vitesse tactile. Les RA et les PC varient avec la fréquence vibratoire et la vitesse d'indentation d'une sonde. Les RA sont les meilleures pour expliquer la vitesse de déplacement d'une brosse sur la peau ainsi que la vitesse d'un point sur une surface lisse, mais les SAI varient aussi dans ses deux situations (PC non étudiés). Finalement, la réponse des afférences périphériques à la vitesse tactile ne semble pas varier sur différentes parties du corps.

Tableau 4 : Caractéristiques des stimuli utilisés dans les expériences d'électrophysiologie de la vitesse*Afférences primaires : chat*

Référence	Stimulus	PS (mm)	Vitesse (mm/s)	Force (N)	Distance (cm)	Peau
Greenspan 1992	Brosse (poils de chameau)	n/a	3.9-1000	0.5	3.2	PI

Afférences primaires : singe

Référence	Stimulus	PS (mm)	Vitesse (mm/s)	Force (N)	Distance (cm)	Peau
Connor et al 1990	Points en relief (patron tétragonal)	1.3-6.2	20-50	0.3	n/d	G
Darian-Smith et al 1980	"	0.55-2.25	40-150	0.2 et 0.6	n/d	G
Darian-Smith et Oke 1980	Grillages	0.5-1	20-180 (P)	0.2-0.6	n/d	G
Franzén et al 1984	Brosse (poils de chameau)	n/a	5-2560	0.5	0.5-8	PI
Gardner et Palmer 1989 a,b	Sondes (144), 0.25 mm (diam)	1.2	30-120	n/d	n/d	G
Goodwin et Morley 1987	Grillages (ratio rainure/crête = 7)	0.75-3	15-480	n/d	n/d	G
Lamb 1983b	Points en relief (matrice rect.)	1-2	40-220	0.4	n/d	G
LaMotte et Srinivasan 1987 a,b	Bosses (H: 0.5 mm, L: 0-3.134 mm)	n/a	10-40	0.2	n/d	G
Lindblom 1965	Sonde, 0.3 mm (diam)	n/a	0.08-80	n/d	?-0.045 (indent)	G
Mountcastle et al 1972	Sonde, 3 mm (diam), 2-400 Hz	n/a	n/a	n/d	0.005-0.09	G
Talbot et al 1968	Sonde, 0.5-3 mm (diam), 2-300 Hz	n/a	n/a	n/d	0.005- 0.56	G

Afférences primaires : humain

Référence	Stimulus	PS (mm)	Vitesse (mm/s)	Force (N)	Distance (cm)	Peau
Edin et al 1995	Différentes brosses	n/a	5-320	0.024-0.370	1.4	PI, G
Essick et Edin 1995	Différentes brosses	n/a	5-320	0.021-0.257	1.4	PI, G
Franzén et Lindblom 1976	Sonde, 2 mm (diam)	n/a	0.067-16	n/d	n/d	G
Franzén et al 1984	Sonde, 2 mm (diam)	n/a	jusqu'à 64	n/d	n/d	G
Knibestol et Vallbo 1976	Sonde, 1 mm ²	n/a	1-100	n/d	0.02-0.04 (indent)	G

Cortex somatosensoriel primaire: singe

Référence	Stimulus	PS (mm)	Vitesse (mm/s)	Force (N)	Distance (cm)	Peau
Costanzo et Gardner 1980	Brosses et bosses (H: 0.5-1 mm)	n/a	20-150	n/d	n/d	G, PI
Hernandez et al 2000	Sonde, 2 mm (diam)	n/a	n/a	n/d	0.05 (indent)	G
Jiang et al 1997	Points en relief (matrice rect.)	2-5	53 et 67	n/d	n/d	G
Luna et al 2005	Sonde, 2 mm (diam)	n/a	n/a	n/d	0.05 (indent)	G
Mountcastle et al 1969	Sonde, 2 mm (diam)	n/a	n/a	n/d	n/d	G
Mountcastle et al 1990	Sonde, 1-2 mm (diam)	n/a	n/a	n/d	0.05 (indent)	G
Romo et al 1996	Sonde, 2 mm (diam)	n/a	12-30	0.2	n/d	G
Salinas et al 2000	Sonde, 2 mm (diam)	n/a	n/a	n/d	0.05 (indent)	G

Sinclair et Burton 1991	Grillages	0.5-2.9	25-150 (actif)	0.05-0.20	8	G
Tremblay et al 1996	Points en relief (matrice rect.)	lisse, 3, 9	49-89	0.04-3.92	10	G

Cortex somatosensoriel secondaire: singe

Référence	Stimulus	PS (mm)	Vitesse (mm/s)	Force (N)	Distance (cm)	Peau
Burton et Sinclair 1990	Sonde, 2 mm (diam)	n/a	1-50	n/d	0.1 (indent)	G
Romo et al 2002	Sonde, 2 mm (diam)	n/a	n/a	n/d	0.05 (indent)	G
Salinas et al 2000	Sonde, 2 mm (diam)	n/a	n/a	n/d	0.05 (indent)	G

Légende : les stimuli ont tous été appliqués sur la peau glabre de la main

Abréviations : G: glabre; n/a: non applicable; n/d: non disponible; PI: pileuse

Colonne vitesse : exploration passive sauf si mentionné autrement

3.3. *Thalamus*

Seulement deux études publiées (Sinclair et al 1991, Burton et Sinclair 1994) ont vérifié l'encodage de la rugosité au niveau d'un nombre restreint de neurones du noyau ventro-postéro-latéral (VPL) du thalamus ($n = 33$). Des enregistrements unitaires ont été faits pendant que les singes exploraient des grillages de 0.5 à 2.9 mm d'espacement. Plusieurs afférences ont une fréquence de décharge qui varie avec l'espacement. Pour celles-ci, la pente de la relation (fréquence vs PS) est toujours positive et il y a aussi une influence de la force de contact dans tous les cas et pour certaines de la vitesse d'exploration. La réponse des neurones de VPL ressemble donc plus à la réponse des afférences périphériques qu'à celle du cortex. En effet, il n'y a pas de neurones qui répondent seulement à la rugosité (indépendance de force et/ou vitesse). Comme il sera vu dans les prochains paragraphes, le cortex contient des neurones ayant des patrons de décharge différents de ceux du thalamus (ex. pente négative entre fréquence de décharge et espacement). Ceci suggère qu'un traitement de l'information a été effectué.

3.4. *Cortex somatosensoriel primaire : Rugosité*

Le prochain relais est le cortex somatosensoriel primaire, S1. Carlson (1981) et Randolph et Semmes (1974) ont démontré que l'ablation de la représentation de la main dans les aires 3 (3a et 3b) ou 1, mais non 2 du S1 entraîne des déficiences pour les tâches impliquant la perception de la texture/rugosité. Les principales aires enregistrées dans les expériences suivantes sont 3b, 1 et 2. L'aire 3a, faisant aussi partie de S1, reçoit toutefois des afférences proprioceptives. Plusieurs neurones

corticaux conservent leur propriétés adaptatives observées au niveau des afférences périphériques (SA, RA). Il sera donc démontré comment les neurones de S1 répondent aux différents stimuli (grillages, points en relief, roues dentées, et matrice de sondes) et donc comment elles diffèrent des afférences primaires. Selon les études, plus de 50% des neurones du S1 ayant un champ récepteur cutané sont sensibles aux changements de texture. La plupart des études présentées utilisent un code intensif (basé sur la fréquence de décharge) pour expliquer la rugosité. Toutefois le groupe de Johnson utilise un code spatial, qui sera considéré à la fin.

Darian-Smith et al (1982), qui ont effectué les premiers enregistrements extracellulaires corticaux lors de l'utilisation de surfaces texturées, ont démontré qu'il y avait peu de différence entre la réponse des neurones des aires 3b et 1 à l'exploration active de grillages (PS de 0.75 à 3 mm) chez le singe. Les neurones de type RA et SA sont toutes deux modulées par les grillages. D'autres études ont confirmé que la fréquence de décharge des neurones des aires 3b et 1 augmente monotoniquement avec la PS (jusqu'à 3 mm) pour les grillages (Burton et Sinclair 1994, Sinclair et Burton 1988, 1991, Sinclair et al 1996) et pour une gamme jusqu'à 5 mm pour les points en relief (Jiang et al 1997). Cette dernière étude a aussi démontré que la relation monotone est présente dans l'aire 2. Les surfaces complètement lisses peuvent aussi moduler la fréquence de décharge de neurones sensibles ou non à la texture (Ageranioti-Belanger et Chapman 1992, Chapman et Ageranioti-Belanger 1991, Sinclair et Burton 1988, Tremblay et al 1996).

L'augmentation monotone de la fréquence de décharge des neurones avec la PS est très fréquente dans S1, mais d'autres patrons de décharge sont aussi

présents. Il y a les neurones non monotoniques, qui sont moins fréquents, où la fréquence de décharge sature à une certaine PS (Burton et Sinclair 1994, Jiang et al 1997, Sinclair et Burton 1988, 1991). Une autre proportion des neurones est modulée par le passage des surfaces texturées au niveau du champ récepteur cutané, mais la décharge est indépendante de la PS. Ces neurones pourraient toutefois être sensibles à une gamme de PS différente.

D'autres facteurs peuvent aussi moduler la fréquence de décharge. Un premier facteur est la vitesse tactile. La proportion de neurones sensibles à la PS qui sont aussi sensibles à la vitesse tactile (gamme totale de 25-100 mm/s) varie entre 50-66% pour le toucher passif (Sinclair et al 1996, Tremblay et al 1996). Sinclair et Burton (1991) ont obtenu une proportion de 23% pour le toucher actif, mais la vitesse tactile n'est pas variée systématiquement. Donc selon ces études il y a quand même des neurones sensibles seulement à la PS, et non à la vitesse tactile. Ceci suggère que le signal de vitesse provenant des afférences périphériques serait filtré pour donner un qui correspond aux données psychophysiques de rugosité subjective, et ce surtout dans l'aire 1. Un deuxième facteur est la force de contact avec la surface texturée. On sait que la fréquence de décharge augmente avec une augmentation de la force (Salimi et al 1999, Wannier et al 1986). La fréquence de décharge covarie avec la force et la PS chez 22 à 30% des neurones (Sinclair et Burton 1991, Tremblay et al 1996). La force n'a pas été variée systématiquement dans ces études, donc seules les variations de force lors de l'exploration ont été utilisées. La seule étude où elle l'a été (gamme de 0.25 à 1N) la proportion des neurones où la force et la PS covarient est de 60%, toutefois les singes y sont anesthésiés et l'échantillon a été très petit, $n = 33$

(Sinclair et al 1996). De plus, les effets observés de la vitesse et de la force dans cette expérience sont variables.

Un troisième facteur est l'effet de la présence ou non d'une tâche tactile. La discrimination tactile a été utilisée dans deux études (Chapman et Meftah 2005, Meftah et al 2002). Tandis que la sensibilité à la PS reste la même selon que l'attention soit dirigée vers la texture ou non, le taux de décharge est plus élevé avec l'attention dirigée. Ceci est une différence importante comparé aux afférences périphériques, qui ne sont pas modulées par l'attention aux stimuli.

Le dernier facteur est le mode de toucher, actif vs passif. Tel que mentionné précédemment, des expériences utilisant les deux modes ont démontré une augmentation de la fréquence de décharge avec l'augmentation de la PS. Toutefois les touchers passif et actif ont été comparés dans Ageranioti-Belanger et Chapman (1992) et Chapman et Ageranioti-Belanger (1991). Il semblerait que la modulation de la fréquence de décharge soit plus faible ou absente en passif qu'en actif. Il y avait toutefois certaines différences entre les deux modes ce qui limitent l'interprétation des résultats, incluant une différence des vitesses de présentation (plus lente en passif) et l'absence d'une tâche de discrimination en passif, et donc un effet possible de l'attention.

Phillips et al (1988) ont vérifié la reproduction des surfaces (mêmes que pour les afférences périphériques) par les SEP corticaux chez le singe exécutant une tâche de diversion visuelle. Tel qu'attendu les cellules SA et RA de l'aire 3b donnent une très bonne résolution (identique aux afférences périphériques pour certains neurones)

mais celle-ci est diminuée dans l'aire 1, proposant que la forme spatiale est peut-être plus représentée dans 3b que 1. De plus, DiCarlo et Johnson (1999) ont démontré que le code spatial est insensible à la vitesse dans 3b. L'indépendance à la vitesse élimine donc la possibilité que le code spatial puisse expliquer la vitesse tactile. Le code spatial signale aussi bien les patrons réguliers et irréguliers (Dicarlo et al 1998, DiCarlo et Johnson 1999, 2000). Les SEP corticaux sont indépendants de la force (0.2 à 0.8 N), ce qui ne correspond pas avec un effet positif de la force sur les estimations de rugosité des humains. La théorie prédit aussi qu'il y ait des champs récepteurs excitateurs et inhibiteurs adjacents, qui ont été observés au niveau de S1 (DiCarlo et al 1998, DiCarlo et Johnson 1999,2000). Toutefois, une inhibition latérale a aussi été observée au niveau des afférences périphériques (Sripati et al 2006) en utilisant une matrice de sondes (spatiotemporal random indentation). Celle-ci pourrait être expliquée par un mécanisme d'origine périphérique (stress mécanique ou temps pour que la peau arrête de se déplacer). Il faut se rappeler aussi que le code spatial est basé sur l'obtention de données par la présentation répétitive d'une surface texturée sur le champ récepteur de la cellule pour y présenter le patron complet (SEP). Ceci n'est pas la méthode utilisée pour l'exploration dans la vie de tous les jours, elle implique plutôt l'activation simultanée de plusieurs récepteurs. De plus, les animaux n'ont pas de tâche tactile dans ces expériences. La preuve au niveau central est présentement manquante pour confirmer un code spatial. L'enregistrement simultané de neurones de S1 ayant des champs récepteurs adjacents serait nécessaire.

En conclusion, un code basé sur la fréquence de décharge est très plausible pour expliquer la rugosité dans les aires 3b, 1 et 2, tandis que le code spatial manque

de preuves. L'idée est que les SAI sont responsables pour la rugosité, et ce en utilisant un code spatial. Ce code est indépendant de la vitesse, ce qui peut expliquer que l'intensité subjective de la rugosité l'est aussi. Toutefois le code spatial est aussi indépendant de la force, tandis que les estimés de rugosité varient avec la force. Nous ne savons pas comment ceci pourrait être transmis par le code spatial. Ce code pourrait toutefois être très utile pour la représentation de la forme spatiale, comme par exemple pour la lecture du braille. Mais peu importe le code, tous les types d'afférences pourraient contribuer à la perception de la rugosité.

3.5. Cortex somatosensoriel primaire : Vitesse

La vitesse tactile a été très peu étudiée au niveau du S1. Zainos et al (1997) ont démontré que la capacité de discriminer la vitesse (sonde déplacée transversalement de 12 à 30 mm/s) est abolie avec une lésion complète de la représentation de la main du S1 controlatéral. Cette observation confirme l'importance de S1 dans l'appréciation de la vitesse tactile.

La vitesse a été étudiée avec différentes approches. Elles peuvent être divisées en toucher passif (animal immobile), tel qu'en utilisant la fréquence de vibration (Hernandez et al 2000, Luna et al 2005, Mountcastle et al 1969, 1990, Salinas et al 2000) ou un stimulus déplacé transversalement sur la peau (DiCarlo et al 1999, Romo et al 1996, Tremblay et al 1996). Le toucher actif est aussi utilisé (l'animal déplace lui-même ses doigts sur des surfaces à différentes vitesses). Cette dernière n'a toutefois pas de changements paramétriques de la vitesse, seulement la variation naturelle de la vitesse durant le toucher actif (Sinclair et Burton 1991). Dans la

plupart des cas, les singes étaient éveillés et exécutaient une tâche tactile ou une tâche de contrôle de l'attention avec distracteur.

Une composante de la vitesse tactile, la vibration à basses fréquences (flutter, 5 à 50 Hz), a fait l'objet des études de Mountcastle et de Romo. Mountcastle et al (1969,1990) ont voulu expliquer la discrimination de la vibration au niveau de S1. Le protocole est toutefois différent entre les deux expériences, soit un singe semi-éveillé (1969) et un singe performant une tâche de discrimination de la fréquence vibratoire (1990). Malgré cette différence, les résultats des deux études suggèrent un code basé sur la périodicité de la fréquence de décharge des neurones RA (SA non contributifs) des aires 3b et 1. Puisque la capacité de discrimination du flutter est très similaire entre l'humain et le singe (Lamotte et Mountcastle 1975), ils suggèrent que leur code, basé sur l'intervalle entre les potentiels d'action, pourrait expliquer la discrimination de flutter chez l'humain. Romo et ses collègues n'ont toutefois pas été capable de confirmer l'hypothèse de Mountcastle. Ils ont trouvé en utilisant une multitude d'approches, dont des microstimulations intracorticales (ICMS), qu'un code basé sur la fréquence de décharge moyenne apporte une meilleur corrélation avec les données perceptuelles. Hernandez et al (2000) et Salinas et al (2000) ont suggéré que ce code se retrouve au niveau des neurones RA des aires 3b et 1. Ce code a été modifié quelque peu (nombre pondéré de potentiels d'action) par Luna et al (2005). Mais peu importe le code, ce sont les neurones RA qui sont responsables de la perception de la vibration (flutter) pour les fréquences de 5-50 Hz au niveau de S1.

Les prochaines études concernent la vitesse de déplacement transversal d'un stimulus sur la peau. Sinclair et Burton (1991) ont étudié les variations de vitesses

(25-150 mm/s) produites par le singe lors de l'exploration active de grillages durant une tâche de catégorisation de la rugosité (voir Tableau 4). Tous les neurones (RA et SA) des aires 3b et 1 (2 non enregistré) sont affectés (pentes positives et négatives) par la vitesse d'exploration. La fréquence de décharge de la plupart des neurones covarie aussi avec la PS, ce qui implique qu'ils pourraient répondre à la fréquence temporelle. Les études suivantes ont varié la vitesse systématiquement (présentation passive) et des résultats similaires sont obtenus. Romo et al (1996) ont montré qu'il y a une augmentation monotone de la fréquence de décharge de neurones RA et SA de l'aire 1 (autres aires non étudiées) avec l'augmentation de la vitesse de déplacement transverse (12-30 mm/s). Ceci est aussi vrai pour les changements de vitesse de surfaces avec points en relief, soit une matrice rectangulaire (tâche de discrimination de rugosité), soit une distribution aléatoire (tâche de détection visuelle) (Tremblay et al 1996, DiCarlo et al 1999 respectivement). Les neurones (RA et SA) des trois aires (3b, 1 et 2) sont sensibles à la vitesse.

Enfin, la proportion de neurones sensibles à la vitesse varie dans chaque aire. Elle est la plus élevée (90-100%) dans l'aire 3b (DiCarlo et al 1999, Tremblay et al 1996) ainsi qu'à 77% dans l'aire 2 (Tremblay et al 1996). Une plus petite proportion (25-50%) est présente dans l'aire 1 (Romo et al 1996, Tremblay et al 1996). Même si les neurones des deux types d'adaptation sont sensibles à la vitesse au niveau du S1, ce sont les RA qui sont prédominantes.

Ces études démontrent que la vitesse est bel et bien signalée dans les trois aires du S1, mais mis à part pour la vibration, son encodage n'a pas été étudié. Il est toutefois connu que la vitesse semble presque toujours covarier avec la PS pour les

matrices de points en relief. Donc même si le signal de rugosité est retrouvé sans le signal de vitesse au niveau du S1, le contraire n'est peut-être pas vrai. Donc des études plus approfondies sont nécessaires pour répondre à ces questions.

3.6. Cortex somatosensoriel secondaire : Rugosité

Tel que mentionné précédemment, S2 est considéré comme hiérarchiquement plus élevé que S1 (Pons et al 1987). En accord avec ceci, la taille des champs récepteurs est beaucoup plus importante dans S2 que dans S1, incluant même les deux côtés du corps. D'autres similarités et différences entre S1 et S2 seront discutées dans les prochains paragraphes. Finalement, des résultats similaires ont été obtenus avec des études utilisant des grillages et d'autres utilisant des surfaces avec des points en relief comme stimuli.

Sinclair et Burton (1993) ont démontré que la fréquence de décharge des neurones de S2 varie avec la PS des grillages (0.5-2.9 mm), lors d'enregistrements faits pendant que le singe fait une tâche de catégorisation. La proportion de neurones sensibles à la texture est toutefois inférieure comparé à S1 (40% vs 60%; Sinclair et Burton 1991). La fréquence de décharge des neurones diminue ou augmente en augmentant la PS (Burton et Sinclair 1994). La relation négative est plus fréquente que dans S1. Jiang et al (1997) ont en partie confirmé leurs observations (voir ci-bas), en utilisant des surfaces contenant des points en relief.

Comme dans S1, certains neurones répondent seulement à la PS, tandis que d'autres répondent aussi à la force et la vitesse. Ceci a été observé initialement en utilisant les variations naturelles de force et de vitesse pendant de l'exploration active

(Burton et Sinclair 1994, Sinclair et Burton 1993). Pruett et al (2000) ont donc utilisé une tâche de catégorisation avec présentation passive des surfaces. Ceci a permis de changer systématiquement la vitesse et la force (voir Tableau 3). Certains neurones sont sensibles aux trois facteurs, d'autres à deux (totalisant 90%), et d'autres seulement à la PS (10%). La combinaison de PS et de force correspond aux résultats psychophysiques sur l'estimation subjective de la rugosité où ces deux facteurs contribuent à la rugosité.

La question à savoir si S2 contient une représentation plus abstraite de la rugosité se pose. Jiang et al (1997) ont démontré que les neurones de S2 peuvent avoir un patron de décharge non gradé, c'est-à-dire que les cellules signalent la présence d'une différence de rugosité et non son intensité. La proportion de ces neurones est à 63% dans S2, tandis qu'elle est à 14% dans S1. Pruett et al (2001) ont principalement rapporté un patron gradé, mais l'inspection de leurs résultats suggère que plusieurs des neurones sont non gradé (cf. Fig. 4, 7, 9, 10 et 11 de leur article). Toutefois, dans Chapman et Meftah (2005), cet effet est peu marqué, et ce probablement dû à la différence dans la tâche. Dans Jiang et al (1997), le signal restait important tout au long de la période de stimulation car le singe devait attendre à la fin pour répondre, tandis que dans la tâche de discrimination de texture de Chapman et Meftah (2005), le singe devait répondre le plus vite possible au changement de texture.

Il semblerait que les neurones de S2 sont particulièrement sensibles au contexte et à l'attention. Il avait été proposé qu'une proportion des neurones de S2 (25%) déchargent seulement durant la tâche et non quand il y a stimulation passive

des doigts, car pour certains neurones, aucune réponse n'est élicitée lors de l'évaluation du champ récepteur (Burton et Sinclair 1994, Sinclair et Burton 1993). Mais d'autres études (Chapman et Meftah 2005, Jiang et al 1997, Meftah et al 2002, Pruett et al 2000, 2001) ont démontré que ce phénomène ne peut être expliqué par le mode de toucher car la stimulation passive est un stimulus efficace pour les neurones de S2 dans le contexte d'une tâche. En accord avec ceci, une influence attentionnelle est fréquemment observée dans S2. En effet, Meftah et al (2002) ont démontré que 62% des neurones du S2 ont une fréquence de décharge plus élevée durant une tâche de discrimination tactile vs discrimination visuelle.

3.7. Cortex somatosensoriel secondaire : Vitesse

Pour ajouter à ce qui a déjà été mentionné dans la section précédente, trois études ont caractérisé l'effet de la vibration et de la vitesse d'indentation sur la fréquence de décharge des neurones de S2. Burton et Sinclair (1990) ont démontré qu'un certain nombre de neurones augmentent leur fréquence de décharge de façon monotonique avec une augmentation de vitesse d'indentation pour la gamme étudiée (1-50 mm/s), chez le singe éveillé ou légèrement sédationné.

Salinas et al (2000) ont démontré que la fréquence vibratoire de 5 à 50 Hz influence les neurones de S2. Elle diffère toutefois de la réponse des neurones de S1 par le fait qu'elles n'ont pas de variations périodiques dans leur fréquence de décharge, un code basé sur la fréquence moyenne est plutôt présent. Il y a moins de neurones qui sont sensibles à la vibration (62% insensibles vs 31% dans S1), mais ceci pourrait être expliqué par une stimulation sous-optimale du champ récepteur vu

qu'il peut être de très grande taille. Romo et al (2002) ont utilisé une tâche de discrimination de flutter dans laquelle deux stimuli sont présentés un à la suite de l'autre et ont proposé que la fréquence de décharge du deuxième stimulus soit influencée par celle du premier pour 40% des cellules. S2 pourrait refléter les exigences comportementales de la tâche plutôt que seulement les détails des attributs physiques du stimulus, ce qui est supporté par Jiang et al (1997) pour la texture.

Tout comme pour la rugosité (ci-haut), les neurones sensibles à la vibration de S2 sont aussi modulées hors tâche (Romo et al 2002, Salinas et al 2000). Ceci a été démontré lors de l'exposition aux deux fréquences vibratoires quand le singe ne reçoit aucune récompense. La seule différence est que la fréquence de décharge est moins élevée hors tâche, mais elle est quand même modulée par la vibration. Ceci pourrait donc être un effet du contexte (aucune récompense) et/ou de l'attention que le singe porte aux vibrations.

3.8. Imagerie fonctionnelle

Grâce aux études chez le singe, nous savons que S1 et S2 sont très importants dans la perception tactile. Des études d'imagerie fonctionnelle chez l'humain ont pu confirmer le rôle de S1 et S2 pour la perception de la rugosité. Burton et al (1997) ont confirmé au TEP (tomographie par émission de positrons) que ces deux régions sont activées par la présentation de grillages. En effet, les parties antérieures (aire 3b) et postérieures (aires 1 et 2) de la représentation de la main de S1 sont activées du côté controlatéral à la main stimulée et aussi ipsilatéral (partie postérieure). L'exploration indirecte des surfaces a aussi été faite avec un plectre de guitare. Dans cette

condition, seulement la partie postérieure du SI controlatéral a été activée (Burton et al 1997). En ce qui concerne S2 controlatéral, l'exploration directe entraîne une activation d'une partie plus antérieure et médiale du S2 qu'avec l'utilisation du plectre. Kitada et al (2005) ont élargi ses observations en ajoutant l'activation de l'insula lors de la présentation de grillages (fMRI: imagerie par résonance magnétique fonctionnelle). De plus, lorsque les sujets ont comme consigne d'estimer la rugosité, le cortex préfrontal s'active (contrairement à hors tâche). Il servirait plutôt au processus cognitif impliqué dans l'estimation subjective de la rugosité.

4. Résumé et plan général de la thèse

Le toucher discriminatif est une habileté complexe qui est dépendante de l'extraction d'information des afférences cutanées dont le signal covarie avec de multiples attributs physiques, incluant la vitesse et la texture. Malgré ce mélange de signal, il est toutefois possible de percevoir les variations de rugosité indépendamment de la vitesse. Ceci peut être expliqué par une extraction du signal de rugosité au niveau central. Il n'est toutefois pas connu si c'est aussi le cas pour la vitesse tactile, car peu d'études y ont été consacrées, donc son encodage n'est peu compris. On ne sait même pas non plus si les humains sont capables d'estimer la vitesse tactile sans indice de durée ou d'étendue de peau stimulée. Les connaissances de base concernant la perception de la vitesse tactile sont très peu nombreuses comparé à celles sur la perception de la rugosité. Cette thèse explore donc la capacité des humains à estimer la vitesse et la rugosité de surfaces en mouvements. Les bases

neuronales de la vitesse tactile sont aussi étudiées en effectuant des enregistrements unitaires dans le cortex somatosensoriel primaire (S1) du singe éveillé.

Un premier but était donc d'établir si les sujets humains sont capables d'estimer la vitesse tactile sans indice de durée ni d'étendue de peau stimulée. Les conditions expérimentales prévues devaient être répétables pour les expériences électrophysiologiques. Les résultats de ces expériences psychophysiques (Ch. 2) ont servi à développer le protocole expérimental ainsi que l'hypothèse de base sous-tendant l'approche expérimentale chez le singe.

Puisque les résultats de l'expérience psychophysique initiale ont suggéré que la perception de la vitesse tactile était dépendante de la PS, mais pas du détail exact des surfaces manufacturées contenant des points en relief (périodique, non périodique), une deuxième hypothèse de travail s'est présentée. Une étude psychophysique chez l'humain (Ch. 3) a été effectuée pour établir si les estimés de rugosité sont aussi indépendants de la disposition des points (périodique vs non périodique).

Finalement, grâce aux hypothèses établies avec les expériences psychophysiques précédentes, des enregistrements ont été effectués dans le S1 (aires 3b, 1 et 2) chez le singe éveillé pour enfin établir les bases de l'encodage neuronal de la vitesse tactile (Ch. 4). Les mêmes gammes de surfaces et vitesses tactiles que chez l'humain ont été utilisées. Des données concernant la représentation de la rugosité tactile dans S1 ont aussi été acquises mais elles ne sont pas présentées ici. Une discussion générale se trouve dans le dernier chapitre.

Article # 1

**TACTILE SPEED SCALING: CONTRIBUTIONS OF
TIME AND SPACE.**

by

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Abstract

A major challenge for the brain is to extract precise information about the attributes of tactile stimuli from signals that co-vary with multiple parameters, e.g. speed and texture in the case of scanning movements. We determined the ability of humans to estimate the tangential speed of surfaces moved under the stationary fingertip, and the extent to which the physical characteristics of the surfaces modify speed perception. Scanning speed ranged from 33-110 mm/s (duration of motion constant). Subjects could scale tactile scanning speed, but surface structure was essential because the subjects were poor at scaling the speed of a moving smooth surface. For textured surfaces, subjective magnitude estimates increased linearly across the range of speeds tested. The spatial characteristics of the surfaces influenced speed perception, with the roughest surface (8 mm spatial period, SP) being perceived as moving 15% slower than the smoother, textured surfaces (2-3 mm SP). Neither dot disposition (periodic, non periodic) nor dot density contributed to the results, suggesting that the critical factor was dot spacing in the direction of the scan. A single monotonic relation between subjective speed and temporal frequency (speed/SP) was obtained when the ratings were normalized for SP. This provides clear predictions for identifying those cortical neurones that play a critical role in tactile motion perception, and the underlying neuronal code. Finally, the results were consistent with observations in the visual system (decreased subjective speed with a decrease in spatial frequency, $1/SP$), suggesting that stimulus motion is processed similarly in both sensory systems.

Introduction

Many years ago, Katz (1925) observed that movement between the skin and the surround is as important to touch as light is to vision. Sensory impressions are more vivid and precise with movement so that, for example, tactile roughness discrimination thresholds are approximately halved with movement (dynamic touch) as compared to without (static touch) (Morley et al. 1983). While we have considerable knowledge about the ability to perceive various qualities of tactile stimuli, including for example light touch, surface roughness, and micro-geometric or local shape (what can be sensed on the fingertip), we know much less about the appreciation of tactile motion itself. This is an important lacuna since tactile motion perception is critically important in everyday life, with a practical example being the ability to hold and manipulate objects. This is in turn dependent on sensory feedback from tactile mechanoreceptors to detect and minimize slip (Johansson 1998).

At a simple level, one would expect that the rapidly adapting mechanoreceptive afferents that play a key role in discriminative touch must be particularly specialized to detect tactile motion. As reviewed by Johnson (2001), these include the PC (Pacinian), RA (rapidly adapting, glabrous skin) and various hair follicle afferents (hairy skin). A complementary role cannot, however, be discounted for the slowly adapting afferents (SAI and II). Even though they are specialized to signal static contact, they also discharge more intensely to moving stimuli, and their signal contains information about tactile motion (Edin et al. 1995). Thus, tactile motion cannot be presumed to depend on activity in only one or several types of peripheral receptors.

The elegant studies of Mountcastle and colleagues provided the first systematic studies of the neuronal and perceptual correlates underlying motion perception, using punctate vibration as the stimulus (LaMotte and Mountcastle 1975; Mountcastle et al. 1972; Talbot et al. 1968). Their experiments showed that RA afferents are particularly sensitive to lower frequencies of vibration (flutter) while PC afferents are exquisitely sensitive to higher frequencies. Vibration does not, however, reflect more than a subclass of the types of tactile motion encountered in daily life. More recent studies have characterized receptor sensitivity to more natural stimuli, including tangential movement (surfaces or local shapes scanned over a skin area) and transverse movement (brush strokes over a fixed length of skin). Such studies have shown that cutaneous mechanoreceptive afferents innervating both hairy skin and glabrous skin, including SAI, SAI, RA and PC afferents, are sensitive to tactile motion (Darian-Smith et al. 1980; Edin et al. 1995; Essick and Edin 1995; Goodwin and Morley 1987; Greenspan 1992; LaMotte and Srinivasan 1987a,b). Yet the afferent signals elicited by tangential movement, specifically moving surfaces, are complex reflecting both surface structure (the roughness and/or shape of the stimuli scanned over the skin) and tangential speed. This leads to the general question as to how the brain extracts precise information about the attributes of tactile stimuli from signals that co-vary with multiple parameters.

We know that human tactile roughness scaling (magnitude estimates) is relatively independent of scanning speed (Lederman 1983; Meftah et al. 2000), indicating that information about surface roughness is extracted from these complex signals – possibly using a spatial code (Connor et al. 1990; Connor and Johnson

1992). As regards tactile motion scaling, in contrast, we have little information as to whether tactile motion can be extracted from signals that co-vary with both texture and speed. There have been a few reports showing that humans can scale the subjective speed of either mechanical pulses on the skin (Franzén and Lindblom 1976) or brush displacement over a fixed length of skin (Essick et al. 1988, 1996). But interpretation of these results was confounded by the fact that stimulus duration covaried with stimulus speed: faster stimuli had a shorter duration. Subjects could, therefore, have based their ratings on either parameter. This is an important gap in our knowledge because such information is critical for identifying the cortical neuronal mechanisms underlying tactile motion perception.

The present study had two aims. First, we determined the capacity of human subjects to scale the tangential speed of surfaces moved under the fingertip (tactile speed), using a paradigm in which stimulus duration was held constant. This was achieved by varying the length of surface presented as a function of speed (faster speeds, longer segment of surface presented). We chose to investigate tactile speeds within the range of speeds often used during tactile exploration, 33 to 110 mm/s (Smith et al. 2002a), corresponding to speeds over which texture estimates are invariant with changes in scanning speed.

The second aim of the study was to identify the extent to which the physical parameters of the stimuli (textured and smooth surfaces) modify the perception of tactile motion. As pointed out above, tactile mechanoreceptors in the glabrous skin do not signal speed independently of surface texture. An invariant representation of tactile texture is extracted from these signals, but we do not know if the brain is also

able to extract an invariant representation of tactile motion. To address this issue, we were motivated by studies in the visual system which have shown that subjective visual speed estimates are decreased when the overall visual stimulus is made sparser, either by decreasing the spatial frequency, $1/SP$ (spatial period) [periodic gratings] or the number of items in the display [dot density] (Campbell and Maffei 1981; Diener and al. 1976; Watamaniuk et al. 1993; cf Smith and Edgar 1990). We therefore systematically varied the physical parameters of our stimuli (SP and dot density) to determine how these factors influence tactile motion perception.

In this study, subjects scaled the speed of textured (raised dot surfaces) and smooth surfaces. Surface texture was varied by changing the spacing between dots, the dot density and dot disposition (periodic or non periodic). The results indicated that subjects can indeed scale the speed of constant duration tactile stimuli, but the spatial characteristics of the surfaces modified speed perception, and this in a similar manner to that seen in the visual system. A preliminary report of these data has been presented elsewhere (Meftah et al. 2005).

Methods

Subjects.

Twenty six naïve paid subjects (17 women and 9 men, all but 2 right-handed for writing, 20 to 35 years old), volunteered to participate in the study. The institutional ethics committee approved the experimental protocol, and subjects gave their informed consent before participating. Each subject participated in one session

of two hours. The task was to estimate the speed of surfaces scanned under their right middle fingertip (D3).

Surfaces.

Ten strips, 2 x 40 cm each, were prepared on flexible letterpress (Jiang et al. 1997): one was smooth (not shown) and the others were textured (Fig. 1A-C), with embossed, cylindrical raised dots (0.8 mm diameter on the top, 1 mm height, Fig. 1D). The physical characteristics of the 9 textured surfaces are summarized in Table 1. As shown in Fig. 1A, one series of textured surfaces (experiment 1, periodic surfaces) consisted of rectangular arrays of dots with identical transverse SPs (2 mm, distance centre-to-centre between adjacent dots in each row) and three different longitudinal SPs (2, 3, or 8 mm between rows), corresponding to the direction of the scan (Fig. 2A, see arrows). Subjective roughness shows a monotonic increase over this range (Meftah et al. 2000) (Note: This contrasts with the U-shaped relation reported by Connor et al. (1990) when dot spacing is incremented in two-dimensions, as opposed to the uni-dimensional change employed here). The second series (experiment 2, non periodic surfaces; Fig. 1B) had the *same number of raised dots* as the first series, but they were distributed quasi-randomly, with densities of 6.3, 16.7 and 25 dots/cm². The latter surfaces were designed by taking the periodic dot matrices and “jittering” the position of the dots while maintaining, on average, the same spacing between adjacent dots (Lederman et al. 1986). The average SP in all directions was 2.0 mm (25 dots/cm²), 2.5 mm (16.7 dots/cm²), and 4.9 mm (6.3 dots/cm²). Finally, the third series (experiment 3, non periodic; Fig. 1C) also consisted of dots distributed quasi-randomly, but with the *same average SP in the*

direction of the scan as in the first series, i.e. 2, 3, and 8 mm. These were prepared by pruning the series from experiment 2 (dots removed) so that the mean dot spacing in the scanning direction was identical to that of the periodic surfaces. Thus, this series preserved the same mean spacing in the direction of the scan, but dot density was lower (Table 1). For all 3 series of surfaces, roughness estimates increase monotonically across the range of dot spacings (Dépeault et al. 2006; Meftah et al. 2000).

Table 1 Spatial characteristics of the textured surfaces.

Surface	Dot Density (dots/cm ²)	Dot Spacing ¹ (mm)
Expt 1 periodic	25	2
periodic	16.7	3
periodic	6.3	8
Expt 2 non periodic	25	2
non periodic	16.7	2.5
non periodic	6.3	4.9
Expt 3 non periodic	25	2
non periodic	14	3
non periodic	2.2	8

¹Mean spatial period in the direction of the scan.

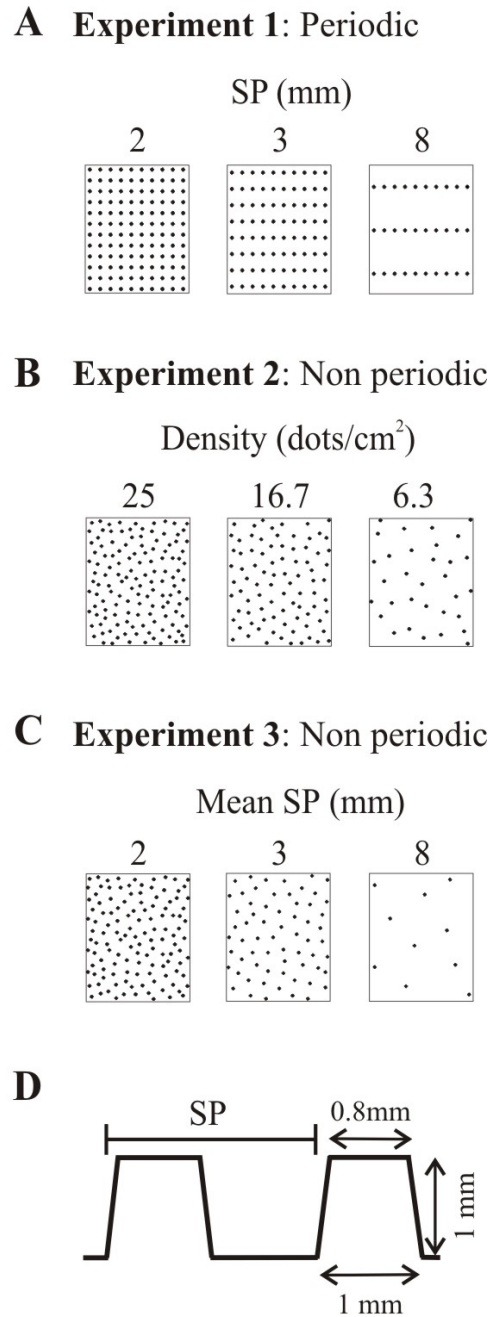


Figure 1 Characteristics of raised dot surfaces. **A:** Periodic surfaces used in experiment 1; spatial period (SP) was constant across the rows (2 mm) and varied between the rows (direction of scan), 2, 3 or 8 mm SP. **B:** The surfaces used in experiment 2 had the same number of raised dots as for experiment 1, but dot disposition was random. **C:** These non periodic surfaces (experiment 3) had the same average SP in the direction of the scan as the periodic surfaces (A), but dot density was lower especially for the roughest surface (see Table 1). **D:** Dot dimensions and SP.

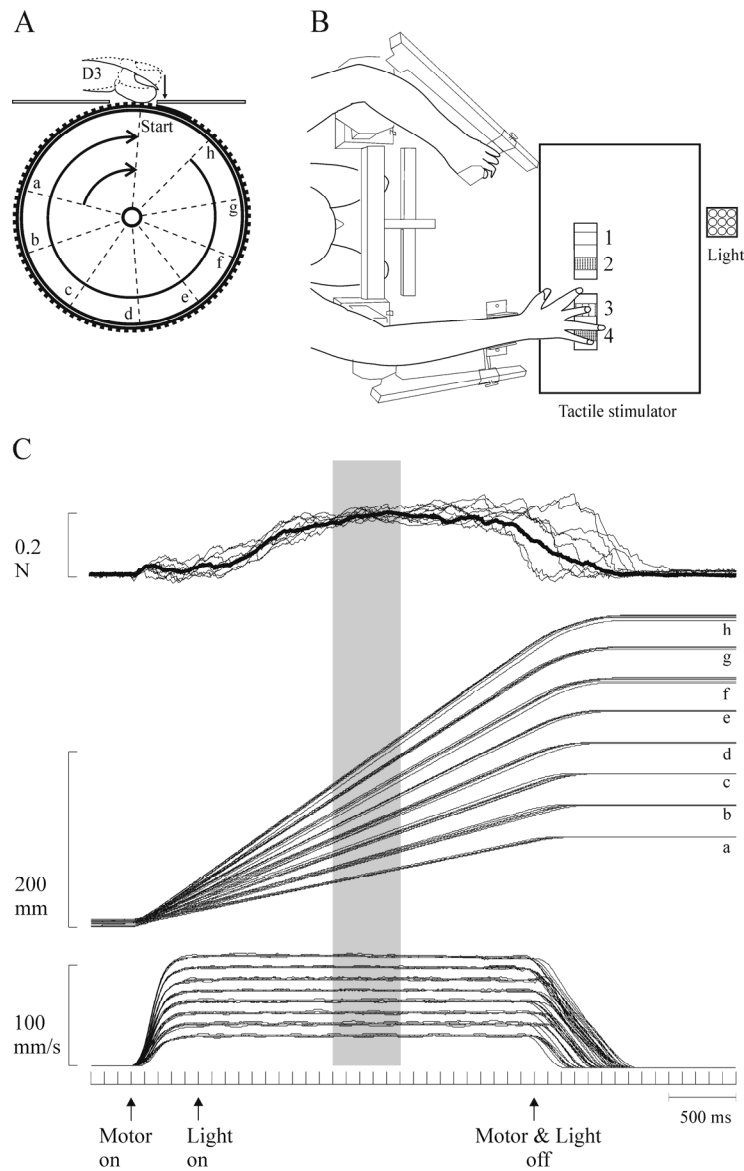


Figure 2 **A:** Lateral view of the tactile stimulator showing one surface (2 x 40 cm) affixed around its circumference. During the trial, the drum was rotated under the finger (see arrows) from the start to the end position (a-h); the length of surface presented varied with the scanning speed (a, shortest segment = slowest speed; h, longest segment = highest speed; see also C). **B:** Subject position during the experiment, with D3 positioned over the surface to be contacted during the upcoming trial (position 3, corresponding to one of the 3 textured surfaces). **C.** Events during the trial along with the force, position and speed measures from 1 subject. All trials are shown for drum position (middle) and speed (bottom). Contact force (top) was variable across trials, so only the mean for each speed (along with the grand mean, bold) is shown. Eight different speeds were tested; for higher speeds, drum rotation was correspondingly increased (a-h). Contact force was measured in a 500 ms window during the force plateau (shaded area).

Tactile stimulator.

The strips were affixed to a tactile stimulator (Fig. 2B, 4 strips tested in experiments 1 and 2; 3 strips in experiment 3). This consisted of a cylindrical drum (40 cm circumference, 12 cm length) mounted on a drive shaft that was rotated by means of a DC motor through a 100:1 reduction gear (Zompa and Chapman 1995). The surfaces were accessible for palpation by the pad of the distal phalanx of the middle finger through two rectangular apertures (6.5 x 2.5 cm each, Fig. 2B). The direction of the scan was proximal to distal relative to D3 (Fig. 2A, arrows).

Experimental setup.

The subject was seated (Fig. 2B), with the tactile stimulator at waist level. Ambient light was reduced to avoid any visual cue concerning the surface and its speed. White noise was delivered through earphones to eliminate any auditory cue from the rotation of the drum. Both arms were comfortably supported on two horizontal manipulanda. The right one was positioned so that, during the inter trial interval, the distal phalanx of D3 rested just above the surface to be scanned. A yellow light (2 x 2 cm) was placed at eye level and 1.2 m distance in front of the subject. This cued the subjects to lower their finger onto the moving surface (see below).

Perceptual task.

Before the experiment, the subjects were informed that surfaces would be displaced under the distal pad of D3 at different speeds. They were asked to estimate the speed of the surface motion. The subjects were free to choose a comfortable

contact force while touching the surface in motion, and were requested to use the same force throughout the experiment. No force feedback was provided during the trials, apart from the occasional reminder to use a relatively constant force. They were not informed about the number of speeds or surfaces used. Six practice trials were first performed to familiarise the subjects with the various events in the trial (see below). The subjects were then provided with sample stimuli so that they could establish their own scale: one surface (3 mm SP or the corresponding non periodic surface) was presented at three different speeds, the slowest, the fastest, and then one intermediate. The subjects were told that these were three illustrative examples, and were asked to estimate the perceived speed of the last trial (intermediate) using any representative whole number. Thereafter, data collection began.

Experimental design.

For experiments 1 and 2, each session consisted of two blocks of trials (textured, smooth); experiment 3 had only a single block of trials (textured). In the first block, the three textured surfaces (periodic or non periodic) were presented at eight different nominal speeds: 33, 43, 53, 65, 76, 86, 98 and 110 mm/s. Speed increments averaged 11 mm/s (range, 10 – 12 mm/s). The actual speed varied slightly from the nominal speed (< 1.2%). Figure 2C shows the superimposed force, displacement and speed profiles from one subject. Each surface-speed combination was repeated six times for a total of 144 trials. A pre-established pseudo-random list of trials that interleaved the three surfaces and the eight speeds was used. In the second block of trials (experiments 1 and 2), only the smooth surface was presented (8 speeds * 6 repetitions, total of 48 trials).

During the inter trial interval, the drum was rotated to the start position (Fig. 2A, Start). The subject was then asked to position D3 over one of the surfaces (position 1, smooth; 2-4, textured). After the subjects signalled their readiness, the trial was initiated by the experimenter. The temporal sequence of events in the trials is shown in Fig. 2C. Drum rotation began 0.3 s after the start of data acquisition; this was followed by the light onset (0.8 s). The light signalled the subjects to quickly lower their finger onto the surface that was already in motion and estimate its speed. The light was extinguished 2.5 s later; this was the cue for subjects to raise their finger, ending their contact with the surface. At the same time, the signal for drum rotation ended. Due to inertia, drum rotation ended 200-600 ms later depending on the speed, generally after contact with the surface ended. Thereafter, the subjects provided their numerical estimate of the perceived speed. At the end of the session, the subjects were debriefed and questions posed as to the strategy for rating speed, as well as the number of speeds and surfaces presented.

One critical element in the experimental design was that the duration of all presentations was identical (3 s), thus ensuring that the subjects had no temporal cue, specifically stimulus duration, on which to base their subjective magnitude estimate of speed. This was achieved by increasing the length of surface presented for higher speeds (see Fig 2A and C, a-h) from 99 mm (33 mm/s, a) to 330 mm (110 mm/s, h). Higher speeds could not be tested, as this would have required more than one revolution of the drum, and so the subjects would have felt the gap where the two ends of the 400 mm long strip met.

Data acquisition and analysis.

The task and data acquisition were under computer control. Digital events (times of onset and offset of drum rotation, light signal), and vertical contact force (200 Hz digitization rate) were recorded for each trial. The subjective magnitude estimate was entered by the experimenter and stored with the trial. If the subject felt uncomfortable or was unable to estimate speed after the trial, the trial was rejected and repeated later. Contact force was visually inspected on-line, and the trial was rejected and later repeated if the contact force during the scan varied by more than ~ 0.2 N.

To pool the data, magnitude estimates were normalised off-line by dividing each subject's responses (raised dot and smooth surfaces) by the arithmetic mean value of all the estimates given for the *raised dot* surfaces during the same session. The grand mean (textured and smooth surfaces) was not used for normalization because one experiment, 3, did not include a block of smooth trials. Thus the results of experiments 1 and 2 would have been skewed relative to the final experiment, making direct comparisons impossible. The normalised values were used for the subsequent statistical analyses.

For each trial, the speed of surface motion was calculated over the time that speed was constant (from 300 ms after motor onset to motor offset, see Fig. 2C). These data were also used to calculate the temporal frequency of the stimulus (speed/mean SP in the direction of the scan). For each trial, we measured contact

force during the scanning period over a 500 ms period of constant force (shaded rectangle, Fig. 2C).

The statistical analyses employed parametric tests since the data were normally distributed (Shapiro-Wilk normality test) and showed similar variances. For the magnitude estimates, an analysis of variance (ANOVA, Systat version 11) was applied to the data from each subject (scanning speed, surface included as factors). For the pooled data, a repeated measures model was used (estimates/scanning speed, surface). To describe the nature of the relationship between subjective magnitude estimates and the objective (tactile) speed of the surfaces, linear regression analyses were applied to the data obtained from each subject. The level of significance was fixed at $P < 0.05$.

Results

All subjects were able to scale the speed of the textured surfaces and showed a monotonic relationship between perceived speed and objective speed (linear regressions, $P < 0.0005$).

Periodic surfaces (experiment 1).

The individual psychophysical curves, mean normalized magnitude estimates as a function of scanning speed, are plotted in Fig. 3A. Inspection of the individual curves indicates that the results were similar for the three periodic surfaces with SPs of 2 mm, 3 mm, and 8 mm. The data of each subject were subjected to an ANOVA: speed was a significant factor for all subjects and SP for 6/8 subjects. No subject showed a significant interaction (speed x SP). The pooled results, plotted in Fig. 4A,

indicate that subjective magnitude estimates of speed were lower for the roughest surface (8 mm SP) as compared to the smoother surfaces. A repeated measures ANOVA applied to the pooled data confirmed that subjective magnitude estimates varied as a function of SP, as well as scanning speed (Table 2), with no interaction between the two factors. The nature of the relationship between subjective speed and objective speed was examined using linear regression analyses applied to the data from each subject. The mean slope (m), intercept (b) and coefficient of determination (r^2) are summarized in Table 3. For all 3 surfaces, the r^2 values were high (0.551 – 0.703). While slopes were closely similar across the 3 surfaces (0.013 – 0.014), a repeated measures ANOVA showed that the intercepts varied across the 3 SPs [$F(2,14) = 4.886$, $P = 0.025$], being lower for the 8 mm SP surface (mean of -0.05) as compared to the other two surfaces (means of 0.15 and 0.12, respectively). The latter impression was confirmed with post hoc contrasts ($P = 0.036$ for both). Overall, subjective magnitude estimates were significantly lower, mean 17.1%, for the surface with the largest SP. A multiple regression analysis indicated that the major part of the variance of the subjective magnitude estimates was explained by scanning speed (75%), as compared to only 18.5% for SP.

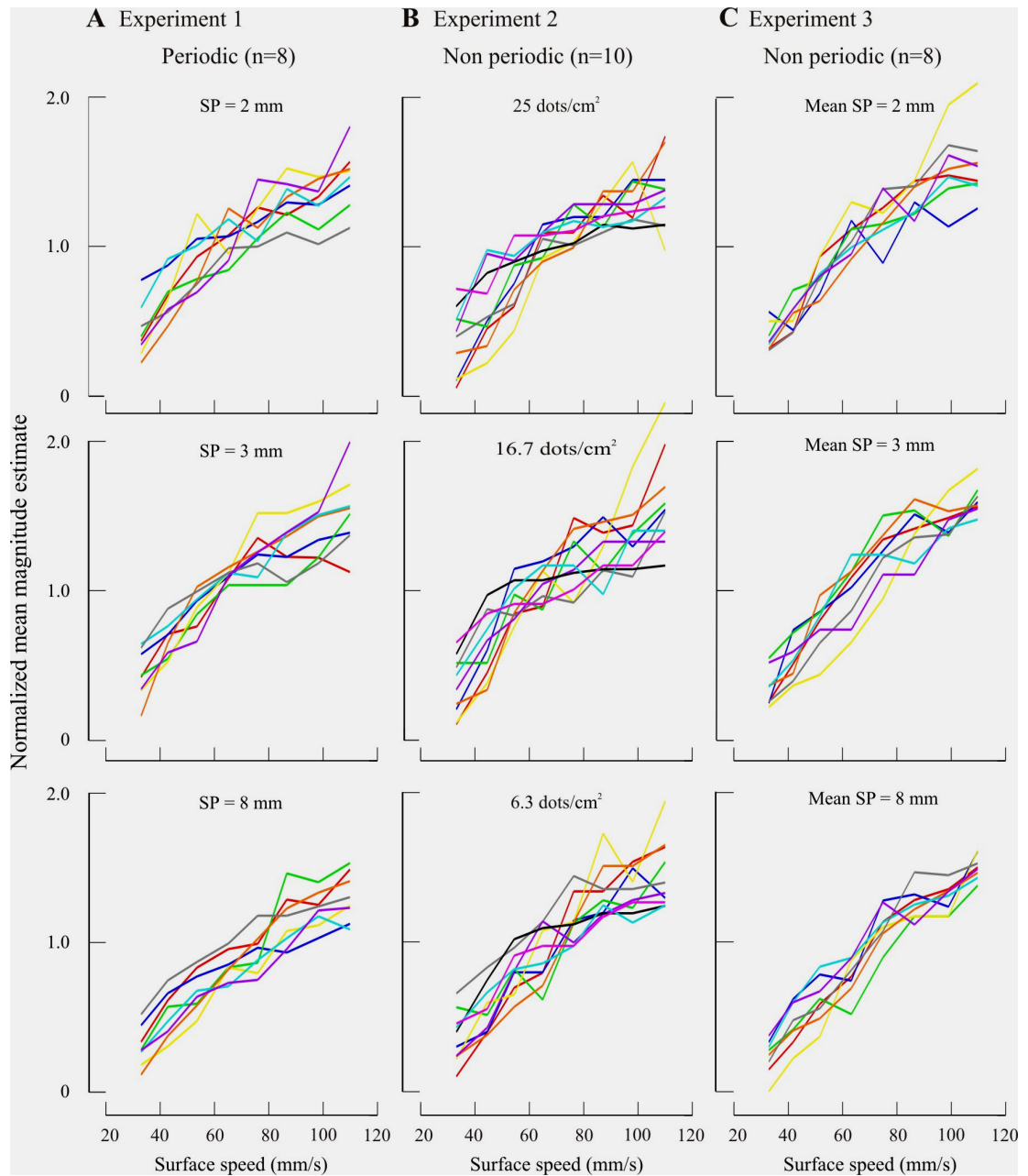


Figure 3 A, B, and C: Individual results from 3 experiments in which subjects estimated the speed of moving textured surfaces. Mean normalized subjective magnitude estimates of speed are plotted in relation to scanning speed. Separate plots are shown for each surface (colour-coded for each subject across the 3 surfaces used in each experiment). Note that different subjects participated in each experiment.

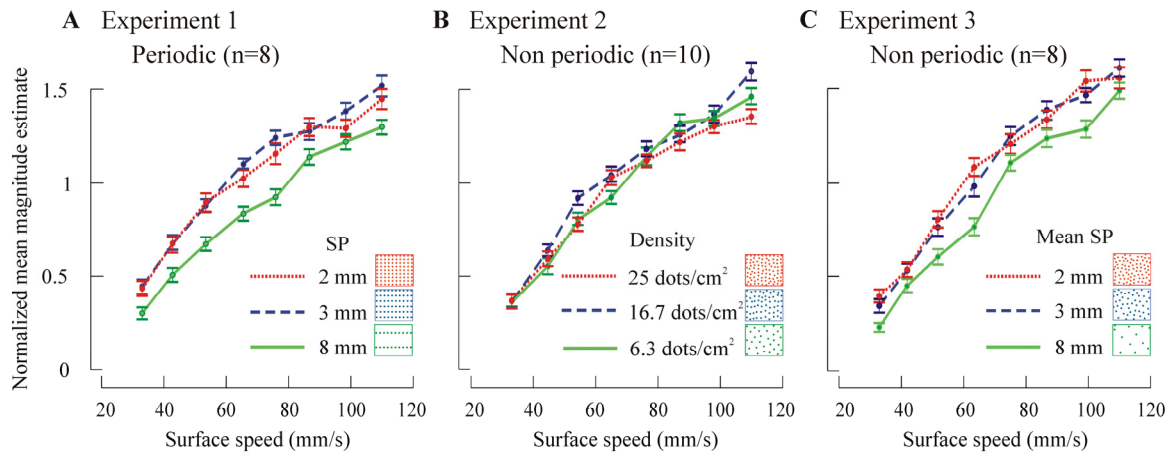


Figure 4 A, B, and C: Pooled data from the 3 experiments. Mean normalized magnitude estimates (\pm SEM across all estimates) are plotted as a function of scanning speed, and the spatial characteristics of the scanned surface.

Non periodic surfaces (experiments 2 and 3).

The surfaces used in experiment 2 preserved the same number of dots as in experiment 1, but their disposition was different, quasi-random versus periodic. The individual results for 10 subjects (different from those used in experiment 1) are plotted in Fig. 3B. Once again, the results were similar for all three non periodic surfaces with densities of 25, 16.7, and 6.3 dots/cm². Speed was a significant factor in all cases, but dot density was only significant in 3 of 10 subjects (ANOVA). None of the subjects showed an interaction between speed and dot density. The pooled results (Fig. 4B) showed there was considerable overlap across the 3 curves. The repeated measures ANOVA (Table 2) was significant for speed but not dot density. Consistent with these observations, the results of the linear regression analyses indicated that neither the intercepts [$F(2,18) = 1.34, P = 0.29$] nor the slopes ($F = 2.33, P = 0.13$) showed a change across the 3 surfaces. Finally, a multiple regression indicated that dot density contributed only 1.2% to the variance in subjective magnitude estimates

of speed, as compared to 75% for tactile motion itself. Thus, subjective speed did not systematically vary across the three non periodic surfaces.

The results of experiment 2 suggested that periodicity, and not the number of raised dots, may have contributed to the underestimation of speed for the 8 mm SP surface in experiment 1. Another explanation for the difference was, however, that dot spacing, and not periodicity, was responsible for the underestimation of speed for the 8 mm SP periodic surface. Dot spacing (SP) in the direction of the scan was different for each series: 2 – 8 mm (periodic) versus 2 – 4.9 mm (non periodic). This factor was controlled in experiment 3 (non periodic surfaces, mean dot spacings of 2, 3 and 8 mm). The individual psychophysical curves are summarized in Fig. 3C, and the pooled data are shown in Fig. 4C. The results were now very similar to those obtained in experiment 1, with subjective magnitude estimates of speed being lower for the roughest surface, 8 mm mean SP, as compared to the two smoother surfaces (2 and 3 mm mean SP). As in experiment 1, the individual ANOVAs showed that speed was a significant factor in all cases, and mean spacing was significant in a majority of subjects (5/8). Both factors were significant in the pooled analysis (Table 2). No significant interactions were found either in the individual or pooled analyses. As for experiment 1, the intercepts of the linear regressions varied across the 3 surfaces [$F(2,14) = 5.853$, $P = 0.014$], and slope showed no change (Table 3). The intercepts were lower for the surface with an average 8 mm SP (-0.26) compared to the other two surfaces (means of -0.07 and -0.15); the difference was, however, only significant between the two extremes (post hoc contrast, 8 versus 2 mm, $P = 0.012$). As in experiment 1, the major part of the variance of the subjective magnitude

estimates was explained by tactile speed (81.8%), as compared to only 14.2% for SP. Overall, subjective speed was, as found for the periodic surfaces, systematically lower, 14.6%, for the surface with the largest average SP, 8 mm. This finding suggests that dot spacing, and not periodicity, was the critical factor for the speed underestimates with the roughest surface.

Table 2 Results of repeated measures ANOVAs for experiments 1 (n=8), 2 (n=10) and 3 (n=8).

	<u>Speed</u>			<u>SP or Density</u>			<u>Interaction</u>		
	F	df ¹	P	F	df	P	F	df	P
Experiment 1	89.16	7, 49	<0.0005	8.34	2, 14	0.004	0.84	14, 98	0.625
Experiment 2	58.42	7, 63	<0.0005	1.53	2, 18	0.243	1.64	14, 126	0.078
Experiment 3	173.89	7, 49	<0.0005	6.33	2, 14	0.011	1.68	14, 98	0.073
Smooth/Expt 1	10.55	7, 49	<0.0005						
Smooth/Expt 2	12.55	7, 63	<0.0005						

¹Degrees of freedom

Smooth surface

In experiments 1 and 2, subjects also estimated the speed of a smooth surface displaced under the finger tip. In order to compare directly across the two sets of results obtained from the same subjects in the same experimental session (smooth versus textured), the smooth estimates were normalized using the corresponding mean from the textured surfaces. The individual and pooled (thick line) psychophysical curves are plotted in Fig. 5. The results were much more variable across subjects than for the main experiments. Moreover, some subjects initially found it difficult to even perceive the movement of the smooth surface. As there was no difference between the results obtained in the 2 experiments ($P = 0.48$, two-way ANOVA), the results were pooled. Overall, subjective magnitude estimates of speed for the smooth surface were $\sim 28\%$ lower than for the corresponding raised dot surfaces ($P < 0.0005$). Most subjects (15/18) could, nevertheless, scale the speed of the smooth surface (linear regressions, $P < 0.05$). The slopes of the regressions were significantly lower than for the corresponding textured surfaces ($P < 0.0005$; see Table 3). This latter result was independent of the normalization procedure because slope was still significantly lower ($P=0.001$) when these data were normalized relative to the mean of all ratings given during the block of trials with the smooth surface. The r^2 values were also lower ($P < 0.0005$), explaining only 28% of the variance in the subjective magnitude of speed, as compared to 55 - 70% for the raised dot surfaces in the same subjects. Finally, although subjects may have changed their rating scale across the blocks of trials (smooth, textured), all subjects commented that the speeds used during the smooth trials were lower than in the textured trials.

Together, the results indicate that subjects had difficulty in scaling speed in the absence of raised dots on the surface.

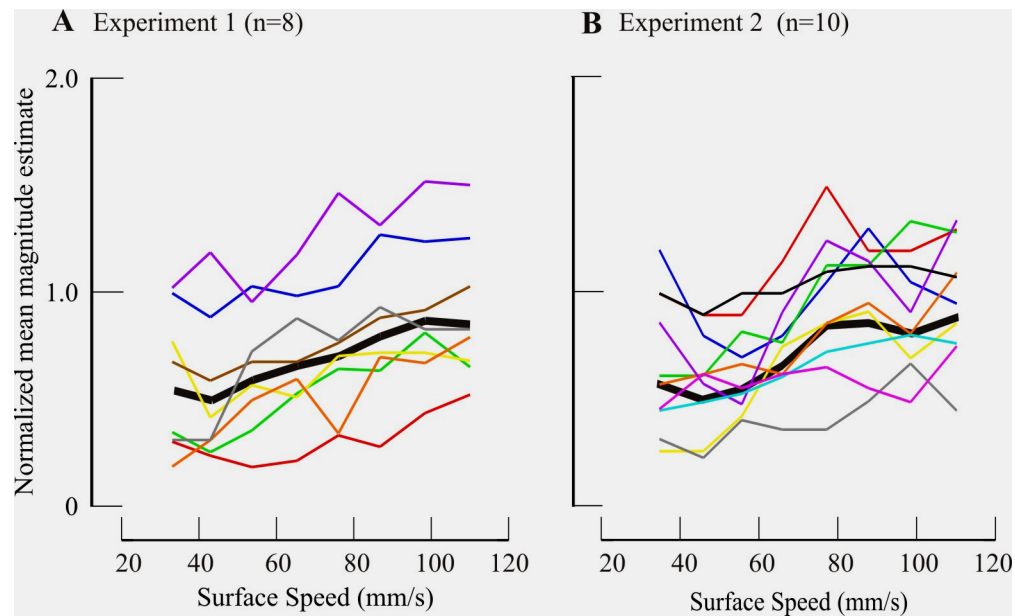


Figure 5 Individual (thin lines) and pooled (thick, black line) results for subjects estimating the speed of a moving smooth surface. Plotted as in Fig. 3 (same colour code). Inter subject variation was high. In addition, subjective speed was lower than for the corresponding texture trials.

Stimulation conditions. For each trial, normal contact force during the exploration was calculated off-line for a period of 500 ms during the scan (shaded rectangle, Fig. 2C). Contact force was under the subject's voluntary control and normal force varied across subjects (ANOVA, $P < 0.0005$). Mean force was higher for the textured surfaces (0.47 ± 0.02 N) than for the smooth surface (0.29 ± 0.02 N) (paired t-test: $P = 0.001$). This observation likely reflects the fact that the coefficient of friction relative to the skin (tangential/normal force) is higher for these raised dot surfaces as compared to the smooth surface (Cadoret and Smith 1996; Smith and Scott 1996; Smith et al. 2002a). In general, subjects used relatively low contact forces, lower than

those used during texture estimation with this same tactile stimulator (Meftah et al. 2000), but comparable to those used during active tactile exploration (Smith et al. 2002b). To determine whether variations in contact force contributed to the results in the main experiments (subjective magnitude estimates for the raised dot surfaces), we categorized the applied force into two categories, low or high contact force, for each speed. The results of one subject are shown in Fig. 6A. Contact force showed no change across the range of speeds tested (left), and magnitude estimates likewise did not vary with contact force (right). Similar results were obtained with the pooled data (Fig. 6B – D). Thus, variations in contact force did not contribute significantly to the results obtained with the textured surfaces.

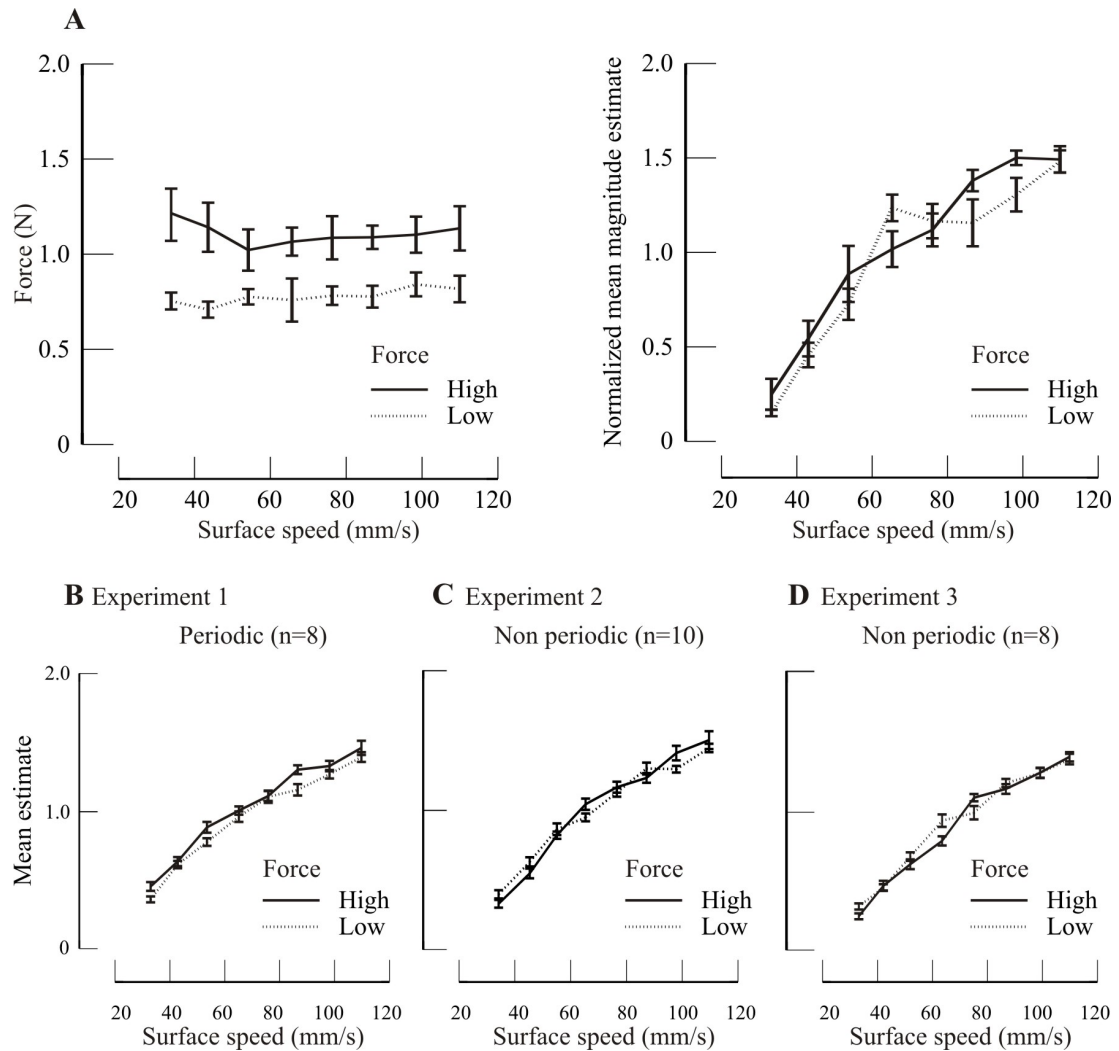


Figure 6 Contribution of vertical contact force to the results. **A:** Results from one subject (experiment 1). On the left, data from each speed were divided into low and high contact forces. Contact force during scanning was low and independent of speed, yet varied across trials (low vs high force). On the right, magnitude estimates for the same subject did not vary with contact force. **B, C and D:** Pooled results from experiments 1, 2 and 3 showing that subjective speed did not vary with contact force, low versus high. All data shown with SEM.

Subject comments. Most subjects (21/26) correctly recognized that each surface touched was different from the others. They estimated that about 7 to 9 different speeds were employed for the textured surfaces, although there were differences between subjects (range, 5 to 15 different speeds). For the periodic surfaces, subjects

reported that the smoothest of the textured surfaces (2 mm SP) seemed faster than the other textured surfaces. For the smooth surface, the subjects judged that there were fewer speeds (4 to 5) than for the textured surfaces and, as mentioned above, they also reported that the speeds were slower, consistent with the estimates given during the psychophysical testing. In addition, subjects often volunteered their estimate while the surface was moving, especially for the smooth surface.

Nature of the relationship between subjective magnitude estimates and tactile scanning speed.

The main analyses were based on the assumption that the relation between subjective speed and tactile speed could best be explained by a linear regression model. This was supported by the results of the single degree of freedom polynomial contrasts performed with the repeated measures ANOVAs (pooled data). In all 3 experiments, the linear relation had a higher F value than did higher order polynomial tests. Nevertheless, power functions have been used in previous studies to describe the relation between tactile speed and either the firing rates of peripheral afferents (Essick and Edin 1995; Greenspan 1992) or speed scaling (Essick et al. 1988). In all cases, the range of scanning speeds was much larger than that used here (e.g.; 5 - 320 mm/s for Essick and Edin; 0.4 – 1000 mm/s for Greenspan). In order to compare the 2 approaches, the pooled data from each experiment/surface were fit to both linear and power functions. The r^2 values with the power functions were systematically higher than with the linear regression analyses, but the difference was very small (mean difference, 0.027). Moreover, the exponents of the power functions were close

to 1 (1.12 – 1.34), i.e. close to a linear function. Together the results suggest that our data were well fit by linear functions.

To determine the extent to which temporal cues related to the surface structure, specifically the frequency with which the raised dots passed over the skin (temporal frequency = speed/mean SP in the direction of the scan), contributed to the results, we plotted the scaling estimates for each surface and each experiment as a function of temporal frequency. Such an analysis has been used previously to argue for the importance of temporal cues to roughness appreciation (Casio and Sathian 2001; Gamzu and Ahissar 2001; Morley and Goodwin 1987). If temporal frequency was the sole determinant of tactile motion estimates, then the subjective magnitude estimates of speed would be expected to show a monotonic increase with temporal frequency. As shown in Fig. 7A-C, however, families of non overlapping curves were obtained for each experiment (green, roughest surface; purple, intermediate; red, smoothest). Estimates reflected more the actual tangential scanning speed (same speeds joined by isocontour lines, see Fig 7A) than the temporal frequency. A 4-fold increase in temporal frequency, for example from 13.8 Hz (8 mm SP at 110 mm/s) to 55 Hz (2 mm SP at 110 mm/s (Fig. 7A), led to only a 12% increase in roughness estimates. These data were subsequently reduced to a single monotonic continuum (overlapping green, purple and red curves, Fig. 7 D-F) by “normalizing” the results to the same spacing (all ratings divided by the mean SP in the direction of the scan), and plotting the results as a function of temporal frequency. To determine the net effect of the transformation, an r^2 total value (3 surfaces pooled together) was calculated for each subject from the linear regression, estimates/SP versus temporal frequency. The

mean values are shown on Fig. 7D-F. Overall, the transformed data explained a significantly higher proportion of the variance in the magnitude estimates, 71 - 83% (paired t-test, $P < 0.0005$), than did the untransformed data, 62 - 72% (Table 3, note that these were separate calculations for each surface, averaged together for the comparison). Moreover, repeated measures ANOVAs demonstrated that the transformation abolished the significant change in intercepts across SP for the two experiments with the same range of mean SP (experiments 1 and 3) [untransformed data, $F(2,28)=10.36$, $P < 0.0005$; transformed data, $F(2,28)=1.89$, $P=0.17$]. Together the results indicate that speed scaling is dependent on temporal frequency, but this ability is consistently modified by the spatial characteristics of the tactile stimuli.

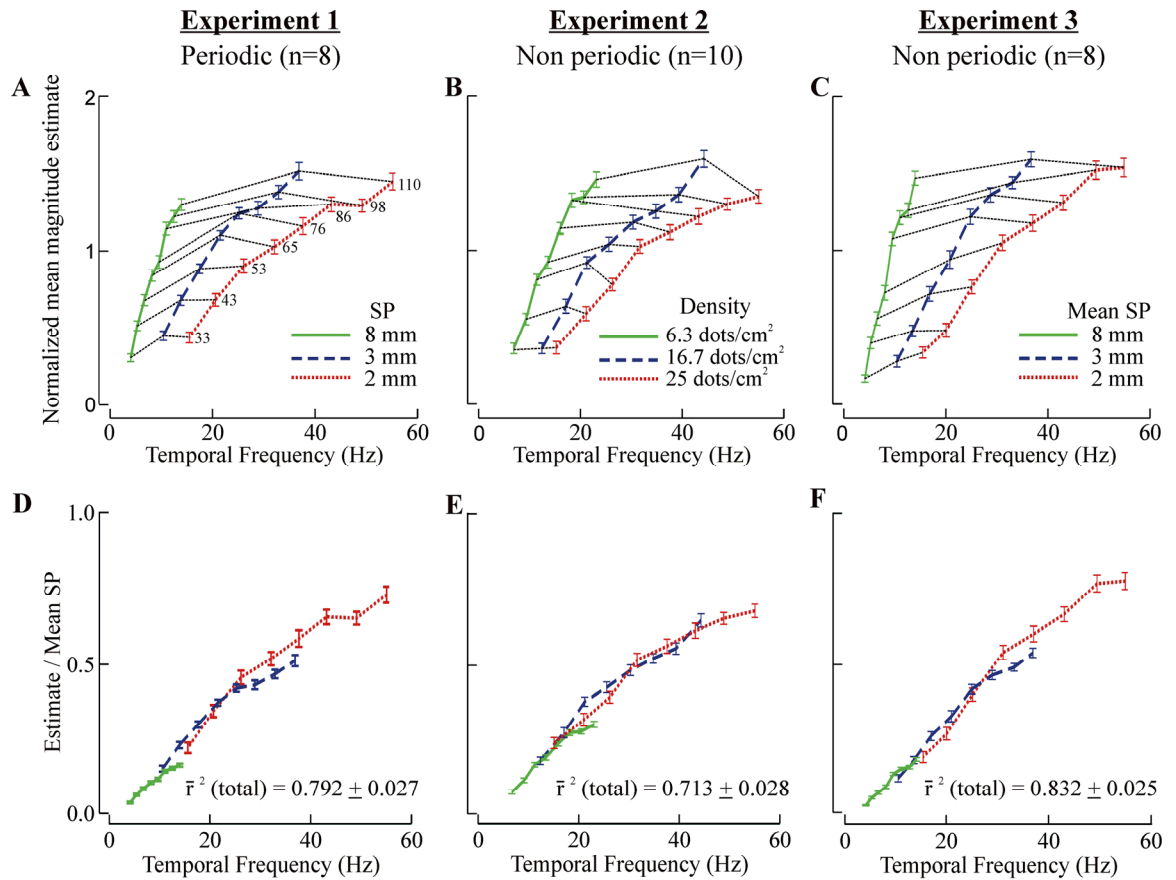


Figure 7 A, B and C: Mean normalized subjective estimates of speed (\pm SEM) plotted, for each surface and each experiment, as a function of the temporal frequency (scanning speed/mean SP in the direction of the scan). Isocontour lines join equivalent speeds (nominal speeds indicated in A). For each experiment, a family of 3 non overlapping curves was obtained. **D, E and F:** The magnitude estimates from A-C were themselves divided by mean SP, and are replotted relative to temporal frequency. This reduced the results from each experiment to a single continuum relative to temporal frequency. The mean r^2 total values (\pm SEM), estimate/SP versus temporal frequency (individual subject analyses), are indicated.

Contribution of periodicity to the results

Although the transformation of the results (above) indicated that periodicity did not contribute to the results, we considered the possibility that the subjective magnitude estimates might have been more reliable (less variable, lower SEM) when

the events were regularly spaced (periodic surfaces) as compared to irregularly spaced (non periodic surfaces). To address this, the data from the two experiments that were matched for dot spacing are plotted together in Fig. 8. The magnitude estimates were pooled across all SPs, and the SEMs were calculated from all trials. Inspection shows that the two curves, periodic (solid line) and non periodic (interrupted line), were superimposed with, if anything, a steeper slope for the non periodic surfaces (see also Table 3). Although the SEMs were not obviously different, we also computed the SEM for each speed and texture in each subject. A repeated measures ANOVA showed a modest increase in the variability of the magnitude estimates for the non periodic surfaces as compared to the periodic surfaces ($P=0.022$), corresponding to a 0.9% increase in variability for the former when expressed as a % of the mean ratings (9.1% for periodic surfaces, 10% for non periodic surfaces). Thus, while stimulus regularity contributed to the results, the effect was small.

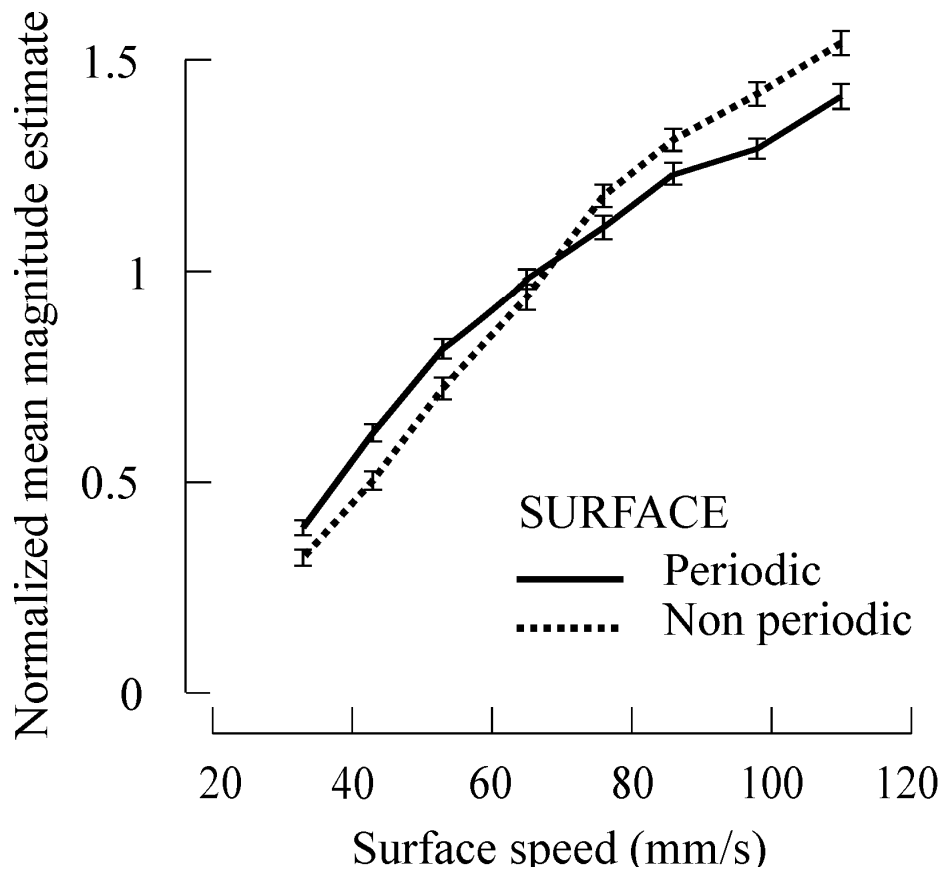


Figure 8 Overall mean normalized subjective estimates of speed (\pm SEM) for experiments 1 (periodic) and 3 (non periodic) plotted as a function of tactile scanning speed. The data from the 3 SPs were pooled (\sim 140 trials per data point; 8 subjects in each experiment).

Table 3 Mean values of the parameters (\pm SEM) describing the linear regressions, mean normalized magnitude estimates versus speed, for each surface in each of the 3 experiments.

	Dot spacing*	Slope	Intercept	r^2
Expt 1, Periodic (n=8)	Smooth	0.005 ± 0.001	0.353 ± 0.108	0.278 ± 0.044
	2	0.013 ± 0.001	0.149 ± 0.096	0.551 ± 0.049
	3	0.014 ± 0.002	0.115 ± 0.099	0.661 ± 0.055
	8	0.013 ± 0.001	-0.049 ± 0.089	0.703 ± 0.025
Expt 2, Non periodic (n=10)	Smooth	0.005 ± 0.001	0.340 ± 0.095	0.279 ± 0.074
	2	0.013 ± 0.002	0.071 ± 0.120	0.586 ± 0.039
	2.5	0.015 ± 0.002	0.012 ± 0.131	0.601 ± 0.039
	4.9	0.014 ± 0.001	-0.031 ± 0.105	0.667 ± 0.030
Expt 3, Non periodic (n=8)	2	0.016 ± 0.001	-0.071 ± 0.061	0.670 ± 0.056
	3	0.017 ± 0.001	-0.147 ± 0.087	0.725 ± 0.026
	8	0.016 ± 0.001	-0.260 ± 0.072	0.756 ± 0.040

*Mean spatial period in the direction of the scan.

Abbreviation: r^2 : coefficient of determination

Discussion

The present study showed that humans can estimate tangential tactile motion across a range of behaviourally relevant speeds, and this in the absence of explicit cues related to stimulus duration. We also demonstrated that subjective magnitude estimates of scanning speed covaried with surface texture, consistent with single unit recordings which indicate that information about speed and surface texture is confounded in the signals of peripheral mechanoreceptive afferents (see Introduction). Figure 7 suggests that speed and texture signals, at least as relates to tactile motion perception, may remain confounded at all levels of processing within the CNS.

Present results

To the best of our knowledge, this is the first demonstration that subjects can scale tactile speed in a situation in which stimulus duration was held constant. Thus, the only source of information on which subjects could base their estimates was tangential motion of the surfaces under the fingertip. All subjects showed a monotonic increase in their subjective magnitude estimates as scanning speed increased, with virtually identical slopes for the psychometric curves across a range of textured surfaces. The ability to scale tactile motion was, however, critically dependent on surface structure. When subjects rated the speed of a smooth surface, their magnitude estimates of speed were significantly lower as compared to the results obtained with textured surfaces in the same subjects. Moreover, while all subjects were able to scale the speed of the textured surfaces, some were unable to

scale the speed of the smooth surface. This latter observation was not explained by lack of familiarity with the task, as testing with the smooth surface occurred, in all cases, after the subject had already performed the experiment using the textured surfaces. While the dramatically lower r^2 values for the psychometric functions (44-45% of the values from the textured surfaces) might have reflected the contribution of other factors to the results obtained with the smooth surface, we believe that this finding more simply reflected the inability of subjects to scale the speed of the smooth surface. Consistent with this explanation, the slopes (smooth) were only one-third of the values for the textured surfaces.

The present results also showed that tactile magnitude estimates of speed were dependent on the spatial characteristics of the scanned surfaces. Specifically, the roughest surfaces (8 mm dot spacing) were estimated to move ~15% slower than the smoother, textured surfaces (2-3 mm dot spacing). This result was independent of dot disposition, since similar results were obtained with raised dots arranged in either periodic arrays of dots or quasi-randomly distributed across the surface. Dot density was likewise not responsible for the speed underestimates seen in the first experiment (periodic surfaces) since we were not able to reproduce this result when subjects rated the speed of non periodic surfaces matched for dot density (experiment 2). In creating the non periodic surfaces, however, the range of dot spacing in the direction of the scan was also altered, decreasing from 2 – 8 mm to 2 – 4.9 mm. The importance of this factor was addressed in the final experiment where we reproduced the initial results, but this time using non periodic arrays of raised dots. Thus, the underestimation of speed for the roughest surface (8 mm dot spacing) was attributed

to the spacing between dots in the direction of the scan, with the critical range being > 4.9 mm, the maximum spacing tested in experiment 2. This effect was, however, small relative to the main effects of tactile speed. Multiple regression analyses indicated that tactile motion explained 75 to 82% of the variance in the magnitude estimates of speed in the 3 experiments, as compared to only 14 – 19% attributed to dot spacing in experiments 1 and 3, and 1.2% in experiment 2.

Comparisons with previous studies

Earlier studies (Essick et al. 1988, 1996; Franzén and Lindblom 1976) reported that subjects can scale tactile speed, but stimulus duration covaried with speed in their experiments. Thus, it was not clear if subjects were scaling speed or stimulus duration. Indeed, Essick et al. actually proposed that stimulus duration was the key factor explaining their results. This likely explains why the mean exponent for the power functions fit to their data (0.61) was lower than the values obtained in the present study (1.12 to 1.34). Another explanation for the different results cannot, however, be discounted: the high exponents obtained here might reflect a difference between hairy and glabrous skin. Consistent with this suggestion, Essick and Edin (1995) reported that ~50% of RA afferents innervating the glabrous skin of the hand have exponents > 1 (mean discharge rate versus speed), while those innervating hairy skin have lower exponents. Further experiments are needed in order to address this latter possibility.

Methodological consideration

The speed range used here covers only partially the range studied by Essick et al. (1988, 1996), 5 to 640 mm/s. We were not able to test speeds > 110 mm/s because we were limited by the length of surface available for presentation (400 mm). This in turn was limited to the physical dimensions of the tactile stimulator. The tested range, 33 to 110 mm/s, nevertheless corresponds to a behaviourally important range of the tactile speeds. For example, subjects use speeds of 10 to 157 mm/s during tactile exploration (Smith et al. 2002a), and 60 to 190 mm/s during Braille reading (Grunwald 1966).

Friction

Friction, the ratio of tangential to normal force, may have been a contributing factor to the present results. The skin of the finger is compliant, and offers resistance to surface displacement. This resistance can moreover be higher for rougher surfaces. Thus, Smith et al. (2002a) showed that the rate of change of tangential force during active tactile exploration increases with surface roughness, at least for periodic surfaces with the same range of dot spacings as tested here. How this contributes to the subjective estimates of speed is not known. We found that normal force was constant across the speeds tested consistent with previous observations (Smith et al. 2002a,b) of invariances in normal force during active tactile exploration of smooth and textured surfaces, but technical limitations of our apparatus did not allow us to monitor tangential force. We can say, on the other hand, that the contribution of friction is likely to be complex: speed was underestimated with the roughest surface,

and this independent of dot disposition (periodic or non periodic). If friction had been a critical factor, then we would have expected a greater effect with the periodic surfaces as the regular and widely spaced rows should have offered more resistance than the randomly distributed dots, and so more friction. The results were, however, independent of dot disposition.

Mechanoreceptors contributing to encoding tactile motion.

For the smooth surface, the initial contact would have produced an initial stretch of the skin, activating discharge in all types of cutaneous mechanoreceptive afferents innervating the glabrous skin, SAI, RA and PC (Srinivasan et al. 1990). During the speed plateau, only SAI afferents would have continued to discharge given their sensitivity to skin stretch, although we cannot exclude a potential contribution from RA and PC afferents since the smallest imperfection on the smooth surface would have been sufficient to activate these receptors (LaMotte and Whitehouse 1986; Srinivasan et al. 1990; see also Bensmaïa and Hollins 2005). We believe that feedback during the speed plateau contributed little to the results since some of the subjects did not even perceive the motion of the smooth surface without prompting. Since subjects often volunteered their estimate while the smooth surface was still moving, we suggest that they likely gathered most of the relevant information from the initial contact with the moving surface. Contact with the moving surface would have been accompanied by both normal and tangential forces on the skin of the fingertip. We suggest that these signals were likely used to estimate the speed of the smooth surface, and that differences across subjects may reflect

differences in skin friction as a result of, for example, difference in skin moisture (see also above).

In contrast, all of the major cutaneous mechanoreceptive afferents contributing to discriminative touch were undoubtedly continuously activated when the textured surfaces were scanned over the skin. It is known that their discharge reflects not only the physical characteristics of the surfaces (texture), but also the parameters of stimulation, specifically speed and contact force (reviewed in Johnson 2001), most likely including tangential force as well as normal force (Birznieks et al. 2001; Smith et al. 2002a). It seems likely that all of these afferents may contribute to tactile speed scaling, although the relative contribution of each remains to be determined. Certainly there is evidence that all afferent types are sensitive to scanning speed, but the results vary depending on the physical characteristics of the stimulus (Edin et al. 1995; Essick and Edin 1995; Goodwin and Morley 1987; Greenspan 1992; Lamb 1983). The closest parallel can be drawn with Lamb's study: he recorded from primary afferents innervating the glabrous skin of the hand in the monkey as raised dot surfaces (1 or 2 mm SP) were displaced across the receptive field at different speeds. Within the range of temporal frequencies (speed/SP) used here, RA and PC afferent mean discharge increased with increased temporal frequency and so could account for the present results. Such a suggestion is consistent with Essick and Edin's (1995) observation that only RA afferents innervating glabrous skin (PC afferents not tested) have exponents > 1 (log mean discharge rate versus log speed), consistent with the exponents found here for the log-log plots (also > 1). Interestingly, SAI afferent discharge in Lamb's study was

constant over the same range of temporal frequencies. To exclude their contribution to the present results, however, a wider range of SPs, up to 8 mm, should be tested under the same conditions since there is some evidence (Goodwin and Morley 1987) that SAI afferents are sensitive to the speed of rougher surfaces (see their Fig. 4).

Roughness and subjective magnitude estimates of scanning speed

The present finding that magnitude estimates of speed covaried with surface roughness is in marked contrast to observations that roughness estimates themselves, measured using the same dot spacings as here (1.5 to 8.5 mm), are *independent* of scanning speed (Meftah et al. 2000). In the latter study, subjects scaled the roughness of periodic raised dot surfaces moved under the immobile fingertip at 50 or 100 mm/s (speeds randomly interleaved). Roughness estimates showed a monotonic increase with dot spacing, but were invariant over a two-fold increase in scanning speed and this for speeds within the range tested here. The latter observations were consistent with the predictions of the spatial variation code proposed by Johnson and colleagues (Connor et al. 1990; Connor and Johnson 1992; Blake et al. 1997; Yoshioka et al. 2001). They proposed that tactile roughness is signalled by differences in the firing rates of nearby SAI afferents, with the transformation into a simple intensive code occurring centrally. The spatial code cannot, on the other hand, explain tactile speed scaling and its dependence on tactile roughness because the code is insensitive to scanning speed (DiCarlo and Johnson 1999). Thus, tactile speed must be dependent on some other neuronal code, most likely a simple intensive code based on the firing rates of the peripheral mechanoreceptive afferents that are sensitive to both roughness and scanning speed (above). Our results also show that speed and texture signals, at

least as relates to tactile motion perception, may remain confounded at all levels of processing within the CNS. Consistent with this suggestion, the r^2 values reported here (Table 3) were lower than the corresponding values for subjective roughness estimates (Meftah et al. 2000), 0.551 – 0.756 versus 0.87 – 0.91, likely reflecting increased uncertainty about the speed estimates. Finally, we suggest that the discharge of central neurones contributing to tactile speed perception should vary with speed and texture in the manner shown in Fig.7D-F (see below).

Implications of the results

At a more general level, it may seem counterintuitive for the spatial properties of stimuli to influence speed perception, since this must ultimately be a temporal property. Nevertheless, the effects of space on speed scaling were reduced to a single monotonic continuum by “normalizing” the results to the same spacing and expressing the results as a function of temporal frequency (Fig. 7D-F). Thus, speed scaling was dependent on temporal, but also spatial, cues. In contrast, applying the same analysis to our previous roughness scaling data, generates a single curve, with a slope approaching 0 (not illustrated). Taken together, we suggest that the discharge of central neurones critically involved in speed or roughness scaling must follow these same patterns. In other words, the neurometric functions (discharge rate/SP versus temporal frequency) should show a monotonic increase for cells that might play a role in speed scaling. The corresponding neurometric functions for cells involved in texture scaling should be flat with a slope approaching 0.

Where this extraction of information occurs is, as yet, unknown. We do know that many neurones in areas 3b, 1 and 2 (S1, primary somatosensory cortex) and S2 (secondary somatosensory cortex) discharge in relation to both surface texture and scanning speed (Jiang et al. 1997; Pruett et al. 2000; Sinclair and Burton 1991, 1993; Tremblay et al. 1996). Moreover, lesions of S1 greatly impair the ability of monkeys to categorize tactile speed (Zainos et al. 1997). The present results provide a clear set of criteria which neurones critical for speed scaling must encounter.

Finally, the appreciation of properties such as speed and texture is not unique to the somatosensory system, but also extends to the visual system. Several studies have shown an interaction between visual speed scaling and the SP of moving gratings (Campbell and Maffei 1981; Diener et al. 1976; cf Smith and Edgar 1990). Most studies reported that a decrease in spatial frequency ($1/SP$) causes a decrease in perceived speed. Our results are consistent with these: the surface with the lowest spatial frequency, 8 mm (0.125) was perceived as moving slower than the surfaces with higher spatial frequencies (0.5 and 0.33 for, respectively, the 2 and 3 mm SP surfaces). In a similar vein, Watamaniuk et al. (1993) reported that decreasing the density of a field of moving dots decreases the perceived speed of visual dot motion. Our results extend this observation to the somatosensory system, but it should be noted that an effect was only seen with the lowest dot density used, 2.2 dots/cm², suggesting that dot density effects may be range limited. Together such findings suggest that important parallels exist between the somatosensory and visual systems as regards the processing of stimulus motion.

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Article # 2

**TACTILE PERCEPTION OF ROUGHNESS: RAISED-
DOT SPACING, DENSITY AND DISPOSITION.**

by

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Abstract

Recently, we showed that tactile speed estimates are modified by the spatial parameters of moving raised-dot surfaces, specifically dot spacing but not dot disposition (regular, irregular) or density. The purpose of this study was to determine the extent to which tactile roughness perception resembles tactile speed with respect to its dependence and/or independence of the spatial properties of raised-dot surfaces. Subjects scaled the roughness of surfaces displaced under the finger. Dot spacing (centre-to-centre) ranged from 1.5 to 8.5 mm in the direction of the scan (longitudinal). Mean dot density varied from 2.2 - 46.2 dots/cm². Dot disposition was varied: repeating rows (periodic) or quasi-random (non-periodic). In the first experiment (n=8), the periodic and non-periodic surfaces were matched for mean dot density. Roughness showed a monotonic increase with 1/dot density, but non-periodic surfaces were judged to be smoother than the periodic surfaces. Subjective equality was obtained when the data were re-expressed relative to longitudinal SP. In the second experiment (n=7), the periodic and non-periodic surfaces were matched for longitudinal dot spacing. Perceptual equivalence was observed when the results were plotted relative to dot spacing, but not 1/dot density. Dot spacing in the orthogonal direction (transverse) was excluded as a contributing factor. Thus, as found for tactile speed scaling, roughness is critically dependent on longitudinal dot spacing, but independent of dot disposition and dot density (over much of the tested range). These results provide a set of predictions to identify cortical neurones that play critical roles in roughness appreciation.

Introduction

Tactile surface texture can vary from smooth to rough, with surface asperities being absent for smooth surfaces (e.g. polished metal or fabrics like satin) and present for rougher surfaces (e.g. abrasive papers or burlap). The physical characteristics of the asperities, or tactile elements, contribute to the subjective impression of roughness (see below). Over the past 35 years, a number of investigations have studied the human ability to estimate the subjective roughness of a wide variety of textured surfaces, with the aim of determining the relative contribution of different physical factors to roughness. Such knowledge has been used to provide critical support for potential neural codes for tactile roughness, most notably the spatial variation code for roughness developed by Johnson and colleagues (Connor et al. 1990; Connor and Johnson 1992; Blake et al. 1997; Yoshioka et al. 2001), whereby local spatial variations in the firing rates of SAI (slowly adapting type I) mechanoreceptors are thought to account for the human perception of subjective roughness. This is a robust code which, being insensitive to scanning speed (DiCarlo and Johnson 1999), can explain observations that tactile roughness estimates are themselves also independent of scanning speed (Lederman 1974; Meftah et al. 2000).

Paradoxically, however, we recently reported that *tactile speed estimates* are dependent on tactile surface texture (Dépeault et al. 2008). Surface structure (texture) is essential because subjects are very poor at scaling the speed of a moving smooth surface. This finding suggests that the same afferent signals contribute, at least in part, to both tactile roughness and speed perception. This suggestion is supported by

our demonstration that tactile speed estimates are significantly modified by the physical characteristics of the textured surfaces. Using rectangular arrays of raised dots (“periodic” surfaces), we found that the surface with the greatest spacing between raised dots, 8 mm centre-to-centre, was judged to be moving 15% slower than surfaces with smaller spacings (2 or 3 mm). In other words, the roughest surface was judged to be moving slower than the smoother surfaces (Meftah et al. 2000). The critical factor underlying this interaction between speed and texture was *dot spacing in the scanning direction*, corresponding to the spatial period, SP, for regularly disposed dots. We excluded the possibility that this result could be explained by the disposition of the dots on the surfaces (regular or irregular) by showing that similar results were obtained using non-periodic surfaces in which case the dots were quasi-randomly distributed (versus periodic surfaces with regularly repeating rows of raised dots). We likewise excluded dot density (number of raised dots/cm²) as a contributing factor, at least over the range tested (6.3 – 25 dots/cm²). Thus, tactile speed estimates, much like tactile roughness estimates, are dependent on the spatial properties of the stimuli. These two sensory abilities diverge, however, in their sensitivity to the temporal properties of the stimuli (above): tactile roughness estimates are invariant across changes in scanning speed while tactile speed estimates – measured over the same range – covary with scanning speed.

The purpose of this study was to determine the extent to which these two perceptual abilities depend on the spatial properties of the tactile stimuli, specifically textured surfaces. This is a fundamentally important question because such

knowledge can give insight into the extent to which these two abilities may rely on common neuronal mechanisms.

While there is abundant evidence that tactile element spacing is critical for tactile roughness (see below), the relative importance of the other factors manipulated in our tactile speed studies (dot disposition, dot density) is less clear and has not been tested systematically. Early evaluations of the contributions of the physical characteristics of surfaces to perceived roughness used abrasive papers. These studies showed that perceived roughness increases as the grit value declines, but these findings are difficult to interpret because 3 factors covary: particle size, density and spacing (Stevens and Harris 1962; Verrillo et al. 1999; Hollins and Risner 2000). Specifically, rougher surfaces have larger particles, with greater spacing and lower density. Because of this difficulty in interpretation, later studies used simple, manufactured surfaces (machined metal plates or etched surfaces) which had the advantage of allowing the experimenter to systematically vary each physical parameter. The results to date indicate that the spacing between tactile elements is a key factor when the size of the tactile elements is kept constant (Lederman and Taylor 1972; Sathian et al. 1989; Connor et al. 1990; Connor and Johnson 1992; Meftah et al. 2000). In contrast, increasing the size of the tactile elements has conflicting effects: an increase in diameter or width leads to a modest decrease in perceived roughness (Lederman and Taylor 1972) while increasing the height of the elements (raised dots) results in increased roughness (Blake et al. 1997). Finally, the importance of the density of the tactile elements, especially for surfaces with randomly disposed elements (like abrasive papers), as compared to element spacing,

has yet to be determined since increased spacing is invariably accompanied by decreased density.

The purpose of this study was therefore to determine the extent to which tactile roughness resembles tactile speed in its dependence/independence on the detailed spatial parameters of raised-dot surfaces. As in our studies on tactile speed perception, subjects scaled the roughness of various textures that differed in dot spacing, dot disposition (periodic, non-periodic) and dot density. As expected, we found that roughness was critically dependent on the spacing between tactile elements; we extended this observation by showing that spacing in the direction of the scan, but not the orthogonal direction, is critical. We found that roughness shares several characteristics with tactile speed, since it is also independent of dot disposition as well as dot density over a wide portion of the range tested. A preliminary report of these results has been presented in abstract form (Dépeault et al. 2006).

Materials and methods

Subjects.

Sixteen naïve paid subjects (8 women and 8 men, 21 to 32 years old, all right-handed for writing except one), volunteered to participate in the study. The institutional ethics committee approved the experimental protocol, and subjects gave their informed consent before participating. Each subject participated in one 2-hr

session. The task was to estimate the roughness of surfaces displaced under their immobile, right middle fingertip (D3).

Surfaces.

The surfaces were prepared on flexible letterpress plate using a photographic process (Fig. 1A) (CML Printing Plates Inc., St. Léonard, QC). They were composed of raised dots [truncated cones: 1 mm high and 0.8 mm diameter (top)]. Examples of the surfaces used are shown in Fig. 1A. In the first experiment (8 subjects, equivalent dot density), dot disposition was systematically varied (periodic or non-periodic, see below) while matching dot density (mean number of dots/cm²) across the range of surfaces. In the second experiment (8 subjects, equivalent dot spacing), dot disposition was again varied, but this time dot spacing in the direction of the scan (longitudinal, measured centre-to-centre) was matched. The dot spacings used (see below) fell within what are generally considered to be relatively coarse surfaces.

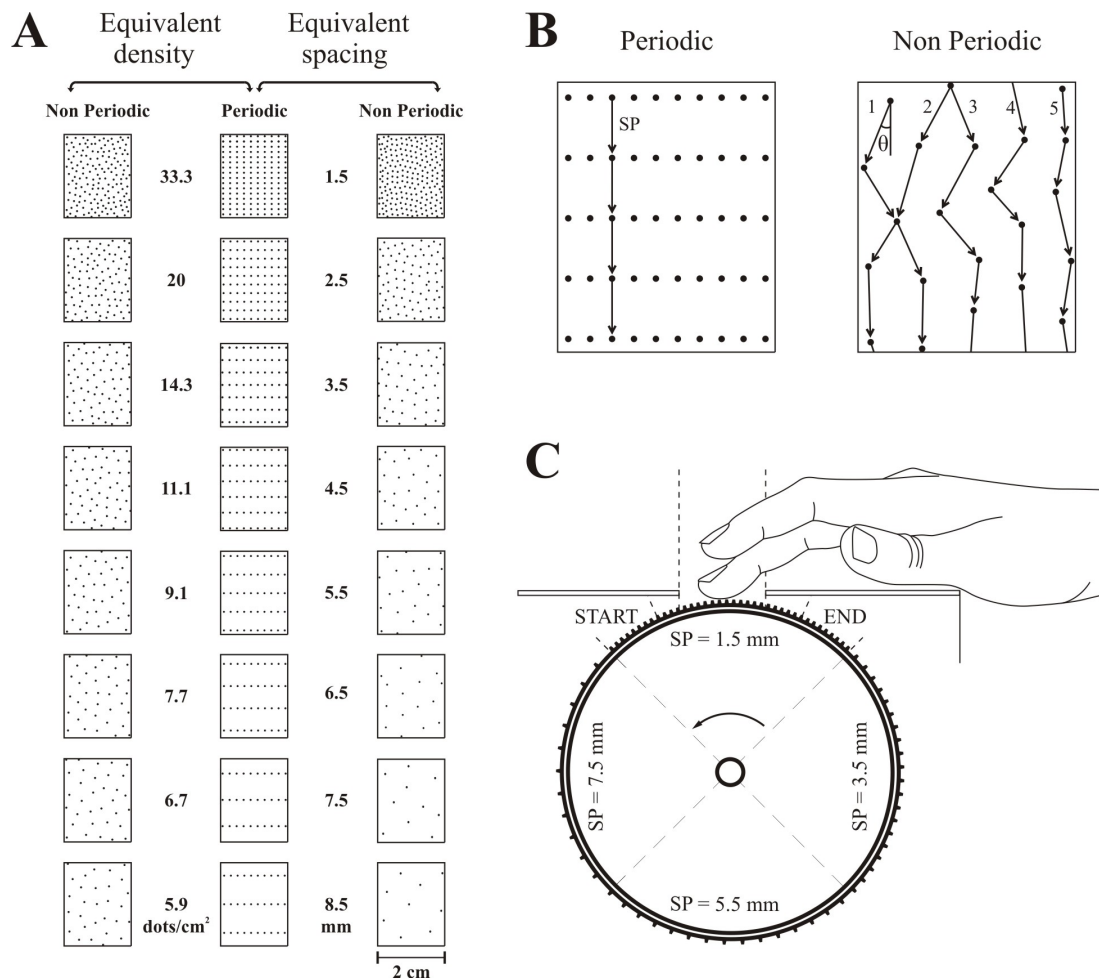


Fig. 1: **A.** Physical characteristics of the surfaces. Shown here are representative examples of the disposition of the raised dots on the surfaces (length truncated) for the surfaces used in experiment 1 (equivalent mean dot density; non-periodic and periodic) and experiment 2 (equivalent mean dot spacing in the direction of the scan; periodic and non-periodic). **B.** For the periodic surfaces (left), longitudinal dot spacing (in the direction of the scan, see arrows) corresponded to the centre-to-centre dot spacing between rows of raised dots. For the non-periodic surfaces (right), the dots were joined by travelling lines in the direction of the scan, and average dot spacing was measured. See Methods for details. Similar measures were made for the orthogonal direction (transverse dot spacing). **C.** Lateral view of the tactile stimulator. The surfaces were affixed around the circumference of the drum (4 strips of 4 textures each/experiment: 2 x periodic and 2 x non-periodic). Access to the surface was via an opening on the top of the stimulator. Surfaces were explored with the right middle fingertip (direction of scan indicated by the arrow). The finger was in contact with the surface only while the drum was moving.

For each experiment, four 40 cm-long strips (2-cm wide) were prepared. Each strip was subdivided into 4 segments of equal length, 10 cm, to give a total of 16 surfaces. Dot disposition was regular for 8 surfaces in each experiment (periodic), and quasi-random (non-periodic) for the other 8 surfaces. The periodic surfaces were the same for both experiments.

For the *periodic surfaces*, dot spacing varied between rows (corresponding to the direction of the scan or longitudinal spacing), from 1.5 mm up to 8.5 mm with 1 mm increments (Table 1 and Fig. 1A). These rectangular matrices of dots had constant dot spacing within each row (transverse spacing, 2 mm). For the first experiment, the 8 non-periodic surfaces had the same numbers of raised dots as the periodic surfaces, so that mean dot density was matched. The non-periodic surfaces were generated by taking each of the periodic dot matrices and “jittering” the dots in the matrix (Lederman et al. 1986) maintaining, on average, the same spacing between adjacent dots (see Fig. 1B, right). Mean dot spacing ranged from 1.5 to 5 mm in the direction of the scan; a similar range was obtained for the orthogonal direction (Fig. 1A and Table 1; paired t-test, $P = 0.16$). For the second experiment, the template for the *non-periodic surfaces* used in experiment 1 was pruned (dots removed) so that the mean dot spacing in the scanning direction was closely similar to that of the periodic surfaces (Fig. 1A; precise values in Table 1). Note that mean dot spacing in the orthogonal direction spanned almost the same range ($P = 0.26$). Thus, this series preserved the same mean spacing in the direction of the scan, but dot density was no longer matched (Table 1).

Table 1 Physical characteristics of the textured surfaces.

Longitudinal spacing (mm)			Transverse spacing (mm)			Dot density (dots/cm ²)		
Periodic	Non-periodic Expt 1 Expt 2		Periodic	Non-periodic Expt 1 Expt 2		Periodic	Non-periodic Expt 1 Expt 2	
1.5	1.5	1.5	2	1.7	1.5	33.3	33.3	46.2
2.5	2.5	2.6	2	2.4	2.5	20.0	20.0	17.3
3.5	3.0	3.5	2	2.8	3.5	14.3	14.3	9.5
4.5	3.5	4.5	2	3.4	4.5	11.1	11.1	6.0
5.5	3.8	5.6	2	3.6	5.6	9.1	9.1	4.1
6.5	4.2	6.8	2	4.3	6.5	7.7	7.7	3.2
7.5	4.8	7.7	2	4.6	7.8	6.7	6.7	2.4
8.5	5.0	8.5	2	4.8	8.2	5.9	5.9	2.2

Measures of dot spacing (non-periodic surfaces).

One key parameter in these experiments was the measure of dot spacing for the non-periodic surfaces. For the periodic surfaces (Fig. 1B, left), dot spacing corresponded to the SP between rows (longitudinal) or across rows (transverse). For the non-periodic surfaces (Fig. 1B, right), the dots were joined by travelling lines in the direction of the scan; from these measures average dot spacing was calculated for each surface. The lines were constrained so that every dot was included in 1, or at most 2 lines. In addition, the path of the line could not diverge from the longitudinal axis of the scan (θ) by $> 45^\circ$. Similar measures were made for the orthogonal direction. Closely identical results were obtained when the measures were repeated using alternate paths, indicating that this objective measure was accurate, reproducible and independent of the chosen path.

Tactile stimulator.

The tactile stimulator is similar to that described by Zompa and Chapman (1995): a cylindrical drum, 40-cm circumference, was mounted on a drive shaft. The 4 strips of surfaces for the experiment were affixed, in close approximation, around the circumference of the drum (Fig. 1C shows a side view with one strip of 4 surfaces) and were accessible via two 6.5 x 2.5 cm windows over the drum. Each strip was identified with a number (1 to 4) affixed to the cover of the stimulator. Drum rotation was controlled by a computer, activating a DC motor through a 100:1 reduction gear. The direction of the scan was proximal to distal relative to D3 (arrow, Fig. 1C), and the mean scanning speed was 96 mm/s. The latter speed is well within

the range of speeds that subjects opt to use during tactile exploration (Smith et al. 2002). Normal force exerted on the drum was measured using a pair of strain gauges.

Experimental set-up and perceptual task.

The conditions (set-up and task) were the same as in Meftah et al. (2000). Subjects were informed that a series of surfaces would be passively scanned under the digital pad of D3. Their task was to evaluate the roughness of each surface following a single scan. Roughness was not defined for the subjects; instead they were specifically asked to use their own personal definition of tactile roughness. Six practice trials were first performed to familiarise the subject with the various events in the trial (see below). The subject was instructed to choose a comfortable contact force, and to use the same contact force across all trials. The subject's scale was then established by presenting three surfaces, covering a range of dot spacings (smoothest, roughest and intermediate). Subjects were told that these were three illustrative examples, and they were asked to assign any whole number that seemed appropriate to the last surface, the only constraint being that the number be proportional to the sensation of roughness. During each experiment, a total of 16 surfaces (8 x periodic, 8 x non-periodic) were presented in a pseudorandom order, with the periodic and non-periodic surfaces interleaved. Each surface was presented 6 times for a total of 96 trials. The lighting in the room was dimmed so that the subjects could not see the details of the surface to be scanned.

Before each trial (and after the drum was repositioned), the subjects were instructed to place their finger above a specific strip (position 1, 2, 3, or 4), which

contained the surface to be scanned. When the subjects indicated that they were ready to start a trial (D3 in position), the trial was initiated by the experimenter. The drum began to rotate and a light in front of the subject turned on; this was the cue for the subject to lower D3 onto the moving surface (see Fig. 1C). The light was turned off at the end of drum rotation, and this was a cue for the subject to lift the finger from the surface. This approach minimized contact with the stationary texture. After the trial, the subjects gave their subjective estimate of the surface's roughness, and this was entered into the computer by the experimenter.

Data analyses.

The methods were identical to those used previously for our study of tactile speed scaling (Dépeault et al. 2008). For each subject, roughness estimates were normalized off-line by dividing the subject's responses by the mean value of all estimates given during the same session. These normalized values were used for the subsequent statistical analyses. The data of each subject were analysed using a two-way analysis of variance (ANOVA). The model included the roughness estimates (dependent variable), with dot spacing or dot density, and dot disposition (periodic or non-periodic) included as factors (level of significance, $P < 0.01$). For the pooled data, repeated measures ANOVAs were employed (mean estimates/ dot spacing or dot density, and dot disposition). To describe the nature of the relationship between subjective roughness and the physical parameters of the surfaces (1/dot density, dot spacing), linear regression analyses were applied to the data obtained from each subject. The regression parameters (slope, intercept and r^2 , the coefficient of determination) were compared across series (periodic versus non-periodic) using

paired t-tests. Statistical analyses used Systat (version 11). For the pooled data, the level of significance was fixed at $P < 0.05$, given the relatively low number of subjects.

Results

All subjects but one were able to scale the roughness of both the periodic and the non-periodic surfaces and showed a monotonic relationship between perceived roughness and spacing (or 1/dot density) (linear regressions, $P < 0.0005$). The results of one subject (experiment 2, female) were excluded as she was not able to scale surface roughness.

Experiment 1: Equivalent dot density

In this experiment, the surfaces were matched for mean dot density (Fig. 1A and Table 1). The pooled data are illustrated in Fig. 2A. For both the periodic and the non-periodic surfaces, roughness estimates showed a monotonic increase with 1/dot density, but the rate of increase (slope) was lower for the non-periodic surfaces. Overall, roughness estimates for the non-periodic surfaces were 26% lower than for the periodic surfaces. The two curves were anchored at the origin, i.e. the lowest nonzero score was assigned to the smoothest surface in each series.

The data of each subject were subjected to a two-way ANOVA: dot density was a significant factor for all subjects ($n = 8$) and dot disposition (periodic versus non-periodic) for 7 of 8 subjects. A repeated measures ANOVA applied to the pooled

data confirmed that both dot density and dot disposition were significant [respectively, $F(7,49) = 116$, $P < 0.0005$; $F(1,7) = 33.5$, $P < 0.001$). There was also a significant interaction (density * disposition, $F(7,49) = 11.1$, $P < 0.0005$) because the data were anchored at the origin (above).

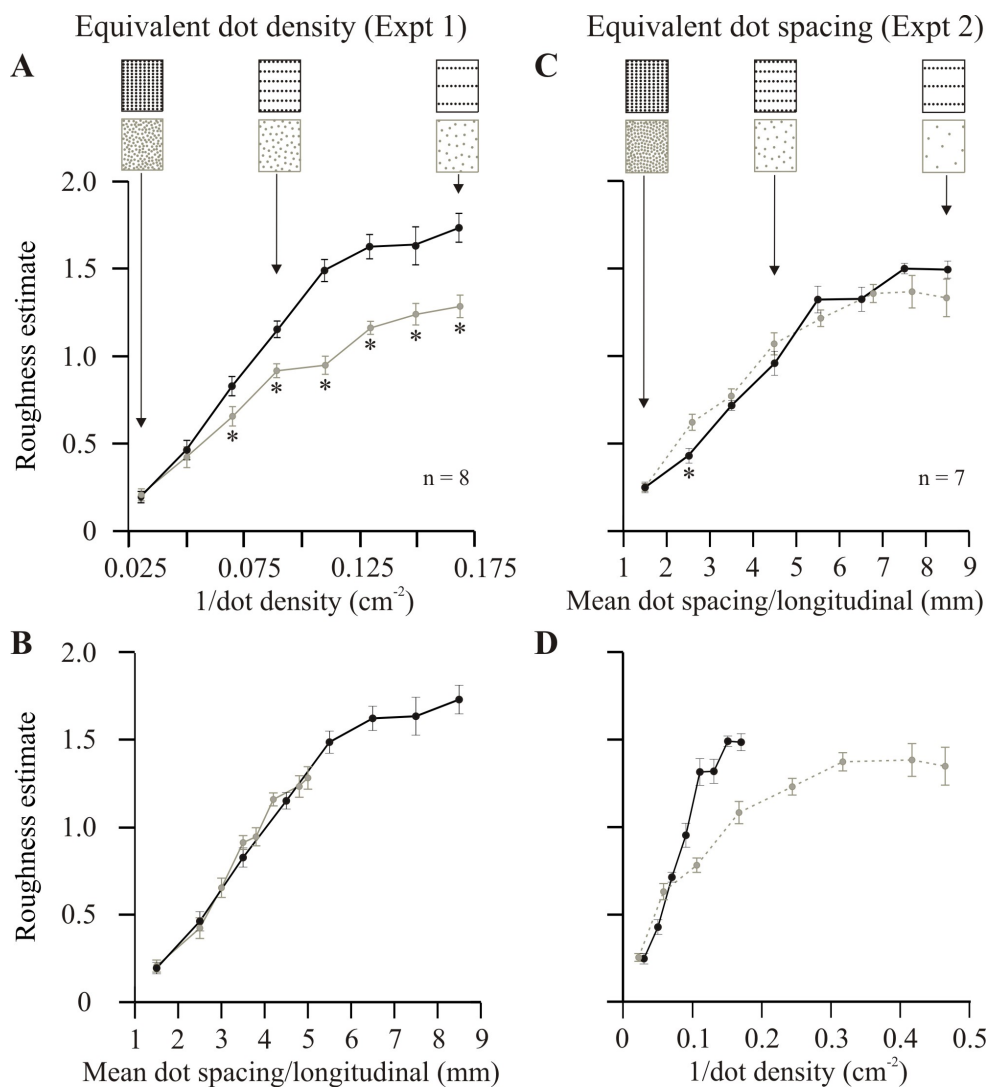


Fig.2: **A,B.** Mean normalized roughness estimates (\pm SEM) as a function of $1/\text{dot density}$ (A) and mean longitudinal dot spacing (B) for the periodic (black) and non-periodic (grey, solid line) surfaces of experiment 1. **C,D.** Normalized mean roughness estimates as a function of mean longitudinal dot spacing (C) and $1/\text{dot density}$ (D) for the periodic (black) and non-periodic (grey, interrupted line) surfaces of experiment 2. The starred values show significant results for paired t-tests ($P < 0.01$) applied to the data in A and C (matched for the relevant physical parameter).

In order to describe the nature of the relationship between perceived roughness and dot disposition, linear regression analyses (normalized roughness estimates versus 1/dot density) were applied to the individual results from each series, periodic and non-periodic. The mean values of the slopes, intercepts and coefficients of determination (r^2) are summarized in Table 2. Slopes were higher for the periodic surfaces, mean of 11.6, then for the non-periodic surfaces, 7.8 ($P = 0.006$). Given that the 2 curves were anchored at their origin, however, the intercepts were similar for both dot dispositions ($P = 0.16$). The r^2 values were high (means of 0.79 and 0.74) and did not vary with dot disposition ($P = 0.38$).

Table 2 Mean values of the parameters (\pm SEM) describing the linear regressions, mean normalized roughness estimates versus 1/dot density or longitudinal dot spacing.

		Slope	Intercept	r^2
Experiment 1 (n=8)				
1/dot density	Periodic	11.6 (0.01)	-0.01 (0.08)	0.79 (0.04)
	Non-periodic	7.84 (0.01)*	0.07 (0.06)	0.74 (0.03)
Dot spacing	Periodic	0.23 (0.02)	-0.01 (0.08)	0.79 (0.04)
	Non-periodic	0.33 (0.03)	-0.31 (0.09)	0.77 (0.03)
Experiment 2 (n=7)				
1/dot density	Periodic	9.67 (0.05)	0.03 (0.05)	0.79 (0.03)
	Non-periodic	2.24 (0.28)*	0.50 (0.05)*	0.64 (0.07)*
Dot spacing	Periodic	0.19 (0.01)	0.03 (0.05)	0.79 (0.03)
	Non-periodic	0.16 (0.02)	0.21 (0.07)*	0.70 (0.07)

Abbreviation: r^2 , coefficient of determination.

* $P < 0.05$ (paired t-tests, periodic versus non-periodic)

As dot density was matched in this experiment, it seemed logical that the difference, periodic > non-periodic, might be explained by dot disposition. Examination of Fig. 1A and Table 1, however, shows that the 2 series also differed in

mean dot spacing measured in the direction of the scan (longitudinal dot spacing) with the periodic surfaces covering a wider range of spacings, 1.5 to 8.5 mm, than the non-periodic surfaces, 1.5 to 5.0 mm. To determine the relative importance of dot spacing to the results, the data were replotted as a function of the average longitudinal dot spacing (Fig. 2B). The difference disappeared, and the 2 curves were now superimposed. The regression parameters were recalculated (Table 2): there was no longer any difference in slopes across the 2 series of surfaces ($P = 0.98$). This finding suggested that the critical factor for subjective roughness was mean dot spacing in the direction of the scan, with little or no contribution from dot disposition, periodic or non-periodic. This suggestion was tested in the second experiment.

Experiment 2: Equivalent dot spacing

In this experiment, the periodic and non-periodic surfaces were matched for average dot spacing in the scanning direction (Fig. 1A and Table 1). The individual results for 7 subjects (different from those used in experiment 1) were similar for the two dot dispositions. The pooled results (Fig. 2C) show that the roughness estimates increased with average dot spacing for both series of surfaces, with the two curves being superimposed.

Dot spacing was a significant factor for all subjects, but dot disposition (periodic versus non-periodic) was significant in only 1 of 7 (two-way ANOVAs). The repeated measures ANOVA (pooled data) confirmed the absence of any effect attributable to dot disposition [$F(1,6) = 0$, $P = 0.99$], and also that roughness

estimates co-varied with mean longitudinal dot spacing [$F(7,42) = 116.8$, $P < 0.0005$]. The interaction term was, as for experiment 1, significant [$F(7,42) = 4.4$, $P = 0.001$]. The linear regression analyses (roughness versus dot spacing) showed that slopes were similar for the periodic and non-periodic surfaces ($P = 0.07$, Table 2). As found in experiment 1, r^2 was high and did not vary with dot disposition ($P = 0.11$). In contrast, the intercepts varied across the two dot dispositions ($P = 0.011$), being higher for the non-periodic surfaces (see Table 2), reflecting the significant interaction found with the repeated measures ANOVA.

Figure 2D replots the same data as a function of $1/\text{dot density}$ for comparison with the results of experiment 1. The two curves no longer overlap, indicating that perceptual equivalence was, as in experiment 1 (Fig. 2A), lost over a large part of the range. The linear regression analyses (roughness versus $1/\text{dot density}$) now showed a significant difference in slopes across the 2 series of surfaces ($P < 0.005$, Table 2). Most importantly, r^2 was significantly higher when the perceptual data were plotted as function of longitudinal dot spacing as compared to $1/\text{dot density}$ for the non-periodic surfaces ($P < 0.005$). The latter observation is consistent with dot spacing in the longitudinal axis being the critical factor for roughness perception.

The latter suggestion was supported by the results of a multiple regression analysis that included longitudinal and transverse dot spacing as variables, along with dot disposition. The partial correlations indicated that longitudinal dot spacing was responsible for the majority of the variance in roughness estimates for both experiments (1, 73.4%; 2, 72.5%). Transverse dot spacing explained only 7-15.8% of the variance, while dot disposition made a negligible contribution (1.9 – 0%).

Experiment 1 versus 2

The importance of dot spacing for the results was further evaluated by plotting the roughness estimates as a function of dot spacing in the direction orthogonal to the scan, i.e. the *transverse spacing* (Fig. 3A and B). For the non-periodic surfaces, roughness estimates increased with an increase in transverse spacing. This was not surprising since dot spacing (longitudinal versus transverse) was closely similar for the non-periodic surfaces in both experiments (paired t-tests, $P > 0.15$, see Fig. 3C). In contrast, transverse spacing was fixed at 2 mm for the periodic surfaces (Fig. 3C); despite this, roughness estimates for the periodic surfaces varied widely, following the changes in longitudinal dot spacing.

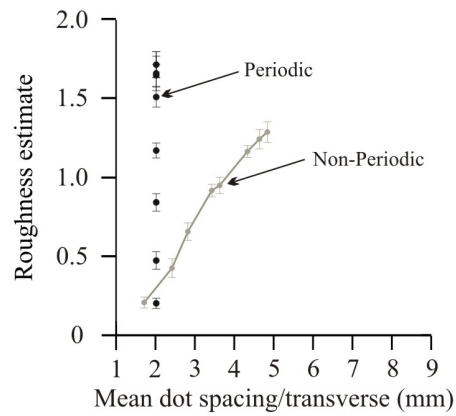
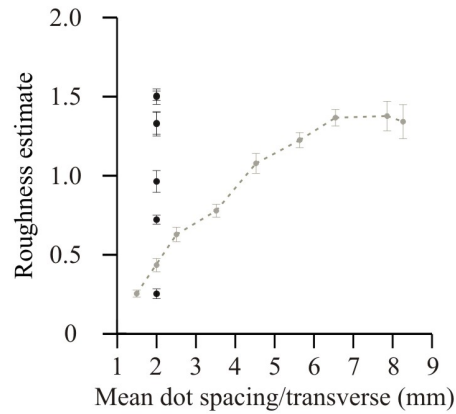
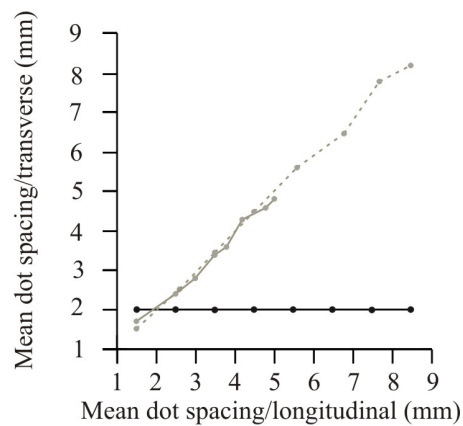
A Equivalent dot density (Expt 1)**B** Equivalent dot spacing (Expt 2)**C** Dot spacing

Fig. 3: **A,B.** Mean normalized roughness estimates (\pm SEM) plotted as a function of mean transverse dot spacing for experiments 1 (A) and 2 (B). **C.** Physical characteristics of the surfaces, mean dot spacing (transverse) versus mean dot spacing (longitudinal). Data for the periodic surfaces are shown in black. Data for the non-periodic surfaces are grey (Experiment 1, solid line; Experiment 2, interrupted line).

Finally, inspection of Figs 2B and C suggests that the scaling of the periodic surfaces differed across the 2 experiments, with a steeper slope and wider range of normalized estimates for experiment 1 as compared to experiment 2. We suspected that this was an artefact of the normalization procedure: data were normalized relative to the grand mean of each experiment, but the results in experiment 1 were biased towards lower values. This was confirmed by renormalizing the periodic data set from experiment 1 relative to its mean. The results are plotted in Fig. 4. Inspection shows that the two curves are superimposed. None of the regression parameters varied across the 2 experiments ($P > 0.7$). Thus, the apparent difference was explained by the normalization procedure.

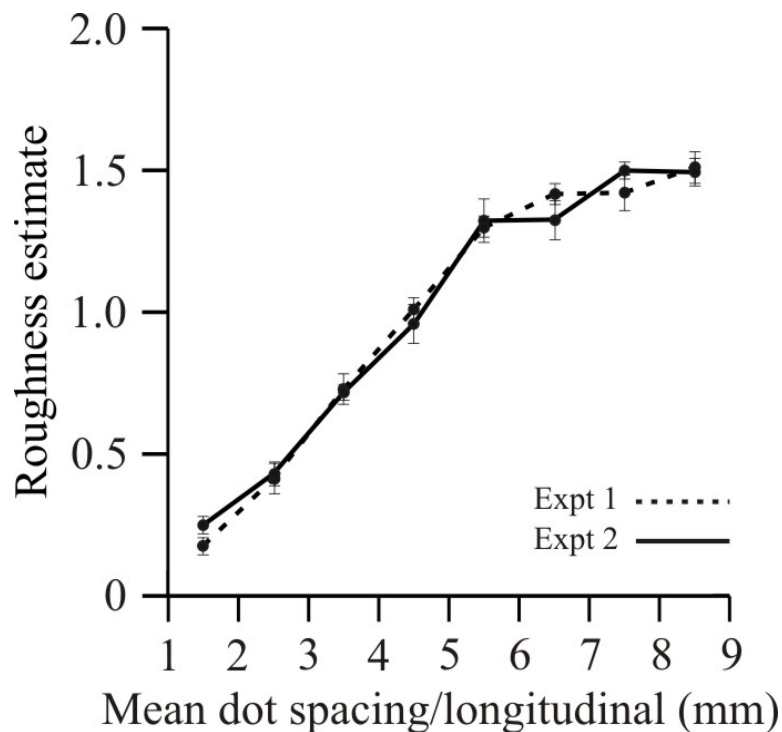


Fig. 4: The roughness estimates of experiment 1 (periodic surfaces) were renormalized for each subject using the mean value of the estimates for only the periodic surfaces, and are replotted with those from experiment 2. Plotted as in Fig. 2B.

Discussion

The results of this study demonstrate that dot spacing in the scanning direction is the critical factor for tactile roughness. Roughness estimates were independent of three other factors: dot spacing in the orthogonal direction to the scans, the disposition of the tactile elements on the surfaces (regular or irregular), and mean dot density, at least over a portion of the tested ranges. Thus, tactile roughness appreciation is very similar to tactile speed appreciation in its sensitivity to the spatial parameters of raised-dot surfaces.

In our experiments, several factors that could have potentially modified subjective roughness were held constant, including tactile element size (dot height and diameter) and the composition of the surfaces, a flexible polymer. In addition, the various surfaces were intermixed in each experiment, thus ensuring that the subjects used the same scale for rating the roughness of the periodic and non-periodic surfaces.

The present results confirm those of Meftah et al. (2000) who reported that roughness estimates show a monotonic increase as the longitudinal dot spacing of periodic raised-dot surfaces is increased up to 8.5 mm. As in our previous study, the rate of rise in perceived roughness with dot spacing declined for spacings greater than 5 mm. We extend these results by showing that closely similar results are obtained using non-periodic raised-dot surfaces, including the less rapid rise in roughness estimates as dot spacing increased beyond 5 mm (Fig. 2). In this study, the relative plateau began at dot spacings ≥ 5.5 mm, in agreement with our previous study and with Lawrence et al. (2007). This appears to be a robust observation since there were

differences in the mode of touch, active touch for Lawrence et al. versus passive touch (our studies), and the physical characteristics of the surfaces [respectively, rectangular gratings versus raised dots; height of the tactile elements, 0.46 mm vs 1 mm; and the composition of the surfaces]. Notably, *none* of these studies (including the present report) found evidence for a U-shaped relation between roughness and tactile element spacing as reported by Connor et al. (1992). The latter study found that perceived roughness initially increased as dot spacing increased, but declined at spacings > 4.5 mm. We previously suggested that this result reflected differences in the physical characteristics of the surfaces, most particularly the fact that dot spacing was varied in two dimensions in Connor et al. as compared to only one dimension (Meftah et al. 2000; Lawrence et al. 2007; the present study).

Of the three factors that were varied here, dot spacing, dot density, and dot disposition (periodic or non-periodic), the first two factors co-varied for the non-periodic surfaces. As dot spacing increased (along or across the direction of the scan), dot density necessarily decreased. Consequently, linear regressions applied to the physical parameters of each set of non-periodic surfaces, dot spacing versus $1/\text{dot density}$, were significant and the r^2 values were all ≥ 0.97 . Dot spacing and $1/\text{dot density}$ also co-varied for the periodic surfaces, but *only* in the longitudinal direction because dot spacing across the rows was fixed (Table 1). In order to sort out the relative importance of dot spacing and dot density to roughness perception, we matched one factor across the periodic and non-periodic surfaces in each experiment, and the results showed convincingly that dot spacing in the direction of the scan was, in these experiments, the key factor for roughness appreciation. This conclusion is

dependent on the accuracy of our measure of longitudinal spacing for the non-periodic surfaces, but we are confident that the objective measure used here was accurate and reliable because closely similar measures were obtained when the chosen paths were systematically varied.

Two earlier studies reported that an increase in dot spacing in the transverse direction (perpendicular to the scan) increases roughness estimates. Connor and Johnson (1992) found that roughness increased over a range of 1.5 to 3 mm, but plateaued at higher spacings (3.5 to 4 mm). Meftah et al. (2000) also found an increase in roughness when transverse dot spacing was increased from 1 to 2 mm but the magnitude of the effect was very small, explaining <1% of the variance in roughness estimates (as compared to 82% for longitudinal spacing), and was limited to the lowest longitudinal spacings tested, 1.5 - 2.5 mm (testing extended up to 8.5 mm). In this study transverse dot spacing was varied over a much larger range, up to 8.2 mm but for the non-periodic surfaces, we could not distinguish between the relative importance of longitudinal and transverse dot spacing because these co-varied (Fig. 3C, coloured curves). Transverse and longitudinal spacing were dissociated for the periodic surfaces. In these cases, transverse spacing was constant, and only longitudinal spacing varied (Fig. 3C, black curve). In both experiments perceptual equivalence with the non-periodic surfaces was obtained when the roughness estimates were plotted as a function of dot spacing in the direction of the scan (Fig. 2), and this despite the fact that transverse spacing was not matched. The implication of this finding is considered below.

While we successfully dissociated dot spacing and dot density over much of the range of spacings tested, the roughness estimates for the surfaces judged least rough (highest dot densities) in each experiment were closely similar, regardless of whether they were plotted as a function of 1/dot density or dot spacing. This was partly explained by the scales being anchored at the origin (similar non-zero estimates given to the smoothest surfaces of each series). Nevertheless, the similarity of the results was not restricted to the “smoothest” surface, but also extended to the adjacent, relatively smooth, surface in each experiment (see non starred data points, Fig. 2A). This observation may reflect the fact that tactile element density is a particularly critical factor for smoother surfaces. Future experiments should explore this suggestion, extending the range of physical features tested here.

A fundamental goal of sensory psychophysics is to understand the neuronal mechanisms that underlie sensory perception, and in this regard discriminative touch is a particularly complex ability since tactile exploration is accompanied by feedback from a number of cutaneous mechanoreceptors, all of which likely contribute to the sensory experience. The principal contribution of the present study lies in the fact that dot spacing, and not dot density or disposition (periodic versus non-periodic), was shown to be the critical factor for roughness sensation. To this, we can add previous observations that subjective roughness is invariant with scanning speed, at least within ranges used during tactile exploration (Lederman 1974; Meftah et al 2000). These results contrast with those of our recent study (Dépeault et al. 2008) which looked at the factors that modify tactile speed estimates. The interest here is that tactile speed is extracted from these same complex afferent signals, and shares

some characteristics with tactile roughness. Specifically, both sensory abilities are independent of dot disposition; in contrast, both are dependent on the presence of surface structure, specifically longitudinal dot spacing. Yet dot spacing has opposite effects: roughness increases as dot spacing is increased, while speed estimates decline. Taken together, these observations suggest that 1) the nervous system must extract this information from the afferent signals and therefore 2) different populations of cortical neurones may be involved in roughness and speed perception. The results provide a clear set of challenges that can be used to identify these cells at the cortical level. In this regard, there is already evidence that some cells in primary somatosensory cortex encode tactile roughness independent of scanning speed (Burton and Sinclair 1994; Tremblay et al. 1996; DiCarlo and Johnson 1999). Future experiments should determine whether such cells maintain their relationship with the spacing of the tactile elements, and independence of scanning speed, for both periodic and non-periodic surfaces.

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Article # 3

**NEURONAL CORRELATES OF TACTILE SPEED IN
PRIMARY SOMATOSENSORY CORTEX**

by

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Abstract

Moving stimuli activate all of the mechanoreceptive afferents involved in discriminative touch but their signals covary with several parameters, including texture. Despite this, the brain extracts precise information about tactile speed, and humans can scale the tangential speed of moving surfaces as long as they have some surface texture. There is, however, an interaction between speed and texture, a relationship that is reduced to a monotonic continuum when estimates are normalized to the same tactile element spacing (SP, spatial period, of raised-dot surfaces) and plotted as a function of temporal frequency (speed/SP). We hypothesized that the discharge of cortical neurones playing a role in scaling tactile speed should covary with temporal frequency in the same manner and that this should be independent of dot disposition (periodic or nonperiodic). Single-cell recordings ($n=119$) were made in the hand region of primary somatosensory cortex, S1, of awake monkeys while raised-dot surfaces (longitudinal SPs, 2-8 mm; periodic or nonperiodic) were displaced under their fingertips at speeds of 40-105 mm/s. Speed-sensitivity was widely distributed (areas 3b, 13/25; 1, 32/51; and 2, 31/43) and almost invariably combined with texture-sensitivity (82% of cells). Of 94 neurons fully tested (periodic and nonperiodic surfaces), the large majority of speed-sensitive cells (60/64) showed a significant monotonic relation with temporal frequency for both surfaces when discharge frequency was normalized by SP. The neurones with the strongest relation to temporal frequency were concentrated in caudal S1, areas 1 and 2, and may contribute to the human ability to scale tactile speed.

Key words: tactile motion, texture, speed scaling, temporal frequency, S1, monkey

Introduction

Movement between the skin and an object activates all tactile afferent types (both slowly and rapidly adapting) that play a role in discriminative touch (Edin et al. 1995; Essick and Edin 1995; Goodwin and Morley 1987; Greenspan 1992; Lamb 1983) and improves tactile perception. For example, tactile roughness discrimination thresholds are halved during dynamic touch, i.e. with movement, as compared to static touch (Morley et al. 1983). While we have a great deal of information about the peripheral and central coding of tactile roughness, little is known about tactile motion coding (speed) and perception, even though it is essential for object manipulation in everyday life.

At the receptor level, a number of studies have characterized the sensitivity of primary cutaneous afferents to movement of surfaces, small shapes (what can be sensed with the finger tip) or a brush over the skin. The results showed that cutaneous mechanoreceptive afferents innervating both hairy and glabrous skin, including rapidly adapting (RA), Pacinian (PC), and slowly adapting type I and II afferents (SAI, SAII), are sensitive to tactile motion (Darian-Smith et al. 1980; Edin et al. 1995; Essick and Edin 1995; Goodwin and Morley 1987; Greenspan 1992; LaMotte and Srinivasan 1987a,b). The signals, however, reflect not only tactile speed but also surface structure (roughness and/or shape of the stimuli scanned over the skin) and tangential and normal forces (Birznieks et al. 2001; Johnson 2001). At present, it is not clear how these signals are processed at higher levels to extract precise information about tactile speed.

Lesions of primary somatosensory cortex (S1) greatly impair the ability of monkeys to categorize tactile speed (Zainos et al. 1997). Consistent with this, a number of studies have shown that S1 cortical neurones are sensitive to tactile motion, and this using a variety of approaches including mechanical indentation of the skin (Esteky and Schwark 1994), sequential stimulation of a fixed length of skin (Gardner et al. 1992; Pei et al. 2010; Romo et al. 1996; Whitsel et al. 1972) and tangential scanning of surfaces over a fixed location on the skin with the subject either immobile, passive touch (DiCarlo and Johnson 1999; Sinclair et al. 1996; Tremblay et al. 1996), or moving, active touch (Sinclair and Burton 1991). The results indicate that sensitivity to the speed of tactile motion is present in all three areas that comprise the primate cutaneous hand representation, areas 3b, 1 and 2. In addition, there is some indication that speed sensitivity is frequently combined with sensitivity to the texture of scanned surfaces. At present, however, we have limited information about the extent to which S1 neuronal discharge has properties consistent with a role in tactile speed perception, and whether the different areas that comprise S1 play differential roles in signalling tactile speed.

This study was prompted by two related observations. First, even though tactile signals are complex and covary with multiple parameters, including texture and speed, human tactile roughness estimates are relatively independent of tactile scanning speed (Lederman 1983; Meftah et al. 2000). This observation indicates that an invariant representation of roughness is extracted from the complex peripheral signals. Second, it appears that the same is not true for human tactile speed estimates. We recently showed that tactile speed scaling is dependent on surface texture in two

important ways (Dépeault et al. 2008): 1) some surface structure (e.g. texture) is essential because subjects have a great deal of difficulty in estimating the speed of a moving smooth surface; and 2) speed estimates for the roughest surface tested (8 mm spatial period, SP, measured in the direction of the scan) were systematically lower than for two “smoother” surfaces (2 and 3 mm SP). In other words, the physical characteristics of the textured stimuli modified the subjective speed of moving stimuli. Identical results were obtained when we contrasted results obtained using periodic arrays of raised dots and pseudo randomly disposed dots (non periodic surfaces matched for the same mean SP in the direction of the scan). Interestingly, the contribution of surface texture to speed scaling was reduced to a single monotonic continuum by normalizing the estimates to the same spacing and expressing the result as a function of temporal frequency (speed/SP). This led us to hypothesize that the discharge of cortical neurones playing a role in scaling tactile speed should covary with temporal frequency in the same manner seen in human subjects, showing a monotonic increase in discharge with temporal frequency. We further expected that the discharge pattern would be independent of the disposition of the raised dots (periodic vs. non periodic).

This hypothesis was tested in the present study by recording from single neurones in S1 cortex of awake monkeys as textured tactile stimuli were displaced at different speeds across the receptive field (RF). The stimuli consisted of raised-dot surfaces that varied in terms of roughness (SP) and dot disposition (periodic, non periodic). The range of tactile speeds was similar to that used in our earlier

psychophysical study, corresponding to speeds often used during tactile exploration (Smith et al. 2002).

Methods

Two monkeys (*Macaca mulatta*; B, 8.5 kg; N, 6.3 kg) were used in the present experiment. Recordings were made from three hemispheres contralateral to the stimulated digits (both sides for monkey B; left for monkey N). The institutional animal care and use committee approved all of the procedures and the guidelines specified by the Canadian Council on Animal Care were followed. During data acquisition, the animal's attention was controlled (Fitzgerald et al. 2006) by having the monkeys perform a simple light discrimination task (see below) while the textured surfaces were displaced beneath the immobile tip of digits 3 and 4 (D34).

Tactile stimulator: The strips of surfaces were affixed to a tactile stimulator, similar to that described by Zompa and Chapman (1995). It is composed of a cylindrical drum (40 cm circumference) mounted on a drive shaft that was rotated by means of a DC motor through a 100:1 reduction gear, controlled by a computer. The different surfaces were accessible through openings (18 X 22 mm;) giving access to the drum. The tactile stimulator was fixed to the primate chair at waist height, in front of the monkey.

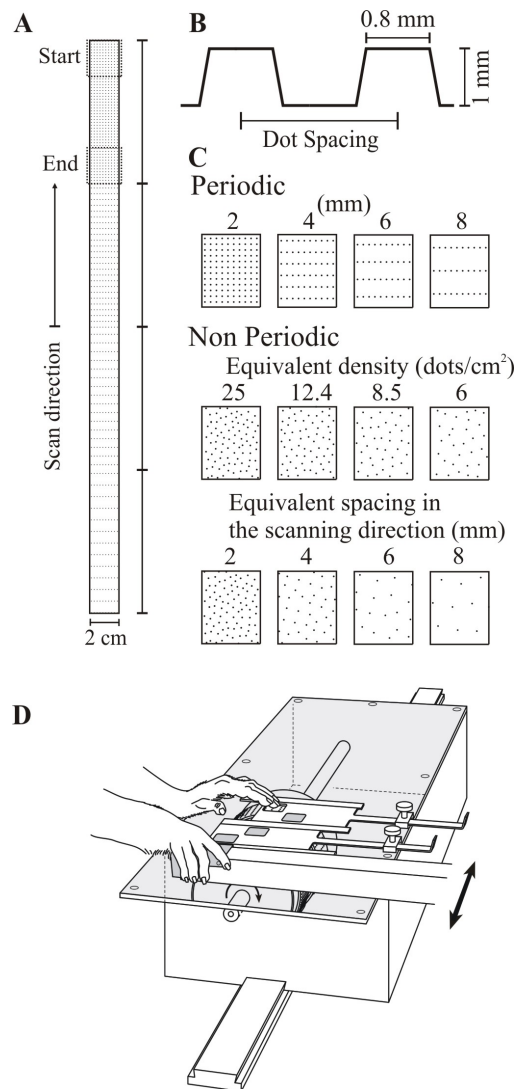


Fig. 1. A: Each series of 4 surfaces (2 x 10 cm) formed a continuous 40 cm strip that was affixed around the circumference of the drum (see D). The start and end boxes show the surface exposed to the fingers at the beginning and end of a trial. The scanning direction was proximal to distal. **B:** Raised dot profile showing the height, diameter, and dot spacing (SP). **C:** *Periodic surfaces* (top) had a constant transverse SP (perpendicular to the direction of the scan) of 2 mm but varying longitudinal SP (in the direction of the scan). *Non periodic surfaces:* The equivalent density series (middle) contained the same number of dots as the periodic series but dot position was jittered (quasi-random distribution); the equivalent dot spacing series (bottom) had almost the same average longitudinal SP as the periodic series but dot density was lower for most surfaces. **D:** The tactile stimulator contained the drum to which the surfaces were attached. A window over the drum gave access to the surfaces. The response lever was attached to the stimulator. Shown here is the position of the monkey's hands during data acquisition. When the series were switched (e.g. periodic for non periodic), the position of the drum was displaced horizontally so that the relation between the surfaces and the stimulated fingers was identical.

Surfaces: The surfaces were prepared on flexible letterpress plate using a photographic process (CML Printing Plates Inc., St. Léonard, QC, Canada). They were composed of raised dots [truncated cones: 1 mm high and 0.8 mm diameter (top), Fig. 1B]. Two series of surfaces were used, one periodic and the other non periodic (see Fig. 1C). Each series consisted of four 10 cm long surfaces that together formed a single 40 cm strip (Fig 1A). The surfaces were drawn from sets used in a previous psychophysical study, and have been described in detail elsewhere (Dépeault et al. 2009). The periodic surfaces were constituted of rows of dots with a constant transverse SP (centre-to-centre) of 2 mm and longitudinal SPs varying from 2 to 8 mm. In the initial recordings, the non periodic surfaces were matched for dot density. These were generated by jittering the periodic dots to produce a pseudorandom arrangement. This maintained the same number of dots, but the average spacing in the scanning direction covered a smaller range, 2 to 4.9 mm. In the later recordings a different set of non periodic surfaces was used, in this case matched for longitudinal SP (Fig. 1C). This set was generated by pruning dots from the first non periodic set.

Speeds: Surfaces were presented using three different speeds that covered most of the range used during tactile exploration in humans (Smith et al. 2002). Initially, nominal speeds of 40 to 85 mm/s were employed. The range of speeds was subsequently extended up to 105 mm/s.

Behavioural task: When the monkeys were first brought to the lab, they were trained to adopt a posture (place one hand on the surface and one on a lever), then accept moving surfaces under their immobile fingers, and finally to perform the visual discrimination task during the drum rotation. This whole process required a total of 4-6 months. The monkeys had to attain a performance of ~90% in the visual discrimination task, which required 5-8 weeks. Lights (red and yellow) were placed in front the monkey at eye level (approximately 35 cm) and the hand ipsilateral to the recorded cortex was positioned on a response lever. The finger tips (D34) of the other hand were placed over the surface in one opening (see Fig 1D) and stayed immobile for all the trials necessary (monitored visually on-line, trial rejected if variation in vertical force ± 0.2 N). Therefore, the correct positioning of the fingers was verified before each trial which was then initiated by the experimenter. After a total hold period of 1 s, a red light turned on, to warn the monkey that the texture would move and that the visual discrimination task would begin in 2 s (see Fig. 2 A and B). The yellow light was first of low intensity and then increased intensity after a delay of 1.5, 2.0, or 2.5 s. The monkey had to detect this change and then respond to it by lifting its hand from the lever to receive a drop of water. The reaction time window for a successful trial was 200-700 ms. Performance of the monkeys during recordings was, on average, 80% trials with reward. Monkey B would often withdraw its fingers from the surfaces when the drum was repositioned, but for each trial, normal contact force during the exploration was calculated off-line and the trace was verified to confirm that there was a uniform contact between the finger tips and the surfaces.

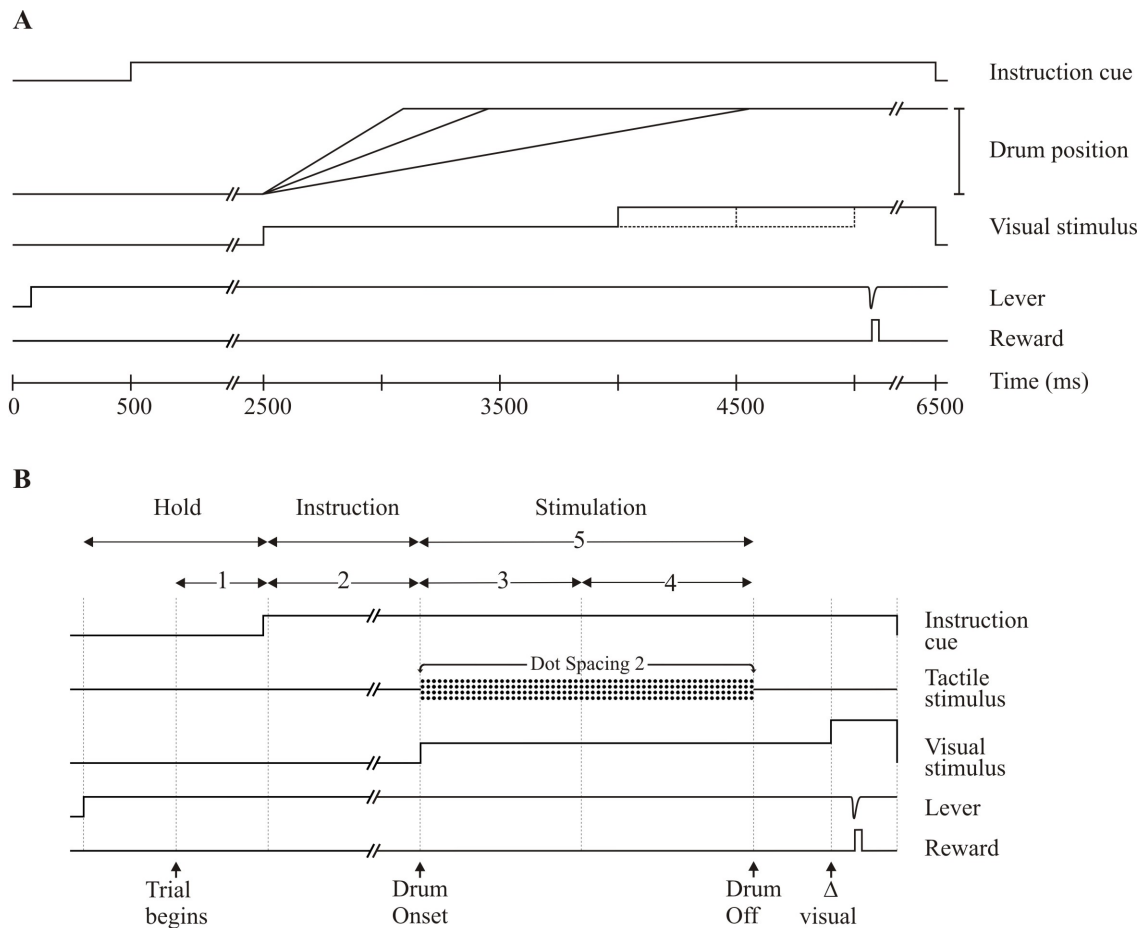


Fig 2. A: Time course of events during a trial (see text for details). **B:** For each trial the discharge frequency was measured in 5 epochs: Epoch 1, hold period; Epoch 2, Instruction period; Epochs 3 and 4, first and second half of Stimulation period; Epoch 5, Simulation period.

Surgical procedures: When the monkey mastered the posture and the task, a chronic recording chamber was placed over the hand representation of the primary somatosensory cortex, contralateral to the stimulated hand. The surgical procedure used here for chamber implantation was described previously (Chapman and Ageranioti-Bélanger 1991; Tremblay et al. 1996). Briefly, after sedation with ketamine + glycopyrolate (15 mg/kg IM + 0.01 mg/kg), the animal was intubated for endotracheal administration of isoflurane (2-3%) Physiological parameters (temperature, heart rate, and respiration rate) were monitored during the surgery.

Antibiotics (enrofloxacin: 5 mg/kg) were administered prior to surgery, and for 10 days postoperatively. Postoperative analgesia was provided for a minimum of 72 h (ketoprofen 0.1 mg/kg and buprenorphine 0.05 mg/kg).

Data acquisition and analysis

Extracellular recordings of single neurones were performed in S1 cortex using glass-coated tungsten microelectrodes (0.2-1 Ω). For each penetration, depths were noted when cell activity was reached, when a cell was recorded and when there were transitions between active and silent zones. The RF properties of each neurone were carefully determined. Cells were initially characterized according to their modality: cutaneous (sensitive to light or moderate touch) and/or deep (responsive to joint movement and/or muscle palpation). Our recordings concentrated on neurones that 1) had a cutaneous RF on the stimulated digit tips (D3 and/or D4) and 2) showed obvious modulation of their discharge rate in response to the moving textures. The extent of the cutaneous RF was mapped with a hand-held probe. For one monkey (N), the mapping was repeated and confirmed using a Von Frey filament ($F=0.02N$). The adaptation rate for each cell was determined: SA neurones continued to discharge for ~ 2 s during static touch while RA neurones showed transient responses to static stimulation, along with discharge during the application and removal of the stimulus. Finally, each cell was tested to see if it was sensitive to the direction of the cutaneous stimulus (moving the probe in different directions across the RF).

Data collection was under computer control (see Tremblay et al. 1996). During each trial, the following data were collected: neural spike intervals, vertical

contact force, drum position, and specific timing of events in the trial (e.g. light change, time of the response). Cell recording started with the last 500 ms of the hold period and lasted for a total of 6.5 s. During each trial, 8 cm of surface were presented (proximal to distal), and drum rotation time was varied to generate a range of speeds (40 – 105 mm/s). The speed was constant throughout the trial (see Fig. 2A). For each cell, there was a total of 120 trials presented pseudo-randomly, consisting of 5 repetitions of each speed-texture combination (3 speeds and 4 textures) for both periodic and non periodic series. The tactile stimulator was displaced horizontally after the first 60 trials (periodic or non periodic series) to expose the next series of surfaces so that the monkey's arm was in the same position throughout.

The activity during the stimulation period (when the surface was displaced under the digit tips) was the focus of this study. Rasters and perievent histograms were used to examine the discharge pattern of each cell. For each trial, mean cell discharge rate was calculated during five different epochs: 1) Hold period corresponding to the 500 ms before the red light turned on; 2) instruction period; 3) first half of the stimulation period; 4) second half of the stimulation period; and 5) complete stimulation period (epochs 3 + 4; see Fig. 2B). The number of spikes during epochs 3 – 5 was also calculated.

For each cell, the following analyses were performed for epochs 3, 4, and 5. First, the mean discharge frequency during epochs 3-5 was compared with epoch 1 to see if there was a significant difference (Wilcoxon test, $P \leq 0.05$) and therefore determine if the cell was modulated by the moving surfaces. Second, an analysis of variance, ANOVA (dependent variable, mean discharge frequency during epochs 3, 4

or 5; independent variables, speed and SP), was applied to the results of each data file (one set of surfaces, periodic or non periodic) to classify cells as speed- and/or texture-sensitive. Third, linear regressions were applied to the data to describe the nature of the relationship between mean discharge frequency and scanning speed. In general, similar results were obtained with epochs 3, 4 and 5. The measure of interest was the strength of the relationship between mean discharge frequency and scanning speed as quantified by the coefficient of determination, r^2 . We chose to concentrate on the measures from the complete stimulation period, epoch 5, in the Results because r^2 values were highest for this measure across the population of speed-sensitive cells. Finally, the linear regressions were repeated using normalized discharge frequency (discharge rate during epoch 5 divided by the grand mean discharge rate across all trials, periodic + non periodic when available) as the dependent variable and temporal frequency (speed/SP) as the independent variable. Further analyses are described in the Results. Statistical analyses used Systat, version 11.0 for Windows (SPSS, Chicago IL). The minimum level of significance for all analyses was $P \leq 0.05$.

Our main analyses were based on the assumption that the underlying neuronal code for tactile speed is mean discharge frequency. We also tested the possibility that a spike count code might provide a better fit to the data. The results (not shown) suggested that the relations were substantially weaker (lower r^2 values, both regression models). Such findings led us to concentrate the population analyses on measures obtained using mean discharge rate.

Histological methods: Electrolytic lesions were performed near the end of the recordings. After that, the monkey was euthanized with an overdose of pentobarbital (35 mg/kg ip) and perfused through the heart with a formol-saline solution. The brain was then removed and parasagittally sectioned in 50 μm slices to be stained with cresyl violet. The areas of SI were distinguished according to the criteria established by Powell and Mountcastle (1959) and Jones et al. (1978).

Results

Recordings were made from three hemispheres of two monkeys in the cutaneous hand region of SI (areas 3b, 1, and 2). A total of 119 cells were recorded, with 94 cells having complete acquisition files for both the periodic and non periodic surfaces (~60 trials for each set of surfaces). Seventy-two neurones were recorded in monkey B; 47 neurones in monkey N. All cells had a cutaneous RF that included the digit tip of D3 and/or D4 and so were stimulated by the moving surfaces. All were sensitive to light touch. The adaptation type was determined for almost all cells using manually applied stimuli: 56 RAs and 62 SAs. Histological reconstructions (see Table 1) showed that the sampling covered all three areas that form the S1 cutaneous hand representation: 25 cells were located in area 3b, 51 in area 1, and 43 in area 2. SA responses were encountered in all three areas (respectively, 44%, 52% and 58% of the sample).

Cell discharge was recorded while the monkey performed the visual discrimination task, ensuring that attention was controlled throughout the time of data

acquisition. When possible (isolation maintained; monkey willing to work), two blocks of trials were recorded for each neurone: one set with the periodic surfaces and the other with the non periodic surfaces (order counterbalanced across sessions). Four different textures were presented in each block, at three different scanning speeds. These data were used to evaluate the extent to which cell discharge covaried with scanning speed, surface texture, and dot disposition (periodic, non periodic). Individual cell examples are presented first, followed by the population analyses.

Table 1. SI cell distribution (n = 119)

	Area 3b	Area 1	Area 2
Monkey B	19	30	23
Monkey N	6	21	20

Single cell examples

The most common response pattern encountered was sensitivity to both surface *texture and scanning speed*. Figure 3A shows a representative cell recorded in area 2. Trials in the rasters and perievent histograms (aligned on scanning onset) were sorted according to dot disposition (top, periodic; bottom, non periodic) and scanning speed. Within each raster, trials are shown in increasing order of longitudinal SP. During the period of drum rotation (thick bar above the raster), discharge frequency showed an abrupt increase shortly after drum rotation began, followed by a modest degree of adaptation during the period of constant velocity

scanning. When scanning speed was increased, from left to right, the discharge rate increased. The change in dot disposition (top vs. bottom), in contrast, had little effect on neuronal sensitivity to tactile scanning speed. Finally, cell discharge increased as SP increased. An ANOVA was applied to the data for each acquisition file (periodic, non periodic). Discharge rate during the stimulation period (epoch 5, Fig. 2) was significantly modulated by both speed and SP ($P \leq 0.003$), both for the periodic and non periodic surfaces. There was no significant interaction between speed and SP.

Speed-sensitivity independent of texture-sensitivity was much less frequently observed. Nevertheless, a few such cells were encountered, and an example from area 2 is presented in Fig. 3B. There was a marked increase in discharge with increasing speed (40 - 105 mm/s). Dot disposition was not an important factor: discharge rates were modestly higher for the data set acquired using the non periodic surfaces (Kruskal Wallis, $P = 0.001$) but the ANOVAs confirmed that speed was a significant factor for both data sets ($P < 0.0005$), while texture was not ($P > 0.15$, see rasters).

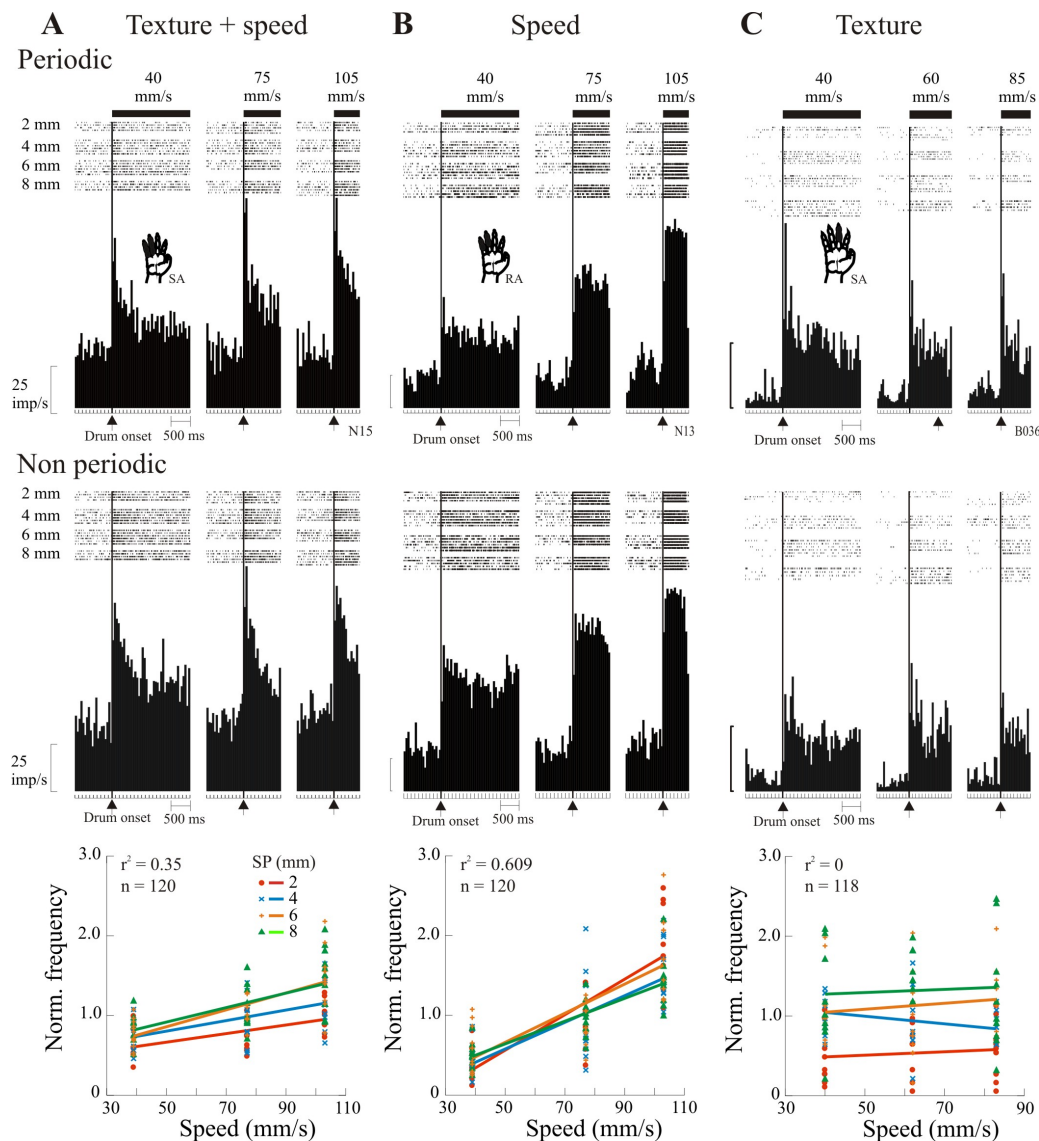


Fig 3. Single cell examples. **A**, Texture + speed-sensitive area 2 cell. **B**, Speed-sensitive area 2 cell. **C**, Texture-sensitive area 3b cell. Top: Rasters and peri-event histograms (50 ms bin width) of neuronal discharge as a function of scanning speed, left to right, and dot disposition (top, periodic; bottom, non periodic). Data are aligned on the onset of drum rotation. Trials in the rasters are sorted in order of SP. The black bar above the raster represents the mean duration of the stimulation period. The receptive field for each cell is shown, with the shaded region corresponding to the region sensitive to light touch. The cells in A and C were categorized as slowly adapting, SA; the cell in B had a rapidly adapting, RA, response to light touch. Bottom: Discharge frequency (epoch 5, Fig. 2) is plotted for each longitudinal SP as a function of scanning speed, along with the corresponding regression. Discharge frequency was normalized by calculating the grand mean for all trials (periodic and non periodic), and dividing discharge frequency by the mean. Cell discharge varied significantly with speed for the texture + speed- (A) and speed-sensitive (B) cells but not for the texture-sensitive cell (C).

Although not the focus of these analyses, a substantial proportion of cells were sensitive only to texture (longitudinal SP) independent of scanning speed. An example is shown in Fig. 3C (area 3b). For both sets of surfaces, cell discharge increased as SP was increased (see rasters). Texture was a significant factor in the ANOVAs ($P \leq 0.01$); speed was not significant ($P > 0.85$) in either case.

Neuronal sensitivity to scanning speed and texture

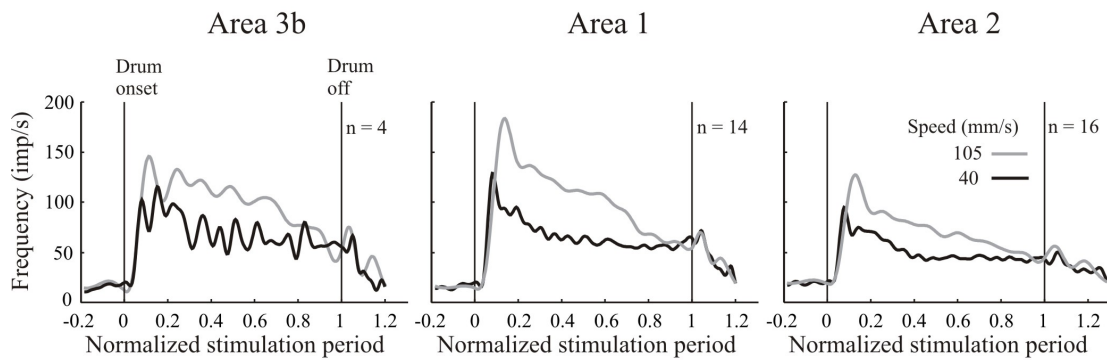
As mentioned above, cell sensitivity to speed and texture was assessed using an ANOVA applied to the data collected with each series of surfaces. The results are summarized in Table 2. The vast majority of cells recorded were sensitive to one or both factors (109/119). Inspection shows that texture-sensitivity was more frequently encountered than speed-sensitivity (95 vs. 76 cells). Speed-sensitivity was frequently combined with texture-sensitivity (62/76, 82%), and rarely seen in isolation (14/76, 18%). In contrast, texture-sensitivity independent of tactile scanning speed was seen in 34% of texture-sensitive cells (33/96).

Table 2. Sensitivity to speed and texture as a function of the cytoarchitectonic area (n = 119 neurones).

	Area 3b (n = 25)	Area 1 (n=51)	Area 2 (n=43)
Texture + speed	12	25	25
Speed	1	7	6
Texture	10	15	8
Ns	2	4	4

Abbreviation: Ns, non significant.

Texture + speed



Speed

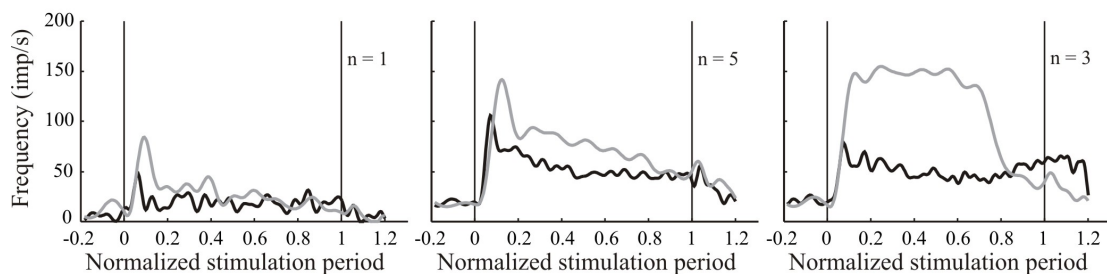


Fig 4. Ensemble averages for cells in areas 3b, 1 and 2 from one monkey (N), showing discharge at slow (40 mm/s, black trace) and fast (105 mm/s, grey trace) speeds. Data are aligned on the onset of drum rotation and normalized to the duration of the stimulation period. Cells were grouped according to their sensitivity to texture and/or speed and their cytoarchitectonic localization within S1. Data from periodic and non periodic surfaces are pooled.

Texture-sensitivity and speed-sensitivity were encountered in all three areas that comprise the S1 hand representation (χ^2 test, $P = 0.64$; Table 2). Figure 4 presents ensemble averages of cell discharge for all of the texture + speed and speed-only cells recorded from one monkey (N: all tested with the same range of speeds and the same surfaces) as a function of the cytoarchitectonic location of the cells. Note that cell discharge was normalized to the average duration of the rotation. For comparison, we only illustrate the response to the lowest and highest speeds (respectively black and grey traces). For the texture + speed cells, the speed signal

showed little change across the 3 areas. Consistent with this, the mean increase in discharge frequency at the highest speed (vs low) was similar in all 3 areas (3b, 64%; 1, 74%; 2, 59%). For the speed-sensitive cells, the increases were also largely similar (increases of, respectively, 80%, 71% and 123%). Note that the larger value for area 2 is explained by the low n and one cell (Fig. 3B).

RA and SA cells were identified in each of the three areas, but there was no obvious trend for the adaptation rate of the cell (RA vs. SA) to influence these categorizations (Table 3). Thus equal proportions of cells that were only texture-sensitive or only speed-sensitive were RA and SA.

Table 3. Adaptation rates of cells (RA/SA,) tested with both sets of surfaces, periodic and non periodic (n=94), as a function of area and speed/texture-sensitivity.

	Area 3b (8 RA/7 SA)	Area 1 (19 RA/23 SA)	Area 2 (14 RA/23 SA)
Texture + speed	5/3	10/11	7/16
Speed	-	3/3	2/4
Texture	3/4	5/8	4/3
Ns	-	1/1	1/-

Nature of the relationship between cell discharge and scanning speed

In order to describe the nature of the relation between discharge rate and speed, linear regressions were applied to the data. For the three single-cell examples (Fig. 3), the results are plotted below. For this graphical representation only,

regressions were fit to the data from each SP. For the texture + speed-sensitive cell (Fig. 3A), there was a monotonic increase in discharge rate as scanning speed increased. The regression curves were parallel, indicating that speed-sensitivity was the same across all textures. There was, however, a systematic effect of SP, so that discharge rates were lowest for the smoothest surface, 2 mm SP, and highest for the roughest surface, 8 mm SP. For the speed-sensitive cell (Fig. 3B), there was also a monotonic increase in discharge rate with speed but in this case the curves were overlapping and independent of SP. For both of these examples, the overall regression was significant ($P < 0.0005$), as were the regressions applied to each set of surfaces (periodic, non periodic). Finally, for the texture-sensitive cell (Fig. 3C), the curves were flat (no relation with speed, $P = 0.96$) and non overlapping, reflecting instead the SP of the scanned surfaces.

Our entire sample of speed-sensitive cells showed an increase in discharge when speed was increased. We characterized the relationship between mean discharge frequency (all SPs pooled) and scanning speed as either graded (monotonic increase as speed increased) or non graded (saturation at higher speeds). For the neurones sensitive only to speed, 12 of 14 were classified as graded (e.g. Fig. 3B). For the texture + speed-sensitive cells, the vast majority (55/62) were also classified as graded (e.g. Fig. 3A). The remaining cells were non graded.

In our human psychophysical experiments, speed estimates were closely similar for periodic and non periodic surfaces. Thus, we expected that neurones involved in tactile speed perception should signal tactile speed independent of dot disposition. A total of 94 neurones were tested for sensitivity to both speed and dot

disposition (Table 3). Of these, 64 were categorized as speed-sensitive, either alone ($n = 12$) or in combination with texture-sensitivity ($n = 52$). The majority of neurones (42/64) were sensitive to speed for both sets of surfaces. The remaining cells, 22/64, were sensitive to speed for only one set of surfaces (11 neurones per set). To determine the extent to which the speed signals were comparable for the periodic and non periodic surfaces, we compared the parameters of the linear regression curves (slope, intercept, r^2). Figure 5 plots the slopes for these regressions (periodic vs. non periodic). Across the sample of 64 speed-sensitive cells, no differences were observed for either the slopes or the intercepts (Wilcoxon tests, $P=0.84$ and $P=0.81$). The r^2 values were slightly higher for the non periodic surfaces ($P = 0.047$). Finally, linear discriminant analyses indicated that there was a significant difference between speed (speed-only and texture + speed combined) and texture-only neurones both as regards slope ($P = 0.0001$) and r^2 values ($P < 0.0005$), but not intercepts ($P = 0.89$). Slopes were higher for speed-sensitive neurones (periodic, 0.45 ± 0.06 ; non periodic, 0.47 ± 0.08) than for texture-sensitive neurones (respectively, 0.06 ± 0.02 and 0.12 ± 0.05). The r^2 values showed a similar trend: speed-sensitive cells (respectively, 0.178 ± 0.019 and 0.21 ± 0.021) $>$ texture-sensitive (0.019 ± 0.004 and 0.024 ± 0.005). To summarize, the majority of neurones were speed-sensitive, usually combined with texture-sensitivity. The higher r^2 values for the non periodic surfaces suggested that the quasi-random distribution of raised dots was a more effective stimulus than the periodically distributed surfaces.

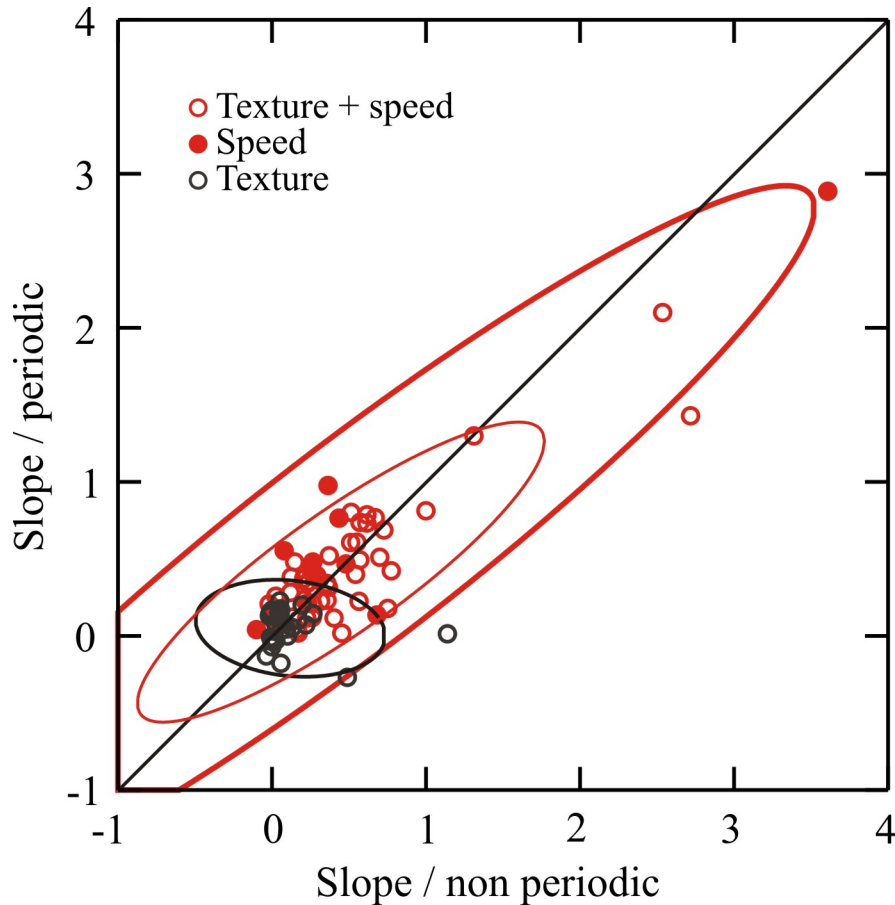


Fig 5. Distribution of slopes for linear regressions (mean discharge rate during epoch 5 vs. speed) for the periodic surfaces (ordinate) as a function of the corresponding slopes for non periodic surfaces (abscissa). Cells were classified as: Texture + speed ($n=52$), Speed-only ($n=12$) or Texture-only ($n=27$). The Gaussian bivariate confidence ellipse (95% probability) is shown for each category. Steeper slopes were obtained for speed-sensitive cells, compared to texture-only cells. The ellipses for the speed-sensitive cells are both oriented along the equality line and cells were equally distributed on either side, $34 >$, $30 <$, consistent with speed-sensitivity being independent of dot disposition.

Nature of the relationship between cell discharge and temporal frequency

One of the main aims of this study was to determine the extent to which discharge frequency covaried with the physical characteristics of the moving textured surfaces, as represented by temporal frequency (speed/longitudinal SP) since this provides a complete description of the skin stimulation. This approach was justified

by our previous observations that human speed estimates are dependent on the physical characteristics of the moving surfaces, an effect that was reduced to a single monotonic continuum by normalizing the estimates to the same spacing and plotting the results as a function of temporal frequency (Fig. 7 in Dépeault et al. 2008).

To pursue this observation, we performed a second set of linear regression analyses. As seen with speed scaling, simple plots of discharge rate as a function of temporal frequency for the two cells illustrated in Fig. 3A-B resulted in families of largely non overlapping curves that reflected the underlying SP of the surfaces (Fig. 6A-B). When discharge rate was normalized by SP, however, the plots were reduced to single monotonic continua in each case (Fig. 6C-D). The net result was that a higher proportion of the variance in cell discharge was explained with this transformation, as compared to the regressions with speed (Fig. 3A-B). For the texture + speed-sensitive cell (Figs 3A and 6C), r^2 doubled, from 0.35 to 0.696. A smaller increase was observed for the speed-sensitive cell (respectively, 0.609 and 0.75, Figs 3B and 6D).

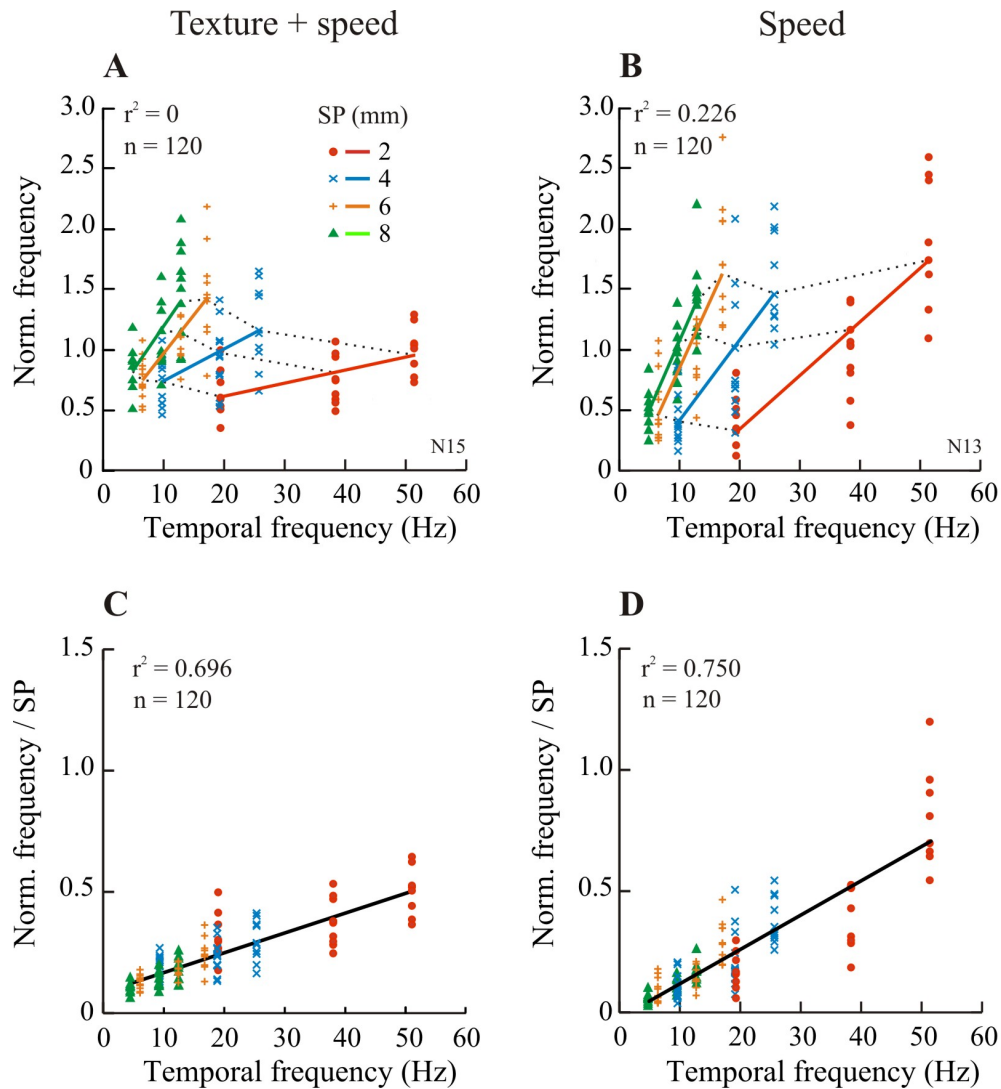


Fig. 6. Single-cell sensitivity to temporal frequency (same speed-sensitive neurones as in Fig. 3). **A-B.** Normalized discharge frequency during the scan plotted as a function of temporal frequency (speed/SP). Separate regressions are shown for each SP, and isocontour lines (dotted) join equivalent speeds. These plots show families of non overlapping curves. **C-D.** Normalized discharge frequency was divided by SP and the data replotted as a function of temporal frequency. This reduced the results to a single continuum that related discharge rate to temporal frequency. The coefficient of variation, r^2 , for the pooled relationship is shown on each panel. The transformation (C-D) substantially increased the r^2 values.

This latter analysis was extended to all of the speed-sensitive cells. As shown in Fig. 7, the r^2 values from the linear regressions were systematically higher for the plots with temporal frequency (discharge normalized by SP) as compared to those

with speed (almost all data points above the line of equality). This impression was confirmed with a paired comparison (Wilcoxon test, $P < 0.0005$). Thus, the relation between discharge rate (normalized by SP) and temporal frequency explained significantly more of the variance in cell discharge than did the relation between discharge frequency and speed. For comparison, Fig. 7 also plots the results from the human psychophysical experiments, small filled symbols (Dépeault et al. 2008). As seen with the single unit data, more variance in the tactile speed estimates was explained by the relation with temporal frequency (estimates normalized by SP) as compared to speed. Moreover, the net improvement was similar for both neuronal and psychophysical data.

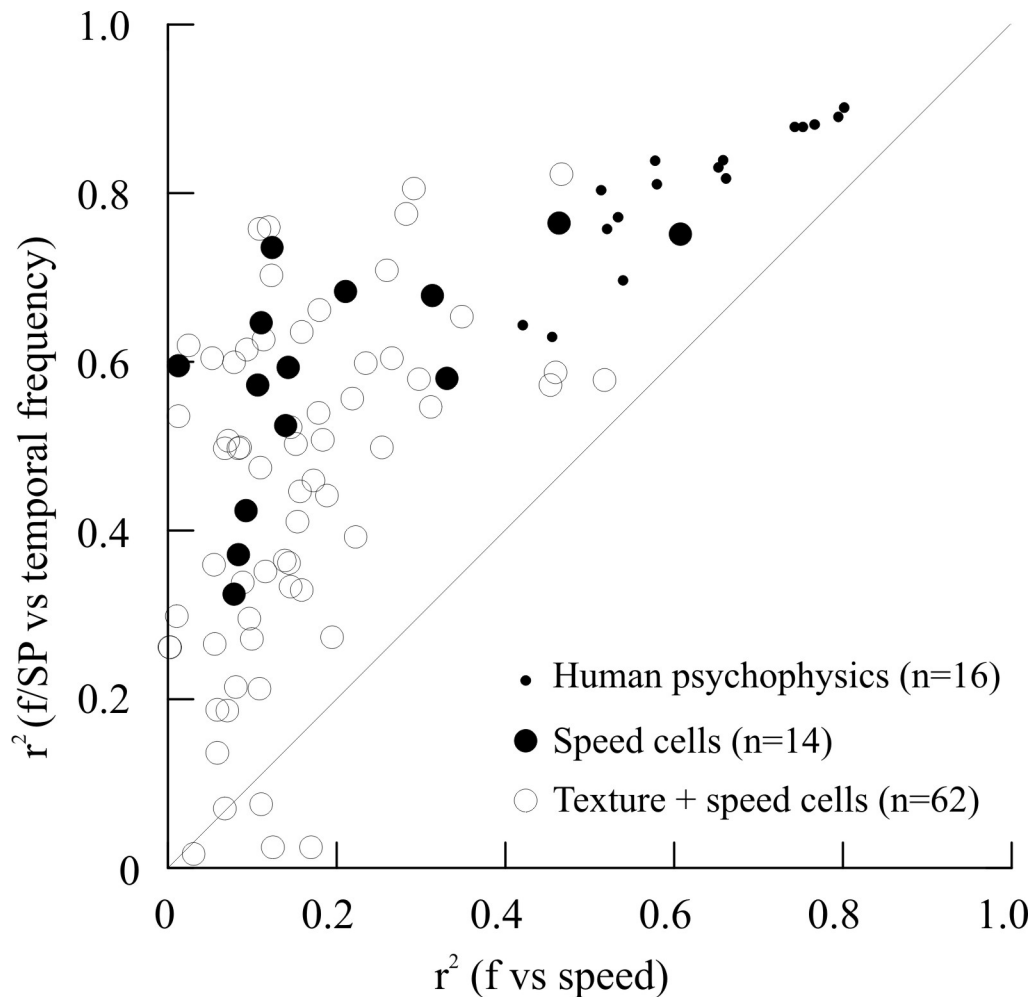


Fig. 7. Results from linear regression analyses (r^2 , coefficient of determination) applied to the texture + speed and speed-only cells. One regression model (abscissa) tested the strength of the relation between discharge frequency and speed, as in Fig. 3. The other (ordinate) tested the strength of the relation between discharge frequency normalized for SP (frequency/SP) and temporal frequency (speed/SP), as in Fig. 6C-D. Only the results of cells with a significant relation to speed are plotted here. For cells with a complete data set (periodic and non periodic, $n=64$), the pooled r^2 is plotted. For the others (only one series tested), the individual r^2 values are shown. For comparison, we plot the corresponding results from the human psychophysical estimates of tactile speed (different subjects for each series, so separate r^2 values for periodic and non periodic surfaces). Note that the r^2 values for the plots with temporal frequency are almost all above the equality line.

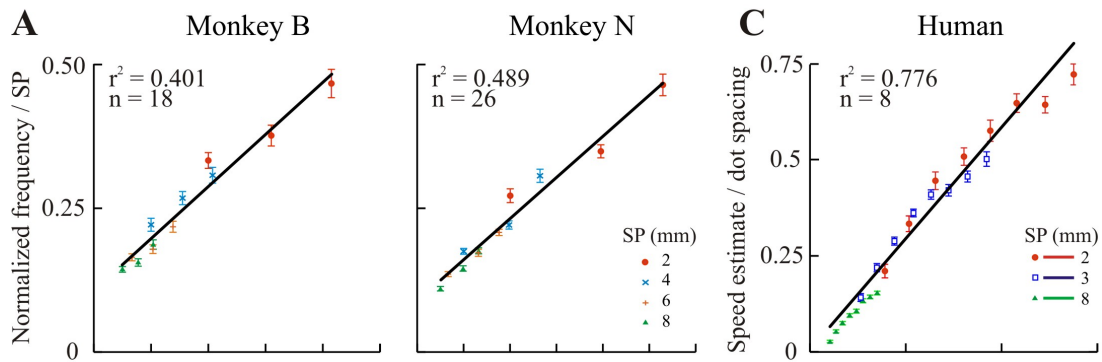
The mean r^2 values (temporal frequency plots) were highest for the speed-sensitive cells (0.65 ± 0.03), lowest for the texture-sensitive cells (not shown, 0.3 ± 0.04), and intermediate for cells sensitive to both parameters (0.46 ± 0.03). A

comparison across the three groups of cells indicated that there was a significant difference in r^2 values (Kruskal-Wallis, $P < 0.0005$). A comparison restricted to those cells sensitive to texture (with vs without speed-sensitivity) was also significant ($P = 0.004$). Finally, speed-sensitive cells (texture + speed and speed-only) with higher r^2 values (≥ 0.4) were mainly restricted to areas 1 and 2 (44/50).

Figure 8A-B shows the pooled relationship between discharge frequency, transformed by dividing by the longitudinal SP (as in Fig. 6C-D), and temporal frequency. Cells were included in this analysis if their discharge covaried with speed and if they were tested with both periodic (A) and non periodic (B) surfaces. Inspection of the results shows that speed-sensitive cells, like the individual examples shown in Fig. 6C-D, show a monotonic increase in discharge rate with temporal frequency, with similar results being obtained in each monkey (left vs. right). Moreover, there was little difference in the results across the two sets of surfaces (A vs B).

Overall, 60 of 64 speed-sensitive cells showed a significant positive relationship with temporal frequency for both sets of surfaces. The remaining showed a significant relation only for one series (2 periodic only, 2 non periodic only). Consistent with our hypothesis, the neuronal results closely match the data from the human psychophysical experiments (Fig 8C, periodic; D, non periodic), suggesting that the discharge of speed-sensitive cells can explain the human perception of tactile scanning speed.

Periodic



Non Periodic

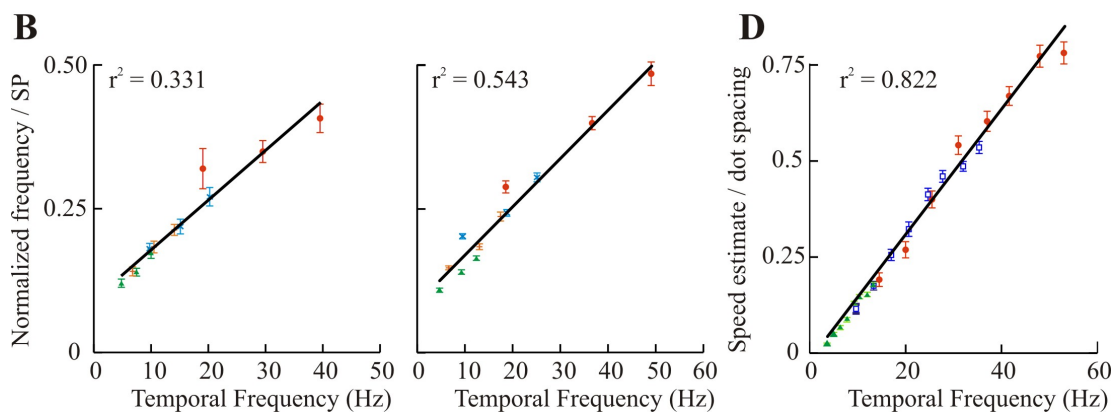


Fig 8. Population analysis of speed-sensitive cells ($n = 64$), **A-B**, and psychophysical results in humans, **C-D**. **A-B**: Neuronal discharge rates [normalized discharge frequency (\pm SEM)/SP] showed a monotonic increase as a function of temporal frequency for both monkeys (B, left; N, right) that was independent of dot disposition since the results were similar for periodic (A) and non periodic (B) surfaces. **C-D**: Normalized subjective estimates of tactile scanning speed (\pm SEM)/SP (8 subjects) also show a monotonic increase with temporal frequency for both periodic (C) and non periodic surfaces (D). Data replotted from Dépeault et al (2008).

Discussion

Consistent with our hypothesis, we identified a population of S1 speed-sensitive neurones that showed a monotonic relation with temporal frequency, independent of the details of dot disposition (periodic vs. non periodic). The neurones with the strongest relations to temporal frequency were concentrated in caudal S1 (areas 1 and 2). Their discharge may underlie the human ability to scale tactile speed.

Sources of tactile speed signals

The sensitivity of peripheral mechanoreceptive afferents to tactile speed has been addressed in a number of earlier studies. As detailed in the Introduction, all of the cutaneous mechanoreceptors that play a role in discriminative touch are sensitive to tactile speed, including afferents categorized as slowly adapting (SAI, SAII) as well as rapidly adapting (RA, PC). In the present study, we categorized each cell according to its adaptation rate since it is known that cortical neurones retain their adaptation properties (Sretevan and Dykes 1983; Sur et al. 1984). In these recordings, no cells with properties consistent with receiving PC inputs were observed (large RF and sensitive to an air puff directed to the field). This is not too surprising since PC-like responses are only rarely encountered in S1 (Hyvärinen and Poranen 1978; Iwamura et al. 1983, 1985; Tremblay et al. 1996). Overall, we found that speed-sensitive neurones had approximately equal proportions of RA and SA (40:60%) responses to maintained touch. Identical proportions were observed for the neurones sensitive only to texture. These findings suggest that all types of afferents contribute to tactile speed appreciation. Although our classification was based on

qualitative responses elicited by manual stimulation, it is interesting that the proportions of SA units identified in areas 3b and 1 (44 and 52%) are fairly close to those reported by Pei et al. (2009) using controlled mechanical stimulation (58 and 46%). Our modestly lower estimate in area 3b may represent sampling bias since SA responses are restricted mainly to middle cortical layers (Sur et al.).

Tactile speed signals in S1 cortex

Speed-sensitivity in S1 bore several similarities to the discharge patterns seen at the level of primary afferents. First, the sign of the relationship between discharge frequency and speed was, in all cases, positive, i.e. discharge rate increased as a function of speed. This observation is consistent with a number of previous studies in S1 which have shown that discharge rates generally increase with increased speed of various stimuli including brushes, scanned surfaces, and simulated moving bars generated with multi-probe arrays (DiCarlo and Johnson 1999; Gardner et al. 1992; Romo et al. 1996; Tremblay et al. 1996; Whitsel et al. 1972). The absence of inhibitory responses to speed in our sample compared to earlier studies (e.g. DiCarlo and Johnson 1999; Sinclair and Burton 1991) can be explained by the sampling procedure since only neurones showing an increase in discharge during surface scanning were tested. Second, cells generally showed a monotonic increase in discharge rate as speed was increased, with little evidence for saturation at higher speeds (~12% of the speed-sensitive cells). The latter was not too surprising since the range of speeds tested, corresponding to speeds used during tactile exploration, was limited. We likewise found no evidence for cells tuned to a particular speed, as seen in the visual system, but this may be a function of the restricted range of speeds

tested (see below). Third, speed-sensitivity was often associated with texture-sensitivity, consistent with the discharge properties of peripheral afferents.

Speed-sensitivity was distributed across all three areas of the S1 cutaneous hand representation, consistent with our previous observations (Tremblay et al. 1996). The proportion of speed-sensitive cells in area 3b, 52%, was lower than that reported by DiCarlo and Johnson (1999), 90%, possibly reflecting their use of a different range of speeds (20–80 mm/s vs 40–105 mm/s here) and/or differences in the physical characteristics of the surfaces (dot height, material, etc.). Our results suggested that there is a trend for a rostrocaudal gradient in speed-sensitivity: area 3b, 52%; 1, 63%; and 2, 72%. Moreover, the speed-only cells were almost entirely restricted to areas 1 and 2. When combined with the observation that areas 1 and 2 contained the large majority of the cells showing a strong relation with temporal frequency (44/50), we suggest that these two areas likely play an important role in tactile speed. We have previously suggested that the rostral areas (3b and 1) are particularly concerned with tactile texture (Meftah et al. 2009), and this in agreement with the work of others (e.g. Connor et al. 1990; Connor and Johnson 1992; Darian-Smith et al. 1982; Sinclair and Burton 1991). We now suggest that caudal S1, specifically areas 1 and 2, is preferentially involved in extracting speed signals. This scenario is supported by the observation that only 24% of texture cells in area 2 were insensitive to scanning speed, as compared to 45% for area 3b and 38% for area 1.

Our observation of speed-only (n=14) and texture-only discharge patterns (n=33) in S1 is consistent with previous reports (Tremblay et al. 1996; Jiang et al. 1997). We have previously suggested (Meftah et al. 2000) that such response patterns

may reflect the result of a central transformation, subtracting either texture or speed on-line from the original texture- and speed-varying signal. To explain the speed-only cells, the necessary speed-invariant texture signal is present in S1, and this may represent the output of the SAI-mediated spatial variation code for tactile roughness (Connor et al. 1990). This code is insensitive to changes in scanning speed (DiCarlo and Johnson 1999) and is thought to be transformed into a mean rate code at some level in the processing of tactile inputs (Johnson and Hsiao 1992). The speed-only cells were mainly found in areas 1 and 2, while the texture-only cells were especially characteristic of areas 3b and 1. Thus, the transformation likely occurs in the more caudal parts of S1 where speed-only cells were found (areas 1 and 2).

Texture-sensitivity in S1 cortex

The discharge of a high proportion of the S1 neurones, 80% of the sample, co-varied with the longitudinal SP of the periodic and/or non periodic raised-dot surfaces. The relationship to SP was not analysed in detail in this report but it is of note that a proportion of these showed a monotonic increase in discharge rate across the range of SPs tested here, 2 to 8 mm (e.g. Fig. 3C). Such a discharge pattern, along with insensitivity to scanning speed (Fig. 3C), is consistent with such a neurone playing a key role in scaling the roughness of textured surfaces since roughness estimates (same surfaces) also show a monotonic increase as SP is increased (Dépeault et al. 2009), and are insensitive to changes in scanning speed (Meftah et al. 2000).

Neuronal code for tactile speed

The main measure of cell sensitivity to tactile speed was the mean discharge rate during the entire stimulation period. We tested the possibility that tactile speed might be signalled in S1 by a spike count code, but our analyses showed that the mean rate code gave superior results to those obtained using the spike count measure. Indeed, for the obviously speed-sensitive neurone illustrated in Fig. 3B, spike count showed no change across the three scanning speeds whereas the discharge rate increased significantly. Our results are consistent with those of Essick and Edin (1995) who showed that primary tactile afferents sensitive to tactile motion use a mean rate code and not a spike count code. Indeed spike counts actually decline as brushing speed increases. Thus, we rejected the possibility that tactile speed is signalled by a spike count code.

The choice of analysis interval (epoch 5, Fig. 2) was in turn based on the results of preliminary analyses that showed that the strength of the relationship between discharge rate during this period and speed was higher than for measures restricted either to the first or second half of the surface scans. Similar results were obtained for the temporal frequency analyses (as in Figs 6-8). We were, however, surprised that the measures based on the first half of the surface presentation did not give stronger correlations. This measure gives greater weight to the initial part of the surface presentation and Luna et al. (2005) had suggested earlier that S1 may rely on a forward weighted code to signal differences in flutter vibration frequencies. Although we cannot discount the possibility that task differences (somatosensory discrimination task in Luna et al. vs. diversionary task here) contributed to our

negative result, the difference can more likely be explained by the neuronal code used – a mean rate code here versus a spike count code for Luna et al. which, as explained above, was not well suited for the present data.

Overall, we suggest that the neuronal basis for tactile speed estimates can best be explained by the discharge properties of the speed-sensitive neurones located in areas 1 and 2. These neurones showed the best fit between mean rate and the temporal frequency of the applied stimuli, with the latter providing a complete description of the spatial and temporal dimensions of the stimuli. Their discharge was likewise independent of dot disposition (periodic = non-periodic), as predicted. It remains to be determined, however, whether all of the speed-sensitive neurones contribute to subjective tactile speed estimates or if the speed-only cells might subserve this function, representing a form of sparse coding (Olshausen and Field 2004). Further experimentation, within the context of a speed psychophysical task is needed.

Finally, our suggestion that speed-sensitive neurones contribute to subjective tactile speed estimates is limited to the range of speeds and surface textures investigated here. The present experiments need to be extended to include finer textures, since these can be more effective stimuli for other types of cutaneous mechanoreceptive afferents, including PC afferents (Bensmaia and Hollins 2003).

Parallels with visual motion

Sensitivity to motion is a general characteristic shared across the major sensory systems (somatosensory, visual, auditory and vestibular). In the present study, we were struck by the general lack of obvious speed tuning. In contrast, speed-tuning in visual cortices has been reported in both cats and monkeys, and this can take many forms including velocity low-pass, high-pass, broad-band and tuned responses (e.g. Orban et al. 1981, 1986). Such tuning is present in retinal ganglion cells (Cleland and Lee 1985). In contrast, primary cutaneous mechanoreceptive afferents (Edin et al. 1995; Essick and Edin 1995; Goodwin and Morley 1987; Greenspan 1992; Lamb 1983) do not show tuning, suggesting that motion is not processed in the same manner in the visual and somatosensory systems. Alternately, the lack of tuning may be a function of the limited range of speeds tested, restricted here to speeds used during active touch. Thus, our testing covered a range of speeds associated with monotonically increasing rates of discharge in cutaneous afferents (Essick and Edin 1995). Saturation of discharge can occur, but this is associated with higher speeds than those tested here.

Motion sensitivity in vision is generally associated with the “dorsal” pathway which is specialized for action (Goodale and Milner 1992; Milner and Goodale 2008; Ungerleider and Mishkin 1982). Within the visual system, motion sensitivity is generally a property of higher order visual areas (e.g. the middle temporal, MT, and medial superior temporal areas, MST) (Britten et al. 1993; Celebrini and Newsome 1994; Liu and Newsome 2005; Wurtz and Duffy 1992). There is some suggestion that somatosensory processing is also organized into dorsal and ventral streams

(Friedman et al. 1986; Mishkin 1979). Although our recordings in S1 were at a relatively low level of processing, it is interesting that the speed-only cells were mainly found in the more posterior areas of S1, areas 1 and 2. Since speed and texture signals are confounded in the discharge of primary mechanoreceptive afferents, this pattern of discharge must represent the result of central processing to extract the portion of the signal related to speed. It is interesting to speculate that these speed-only cells might preferentially project to posterior parietal cortex, and so the dorsal stream, rather than to S2 (the ventral stream). The present recordings were extended to include S2 to determine the extent to which the properties seen in S1 are also seen in S2 (unpublished observations, Cybulska-Klosowicz A, Meftah EM and Chapman CE). Preliminary analyses do not, however, support this suggestion since speed-only cells are also found in S2, and this in about the same proportion as seen in S1. An alternate interpretation is that both streams of processing require basic information about tactile motion both for planning and executing movements (dorsal stream) and for perception (ventral stream).

As also seen in the visual system (Campbell and Maffei 1981; Diener et al. 1976; cf Smith and Edgar 1990), tactile speed scaling varies with the physical characteristics of the moving patterns, and so is dependent on both temporal and spatial cues (Dépeault et al. 2008). Specifically, a decrease in spatial frequency ($1/SP$) causes a decrease in perceived speed. As we had predicted earlier, the present study has shown that the stimulus-response functions of S1 neurones sensitive to scanning speed showed a monotonic increase as a function of temporal frequency, consistent with speed-sensitive S1 neurones playing a key role in tactile speed

perception. In contrast, and as also predicted, neurones sensitive to texture-alone (e.g. Fig 3C) showed no sensitivity to temporal frequency with the slope of the neurometric function approaching 0. Together such findings suggest that important parallels exist between the somatosensory and visual systems as regards the processing of stimulus motion.

Concluding remarks

We identified a population of neurones, mainly located in areas 1 and 2, with discharge properties consistent with playing a role in scaling tactile speed. Specifically, their discharge rate when normalized for SP showed a monotonic relation with temporal frequency. This relationship was moreover, as predicted by our psychophysical results (Dépeault et al. 2008), independent of the disposition of the raised dots that formed the surfaces (periodic, non periodic). Our results also suggest that the underlying neuronal code is a simple rate code, the same code that is used by the primary mechanoreceptive afferents that are sensitive to tactile speed (Essick and Edin 1995). This latter observation raises an interesting question. Work from Johnson and collaborators (Connor et al. 1990; Connor and Johnson 1992; Yoshioka et al. 2001) has promoted the hypothesis that tactile roughness is not signalled by a mean rate code, but by a spatial variation code. The latter code has the interesting property of being insensitive to scanning speed (DiCarlo and Johnson 1999), and so can account for the invariance of roughness estimates at different speeds (Lederman 1983; Meftah et al. 2000). So, do peripheral afferents use different neuronal codes to signal various physical attributes, a spatial variation code for texture and a mean rate code for speed and force (e.g. Wheat et al. 2010)? We are

currently investigating the neuronal code for tactile roughness, re-examining the mean rate code.

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DISCUSSION GÉNÉRALE

Grâce à ces expériences, nous avons pu suggérer des bases neuronales expliquant l'intensité subjective de la vitesse tactile. L'hypothèse établie dans l'étude de l'article 1, comme quoi les cellules sensibles à la vitesse dans S1 devraient avoir une relation linéaire avec la fréquence temporelle, a été confirmée. Donc la grande majorité des neurones sensibles à la vitesse sont aussi sensibles à la rugosité. De plus, tel qu'attendu, la relation est généralement indépendante de la disposition des points.

1. Article # 1

Cette étude a démontré que les sujets sont capables d'estimer la vitesse tactile, sans indice de durée ni de distance. De plus, la présence d'éléments tactiles semble très importante pour l'estimation de la vitesse, puisque les sujets ont beaucoup de difficulté à estimer la vitesse tactile d'une surface lisse. L'espacement des éléments tactiles dans le sens de l'exploration influence toutefois les estimés (sous-estimation de la vitesse pour le plus grand espacement comparée aux surfaces de petit espacement). Une relation linéaire est obtenue lorsque les estimés sont normalisés en les divisant par l'espacement et qu'ils sont exprimés en fonction de la fréquence temporelle. Finalement, la disposition des points n'affecte pas la perception de la vitesse tactile. Ces données ont permis d'émettre des hypothèses concernant l'encodage probable de la vitesse tactile, soit que la fréquence de décharge, des neurones du S1 encodant la vitesse tactile, devrait varier avec la fréquence temporelle, et ce indépendamment de la disposition des points.

2. Article # 2

Les résultats du premier article (périodique = non périodique) suggéraient que les estimés de rugosité devraient aussi être égaux pour les deux séries de surfaces. Cette hypothèse a été vérifiée, et validée, dans cette étude. Effectivement, les sujets percevaient les surfaces périodiques et non périodiques comme ayant la même rugosité, et ce quand les dispositions de points étaient équivalentes pour l'espace longitudinal moyen (deuxième partie de l'étude). La première partie de l'étude a comparé les surfaces périodiques à des surfaces non périodiques densité équivalente. Cette étude suggère donc que les neurones jouant un rôle dans la perception de la rugosité subjective devraient avoir une relation monotone avec la PS et ce indépendamment de la disposition des points.

3. Article # 3

L'hypothèse développée dans le premier article a été testée ici grâce à l'enregistrement de la décharge de neurones cutanés du S1 chez le singe lorsque des surfaces périodiques et non périodiques étaient présentées sous le bout des doigts. Les résultats ont confirmé l'hypothèse et on a aussi identifié un petit nombre de neurones sensibles seulement à la vitesse tangentielle. Ces cellules ne signalaient pas les changements de PS pour la gamme utilisée. La sensibilité à la vitesse était distribuée dans les trois aires étudiées (3b, 1 et 2), mais était plus fréquente dans la partie postérieure de S1 (aires 1 et 2).

4. Forces de ces études

Une des principales forces est que l'étude psychophysique initiale chez l'humain (Article 1) a permis de générer deux hypothèses claires pouvant être testées avec une étude psychophysique supplémentaire (Article 2) et avec les données neuronales (Article 3). Ces résultats s'inscrivent donc dans une approche expérimentale, introduite par Mountcastle avec ses études sur la perception et l'encodage de la vibration, visant à comprendre les mécanismes neuronaux de la perception.

Tandis que les résultats neuronaux ont confirmé notre hypothèse (sensibilité des neurones à la fréquence temporelle), il est quand même à noter qu'une faible proportion des neurones était sensible à la vitesse tactile seulement pour les surfaces périodiques et pas du tout pour les surfaces non périodiques, ou vice versa. Ces neurones représentent environ 15% des neurones ayant eu une évaluation complète, soit 14/ 94. La proportion de cellules sensibles à seulement une série était identique dans chaque aire (3b, 20%; 1, 19%; 2, 22%). Au total, il y avait un nombre égal sensible pour les périodiques seulement ($n = 9$) et pour les non périodiques ($n = 10$). Une explication de ce phénomène pourrait être que l'isolement de la cellule n'a pas été maintenu tout au long de l'enregistrement. Ceci est toutefois peu probable car la forme du potentiel d'action était observée tout au long de l'enregistrement et elle restait la même. De plus, le champ récepteur était réévalué à la fin de l'enregistrement, si possible, et celui-ci aussi restait le même. Donc ce type de patron de décharge suggère que la vitesse tactile pourrait être représentée par un code

populationnel, nécessitant la contribution de plusieurs neurones pour donner une représentation centrale de la vitesse tactile.

Les résultats de la deuxième étude psychophysique (Article 2) démontrent aussi une indépendance des estimés de rugosité en fonction de la disposition des éléments tactiles (périodiques vs non périodiques). Cette observation sert comme base pour l'hypothèse applicable aux analyses de sensibilité à la texture au niveau des neurones de S1. Notre hypothèse est que les neurones de S1 jouant un rôle dans l'estimation de la rugosité subjective des surfaces texturées devraient montrer une relation monotonique entre leur taux de décharge et la PS (2 à 8 mm), et ceci indépendamment de la disposition des points en relief, périodique ou non périodique. La décharge devrait également être indépendante de la vitesse tactile, en concordance avec l'invariance de la rugosité avec la vitesse tactile (Lederman 1974, 1983, Meftah et al 2000). Les analyses préliminaires démontrent que, comme pour la sensibilité à la vitesse, la sensibilité à la rugosité est une fonction distribuée, impliquant les neurones dans les trois aires de S1 (3b, 1 et 2). Une grande proportion des neurones est sensible à la texture (80% de l'échantillon), le tiers étant indépendant de la vitesse. De plus, les deux tiers des neurones sensibles à la texture le sont pour les deux séries de surfaces. La proportion des cellules indépendantes à la vitesse ayant une relation « graded » (relation monotonique avec la PS), pour les deux séries de surfaces est toutefois faible. Un patron « non graded » (saturation de la réponse pour les PS élevées) est plus fréquent et il y a même quelques exemples de courbe en U inversé. Une analyse plus approfondie est en cours. Ceci est un bon exemple de la variété de réponses des neurones corticaux et donc de la richesse de la perception tactile.

5. Comparaison entre la vitesse tactile et la vitesse visuelle

Le cortex visuel est vaste et séparé en au moins neuf aires (Van Essen et al 1982). La perception de la vitesse a beaucoup été étudiée dans le système visuel et il semblerait que plusieurs aires soient responsables de son traitement. Une serait plus importante que les autres, c'est l'aire MT (medial temporal) qui est aussi nommé V5 (Baker et al 1981, Maunsell et Van Essen 1983). Ses neurones sont sensibles à plusieurs caractéristiques du mouvement, surtout la direction du mouvement des barres ou points aléatoires ainsi que leur vitesse. En effet, des lésions (Newsome et al 1985) ou des inactivations temporaires en utilisant des stimulations magnétiques transcrâniennes (McKeefry et al 2008) dans cette aire entraînent une diminution de la capacité à discriminer la vitesse visuelle. La réponse à la vitesse tactile semble toutefois présente dans toutes les régions somatosensorielles (trois aires de S1 : 3b, 1 et 2, ainsi que S2; la sensibilité ailleurs – aires 5 et 7 – reste à déterminer). Les prochains paragraphes vont donc comparer l'encodage de la vitesse tactile et visuelle.

Trois patrons d'encodage de la vitesse sont présents dans le système visuel, incluant des courbes en U inversé (sensibilité à une gamme restreinte de vitesses; aucune réponse aux vitesses visuelles supérieures ou inférieures à la zone sensible), de courbes de sensibilité à basses vitesses seulement (aucune réponse aux vitesses supérieures) et de courbes de sensibilité à une grande gamme de vitesses (à très hautes vitesses, les neurones ne répondent plus) (Lagae et al 1993). Au niveau tactile (cortical), nous n'avons vu que deux patrons d'encodage, monotonique (une relation monotonique entre la fréquence de décharge et la vitesse tactile) et non monotonique (similaire au patron monotonique, mais avec saturation de décharge à partir d'une

vitesse tactile). La plupart des neurones sensibles à la vitesse ont montré un patron monotonique (88%), les autres étant classifiés comme non monotonique. Nous suggérons que le patron monotonique ressemble au patron de sensibilité à une grande gamme de vitesse. Il se peut que notre patron non monotonique ressemble au patron de sensibilité à basses vitesses, mais le taux de décharge ne tombe jamais à zéro comme c'est le cas pour les neurones visuels. Ceci est possiblement expliqué par l'utilisation d'une gamme restreinte de vitesses tactiles dans nos études. Il est donc possible que des courbes en U inversé puissent être observées en utilisant une gamme de vitesses beaucoup plus grande. En effet, les fréquences temporelles utilisées dans nos expériences atteignent environ 50 Hz, ce qui couvre très peu la gamme possible si nous considérons que les afférences PC sont sensibles à des fréquences pouvant aller jusqu'à 400 Hz. La gamme de 50 à 400 Hz reste donc à être explorée et des courbes en U inversé pourraient y être observées. Une limitation méthodologique, reliée au moteur contrôlant la rotation du tambour, empêche toutefois de présenter des surfaces texturées à vitesse plus rapide. Une autre limitation de nature sécuritaire est que la main de l'animal n'est pas fixée, donc des vitesses rapides pourraient entraîner un risque de lésions aux doigts des singes (entraînement des doigts à l'intérieur du stimulateur).

Une autre caractéristique commune à la perception de la vitesse tactile et visuelle est l'effet de la texture. Dans les deux systèmes, l'intensité subjective de la vitesse est diminuée en augmentant l'espacement entre les stimuli, que ce soit en diminuant la fréquence spatiale ($1/PS$) pour les stimuli visuels périodiques (Campbell et Maffei 1981, Diener et al 1976, cf. Smith et Edgar 1990) ou en diminuant le

nombre d'éléments visuels pour les champs de points aléatoires en mouvement (Watamaniuk et al 1993). Donc le signal de vitesse ne serait pas indépendant du signal de texture dans ces deux modalités. Tel que démontré dans le troisième article, la grande majorité des cellules sensibles à la vitesse le sont aussi à la texture dans S1. Ceci a aussi été observé dans l'aire MT, soit que l'encodage de la vitesse visuelle dépend de la fréquence spatiale d'une onde sinusoïdale (Priebe et al 2003).

6. Effet de l'attention

L'attention peut modifier la perception de stimuli tactiles, visuels et auditifs. Nous avons aussi quelques connaissances sur les mécanismes neuronaux impliqués, par exemple pour la rugosité et la vibration tactile. Il n'y a toutefois aucune donnée concernant l'effet de l'attention sur la perception de la vitesse tactile.

La plupart des connaissances sur l'effet de l'attention sur le traitement des données sensorielles proviennent des études dans le système visuel. L'attention module la réponse neuronale aux stimuli visuels et ce dès V1 (cortex visuel primaire), qui est un des premiers relais d'analyse de l'information visuelle. Elle a toutefois plus d'effet dans les stades plus avancés du traitement de l'information (V4, cortex inférotemporel; révisé dans Desimone et Duncan 1995, Kanwisher et Wojciulik 2000).

C'est relativement récemment qu'il a été démontré que l'attention sélective rehausse la perception de stimuli tactiles (Johansen-Berg et Lloyd 2000, Johnson et Haggard 2003, Post et Chapman 1991, Spence et McGlone 2001, Zompa et Chapman

1995). Par exemple, les sujets sont plus rapides à détecter un stimulus vibrotactile quand l'attention est sur la main stimulée vs l'autre main (Spence et McGlone 2001). Ce phénomène est de l'attention spatiale. L'attention peut également être dirigée vers différentes modalités (attention intermodale) : les réponses sont plus rapides quand l'attention est dirigée vers la modalité tactile, en comparaison aux situations d'attention divisée (ex. visuelle et tactile) ou mal-dirigée (Post et Chapman 1991). Les sujets répondent également avec plus de précision quand l'attention est dirigée vers les stimuli tactiles (tâche de discrimination de la rugosité; Zompa et Chapman 1995).

Au niveau neuronal, certaines cellules de S1 et S2 (en plus grand nombre) sont sensibles à l'effet de l'attention (Burton et Sinclair 2000, Burton et al 1997, Chapman et Meftah 2005, Hsiao et al 1993, Meftah et al 2002, Romo et al 1996, Salinas et al 2000, Steinmetz et al 2000). La distribution de l'effet de l'attention dans S1 aurait une légère augmentation rostro-caudale dans certaines études (Hyvarinen et al 1980, Meftah et al 2002). Tandis que d'autres études suggèrent une distribution uniforme (Burton et Sinclair 2000, Hsiao et al 1993), ces deux études n'avaient toutefois pas exploré l'aire 2.

L'effet de l'attention sur les neurones corticaux de S1 et S2 n'est toutefois pas le même d'une expérience à l'autre. Par exemple, des études montrent que la fréquence de décharge augmente quand l'attention est dirigée vers le stimulus tactile (Chapman et Meftah 2005, Hsiao et al 1993, Meftah et al 2002, Romo et al 1996, Salinas et al 2000). Burton et Sinclair (2000) ont toutefois observé une suppression de la fréquence de décharge comme effet prédominant de l'attention. Il faut

mentionner que les stimuli et tâches varient beaucoup d'une expérience à l'autre: discrimination de la rugosité, de la forme locale, de la vibration et de la douleur thermique, et la catégorisation de la vitesse d'une sonde.

De plus, l'effet de l'attention est différent entre S1 et S2. Pour la tâche de discrimination de la rugosité de l'équipe de Chapman, la fréquence de décharge est augmentée seulement durant le changement de texture dans S1 (période comportementalement importante), tandis qu'elle est augmentée tout au long de l'essai dans S2 (Chapman et Meftah 2005, Meftah et al 2002). Ceci pourrait représenter une modulation en deux étapes, soit un stade initial dans S1, et un autre dans S2.

Il est donc très probable qu'il y ait un effet de l'attention sur la vitesse tactile. Au niveau du S1, l'attention pourrait moduler la fréquence de décharge des neurones selon le contexte (tâche vs non tâche). Dans le troisième article, la tâche utilisée était une discrimination visuelle, donc l'attention était contrôlée mais non dirigée vers le stimulus tactile. Avoir utilisé une tâche de discrimination de la vitesse tactile aurait probablement augmenté la fréquence de décharge des neurones. L'impact d'un tel effet est probablement minimal. En présumant que les effets sont similaires aux effets sur la sensibilité neuronale à la rugosité tactile, on peut attendre aucune modification des pentes des régressions linéaires (fréquence de décharge en fonction de la vitesse tactile); les interceptes, par contre, pourraient être plus hauts si on avait utilisé une tâche de discrimination de la vitesse tactile.

7. Utilisation du singe comme modèle

Les études électrophysiologiques sont limitées chez l'humain car évidemment, il n'est pas éthique d'effectuer des enregistrements dans leur cerveau à l'exception des interventions neurochirurgicales. De tels cas ne se présentent que rarement, et souvent les structures enregistrées sont touchées par une pathologie : par exemple, les noyaux gris centraux dans le cas d'intervention pour implanter des électrodes de stimulation afin de contrôler les symptômes associés à la maladie de Parkinson, électrostimulation cérébrale profonde. Un modèle animal est donc nécessaire pour permettre d'étudier les bases neuronales des résultats perceptuels.

Plusieurs observations indiquent que le singe est un bon modèle pour étudier la perception somatosensorielle. Premièrement, ils ont des capacités perceptuelles similaires. Par exemple, Mountcastle et al (1972) ont démontré que le seuil de détection de la vibration (2-400 Hz) au niveau de la main est identique entre le singe et l'humain. En ce qui concerne le seuil de discrimination de la vibration, il est aussi similaire : les deux espèces peuvent discriminer une différence d'environ 10% entre deux fréquences vibratoires (LaMotte et Mountcastle 1975). Pour la discrimination de la texture, le seuil est d'environ 20-25% chez les deux espèces (Meftah et al 2002, Sinclair et Burton 1991b, Zompa et Chapman 1995). Ces résultats ont été obtenus avec un seul passage sur la surface, mais des seuils plus bas (environ 5%) pourraient être obtenus avec une exploration illimitée (Lamb 1983a).

Deuxièmement, les caractéristiques physiologiques des afférences périphériques sont similaires chez le singe et chez l'humain. En utilisant la technique

de microneurographie, Phillips et al (1992) ont enregistré les patrons d'activité des quatre types d'afférences (RA, PC, SAI et SAII) de la peau glabre chez l'humain en réponse à la présentation de différentes surfaces texturées. Les surfaces étaient très similaires à celles de Connor et al (1990), des patrons de points tétraogonaux. Les patrons de décharge sont très similaires pour tous les types d'afférences (RA, PC, SAI) chez l'humain et le singe. Les SAII (absents dans la peau glabre du singe), quant à eux, ressemblent aux afférences PC. Ces résultats suggèrent que l'encodage sensoriel en périphérie et probablement même à des niveaux hiérarchiques plus élevés est très similaire entre les deux espèces, et donc que le singe serait un bon modèle à utiliser pour expliquer la perception de la rugosité et de la vitesse tactile chez l'humain.

8. Estimation de la vitesse d'une surface lisse

L'étude présentée dans le Chapitre 2 a démontré que les sujets humains avaient beaucoup de difficulté à estimer la vitesse de la surface lisse, toutefois cette tâche n'était pas totalement impossible. Donc, quels facteurs auraient pu donner des indices de vitesse? Il y a trois sources potentielles d'information. Premièrement, seuls les SAI déchargent pendant le déplacement continu d'une surface lisse (Srinivasan et al 1990), mais on ne sait pas si leur décharge varie avec la vitesse de présentation car Srinivasan et al n'avaient utilisé qu'une seule vitesse (10 mm/s). Tremblay et al (1996) ont utilisé une surface lisse présentée à différentes vitesses lors d'enregistrements dans le S1, mais l'analyse est plutôt concentrée sur les surfaces

texturées. Par contre, l'observation des figures ne supporte pas l'idée que la décharge des neurones du S1 (incluant les SA) reflète la vitesse de présentation d'une surface lisse. Deuxièmement, il est possible que les RA et PC aient été recrutés pendant le déplacement de la surface lisse en raison de la présence d'imperfections sur la surface (LaMotte et Whitehouse 1986, Srinivasan et al 1990; voir aussi Bensmaïa et Hollins 2005) et donc plus d'information concernant la vitesse tactile. On ne peut pas ignorer cette possibilité, mais nous avons utilisé le même stimulateur tactile que Tremblay et al, et la surface lisse était fabriquée de la même façon. Finalement, le déplacement initial de la peau (glissement ou 'slip') lié à l'accélération du tambour pourrait être un facteur. Srinivasan et al (1990) ont démontré que l'étirement initial de la peau par une surface lisse active tous les types de mécanorécepteurs de la peau glabre chez le singe (SAI, RA et PC), ce qui pourrait correspondre à la source d'information principale. En ce qui concerne nos résultats, l'examen de la Figure 5 du premier article (estimés en fonction de la vitesse pour la surface lisse) démontre que la plupart des sujets étaient seulement capables de distinguer les vitesses lentes des vitesses rapides (deux catégories). Donc peu importe la source d'information, la capacité à estimer la vitesse d'une surface lisse est très limitée.

9. Directions futures

D'autres expériences peuvent découler de cette thèse pour augmenter la compréhension de la perception de la vitesse tactile (psychophysique et neuronale). Quelques exemples seront mentionnés dans les prochains paragraphes: 1) l'effet de la

force tangentielle et de l'attention sur la perception de la vitesse, 2) la capacité de discriminer la vitesse tactile, 3) l'encodage de la vitesse dans S2, ainsi que 4) les neuroprothèses.

Une mesure dynamique des forces (normale et tangentielle) durant une expérience sur la vitesse tactile pourrait être très intéressante. Les changements de force (et aussi de friction) sont très importants dans la manipulation d'objets (dont les glissements entre objet et peau) et l'exploration tactile. Ils semblent aussi présents avec les variations de vitesse pendant l'exploration d'une surface (Poisson Fortier et Smith non publié). Il a aussi été démontré que le taux de changement de la force tangentielle augmente avec une augmentation de l'intensité subjective de la rugosité pour les surfaces ayant des points en relief (disposition périodique) (Smith et al 2002). La contribution serait probablement complexe puisque les changements de force tangentielle sont probablement beaucoup plus importants avec les rangées de points des surfaces périodiques, comparativement aux surfaces non périodiques. L'absence de différence dans l'estimation de la vitesse entre les surface périodiques et non périodiques suggère que les variations dans la force tangentielle ne semble pas un facteur clé expliquant l'estimation de la vitesse. Le rôle, si présent, des variations de la force tangentielle dans l'estimation de la vitesse nécessiterait la confection d'un stimulum sensible aux forces et pouvant présenter des surfaces a différentes vitesses.

L'estimation de la vitesse tactile a été étudiée dans cette thèse. Toutefois, les sujets peuvent estimer l'intensité de stimulation d'un nombre restreint de stimuli seulement, tandis que le nombre de combinaisons qu'on peut discriminer est énorme.

Le seuil de discrimination correspond à la plus petite différence pouvant être perçue adéquatement (75% de réussite) entre 2 stimuli. Il suit habituellement la loi de Weber, où $\Delta S/S = k$ (S : stimuli; k : constante), donc la différence est une fraction de la valeur du stimulus standard. Par exemple, pour la discrimination de la rugosité (PS), il est d'environ 2 à 5% (Lamb 1983a, Morley et al 1983), tandis que pour la perception de la raideur générée par un moteur externe, il est de 23% (Jones et Hunter 1990). En ce qui concerne la vitesse, nos connaissances sont présentement limitées. Romo et collègues ont développé une tâche de catégorisation de la vitesse d'une probe déplacée sur la peau (Merchant et al 1997; Romo et al 1996). Les singes étaient capables de discriminer des vitesses de 20 et 22 mm/s (10%). Ces études avaient deux limites : des plus petites différences n'ont toutefois pas été utilisées et la durée variait entre les vitesses (longueur de peau stimulée constante à 6 mm), donc il est impossible d'éliminer sa contribution aux résultats.

Additionnellement, l'effet de l'attention sur la perception de la vitesse et son encodage n'a jamais été étudié. Puisque l'attention a un effet sur la perception de la rugosité et la vibration tel que mentionné ci-haut, on s'attend à ce qu'elle ait aussi un effet sur la perception de la vitesse tactile. Donc, par exemple, on s'attend à ce que les sujets puissent plus facilement discriminer deux vitesses tactiles lorsque l'attention est dirigée sur cette tâche. De plus, des enregistrements au niveau des neurones corticaux pourraient démontrer un effet additif dans le S1 tandis que ce serait un effet multiplicatif au niveau de S2, selon les observations avec la rugosité de Chapman et Meftah (2005). Ceci permettrait donc de vérifier si cet effet (additif dans S1 vs multiplicatif dans S2) peut être généralisé à d'autres sous-modalités tactiles.

De plus, la question suivante se pose: est-ce que tous les neurones sensibles à la vitesse dans S1 contribuent à la perception subjective de la vitesse? Une interprétation de nos résultats est que toutes les cellules sensibles à la vitesse contribuent à l'estimation de la vitesse tactile. Ce serait donc un encodage populationnel distribué à travers tous les neurones, similairement à celui de la directionalité du mouvement dans l'aire 4 (Georgopoulos et Massey 1988). Il y avait toutefois une grande variabilité de sensibilité à la fréquence temporelle, et ce surtout pour le groupe vitesse + texture où 35% ont un r^2 plus petit que 0.4 (décharge vs fréquence temporelle). Une possibilité est que ces cellules pourraient toutefois jouer un rôle dans la perception de la texture ou une plus petite proportion qui contribuerait à l'estimation de la vitesse tactile. Donc les neurones répondant aux critères établis dans l'article 1 correspondent à une petite proportion, mais ceci serait consistant avec la suggestion que les caractéristiques d'un stimulus sont encodées par un petit nombre de neurones seulement (sparse coding: Rolls et Tovee 1995). Les données présentes ne peuvent distinguer entre ces possibilités, des enregistrements durant une tâche comportementale seraient nécessaires et probablement dans des aires hiérarchiquement plus hautes, tel S2, pour corréler les réponses neuronales et comportementales.

Enfin, les résultats de ces études sont aussi pertinents pour la conception de dispositifs neuroprothétiques (stimulant la périphérie ou le cortex) qui substituerait des pertes fonctionnelles, ex. amputation ou quadriplégie. Nos résultats suggèrent qu'un simple code basé sur la fréquence de décharge pourrait expliquer la perception de la vitesse tactile chez l'humain (article 3). Sutula et al (sous

presse) ont aussi suggéré que la perception de la rugosité tactile est basée, au moins en partie, sur le même type d'encodage. Ces connaissances sont très importantes en ce qui concerne les neuroprothèses puisque la seule méthode connue pour activer le tissu neuronal est la stimulation électrique. Cette approche prend pour acquis que le système nerveux soit capable d'interpréter ce code. En effet, il est connu que les humains et les singes peuvent discriminer les différences d'intensité et/ou de fréquence de stimuli électriques appliqués respectivement sur la peau ou le cortex du S1 (Chapman et al 1987, Romo et al 1998).

Le domaine des neuroprothèses est en grand essor (Green et al 2011a,b). Beaucoup d'emphase est attribuée au remplacement de la fonction motrice, mais le feedback sensoriel est tout aussi important. En effet, le premier dispositif neuroprothétique qui a réussi est l'implant cochléaire. Dans le cas de l'amputé, le manque de feedback sensoriel entraîne des différences entre un membre naturel et un membre artificiel pour ce qui est du contrôle et de l'intégration à l'image corporelle. Ceci fait que le taux d'acceptation des prothèses est très faible chez les amputés. De plus, même avec des amputations datant de plusieurs années, les nerfs sensoriels dans le moignon seraient encore fonctionnels pour opérer une prothèse sensori-motrice (Horch et al 2011). Dans cette dernière étude, l'utilisation de la position des doigts de la prothèse via la stimulation des afférences proprioceptives permet au sujet de discriminer parmi des objets différents. La capacité de discrimination de textures virtuelles est aussi observée chez le singe en utilisant une interface cerveau-machine (implants de microélectrodes dans S1 et M1) correspondant à un membre virtuel (O'Doherty et al 2011). Donc le fait de connaître l'encodage neuronal de la vitesse et

de la rugosité, en autres, permettrait d'intégrer la transmission de leur signal entre une prothèse et le système somatosensoriel et donc faciliter la manipulation et la reconnaissance d'objet et probablement permettre une meilleure acceptation des prothèses du membre supérieur.

10. Conclusions et sommaire

La perception de la vitesse tactile ainsi que son encodage ont été étudiés dans cette thèse. Il a été démontré que les sujets humains sont capables d'estimer la vitesse tactile d'une surface en déplacement sans indice de durée ni de distance. De plus, l'intensité subjective de la vitesse est indépendante de la disposition des éléments tactiles. Ceci est aussi vrai pour la perception de la rugosité tactile. Les résultats psychophysiques ont permis d'établir des hypothèses solides concernant l'encodage neuronal de la vitesse et de la rugosité tactile au niveau du S1. L'hypothèse sur la vitesse tactile a été confirmée; l'autre hypothèse, sur la rugosité tactile, est toujours en étude. Des cellules sensibles à la vitesse tactile et plus ou moins à la texture ont été identifiées. De plus, elles avaient une relation linéaire avec la fréquence temporelle, et ce indépendamment de la disposition des éléments tactiles. Les résultats des trois articles présentés dans cette thèse amènent de nouvelles connaissances et permettent d'émettre de nouvelles hypothèses pour des études futures, tel que mentionné ci-haut, afin de continuer à élucider les mystères du cerveau.

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