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Études des substrats neurologiques de la stéréopsie chez le chat.

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Lorsqu'un organisme contemple une scène visuelle donnée, l'espacement latéral de ses yeux fait en sorte que les images de cette scène visuelle qui s'imprime sur ses deux rétines sont légèrement disparates. Cette disparité spatiale horizontale entre les deux images rétiniennes permet l'émergence de la stéréopsie (Wheatstone, 1838), c'est à dire la perception claire et précise de la profondeur et l'impression saisissante de la tridimensionnalité des objets.

Les expériences électrophysiologiques de Hubel et Wiesel (1959, 1962) démontrent que les inputs visuels sont combinés au niveau de la cellule nerveuse, et ce à un niveau précoce de l'analyse visuelle, soit dans le cortex visuel primaire. Les expériences de Barlow et al. (1967) démontrent que ces cellules binoculaires répondent optimalement à certaines disparités spatiales, ce qui laisse supposer que la stéréopsie est basé sur l'encodage neuronal des indices de disparité spatiale.

Des cellules binoculaires se retrouvent non seulement dans le cortex visuel primaire, mais aussi dans les aires extrastriées et dans certains noyaux sous-corticaux du chat et des autres mammifères supérieurs. Cependant, il existe peu de données sur la sensibilité à la disparité spatiale des cellules binoculaires situées hors du cortex visuel primaire. L'objectif de cette thèse est donc d'étudier l'encodage des indices de disparité spatiale le long du système visuel du chat et de proposer des implications fonctionnelles pour les différentes régions visuelles dans la perception stéréoscopique.

Des enregistrements électrophysiologiques ont été effectués dans les aires 17/18, dans l'aire 19, dans l'aire postéro-médiale de la fissure suprasylvienne latérale ainsi que dans le collicule superieur du chat normal et du chat Siamois. Les réponse à la disparité spatiale des cellules binoculaires des différentes régions visuelles étudiées sont comparées selon trois paramètres: le

pourcentage de cellules sensibles à la disparité spatiale, la répartition des cellules sensibles dans les quatre classes de détecteurs de disparité spatiale et la sélectivité des cellules (telle que mesurée par la pente ou la bande-passante des profils de sensibilité à la disparité spatiale de celles-ci). Toutes les manipulations physiologiques ont été effectuées en accord avec les règles proposées par le Conseil Canadien de la Protection des Animaux et celles du *National Institute of Health* pour ce qui est du soin et de l'entretien des animaux supérieurs durant les expériences en sciences neurologiques. De plus, les protocoles expérimentaux ont été approuvés par le comité institutionnel des bons soins aux animaux.

Dans les aires 17/18, plus de 70% des cellules binoculaires sont sensibles à la disparité spatiale et celles-ci sont équitablement réparties entre les quatre classes de détecteurs de disparité. De plus, leur sélectivité à la disparité spatiale est extrêmement fine, beaucoup plus que dans toute autre aire visuelle. Cette sélectivité fine reflète l'apport des inputs de type X vers le cortex visuel primaire et va de pair avec les petits champs récepteurs et la haute résolution spatiale des cellules de ces aires. Ainsi, les cellules sensibles à la disparité spatiale dans le cortex visuel primaire semblent former un substrat idéal pour la perception de la stéréopsie fine.

L'aire 19 ne contient que 34% de cellules sensibles à la disparité spatiale et la sélectivité de ces cellules est plus grossière que celle des cellules du cortex visuel primaire. Ainsi, la contribution de l'aire 19 dans les mécanismes stéréoscopiques de perception de la profondeur et de la troisième dimension semble limitée. L'aire 19 contient néanmoins une importante proportion de cellules binoculaires, lesquelles ont de petits champs récepteurs et des propriétés spatiales assez fines. En ce sens, cette aire pourrait servir de substrats à d'autres aspects de la vision binoculaire, tels que la fusion binoculaire et l'intégration des différents indices de profondeurs.

La détection et l'analyse des indices de disparité spatiale semblent s'effectuer de manière similaire dans l'aire postéro-médiale de la fissure suprasylvienne latérale et dans les couches superficielles du collicule supérieur du chat normal. En effet, ces deux régions visuelles contiennent une forte proportion de cellules sensibles à la disparité spatiale (73% dans l'aire postéro-médiale de la fissure suprasylvienne latérale et 64% dans le collicule supérieur), et la majorité de ces cellules sensibles sont de type excitatrices. Les cellules sensibles à la disparité spatiale de ces deux régions visuelles sont aussi caractérisées par une sélectivité moins fine qui reflète leurs piètres propriétés spatiales et qui laisse supposer certaines contributions à des aspects plus grossiers de la stéréopsie, tel que la localisation de stimuli dans l'espace tridimensionnel. Les cellules sensibles à la disparité spatiale de ces régions visuelles jouent aussi probablement un rôle dans le contrôle de la vergence et de l'accommodation.

Ainsi, nos résultats suggèrent que chez le chat normal, l'analyse stéréoscopique d'un stimulus s'effectue en deux temps: la localisation dans l'espace tridimensionnel, la fovéation et le maintien de la fixation, sous contrôle des mécanismes suprasylviens et colliculaires, puis l'analyse précise de son relief et la reconstruction de sa "solidité" stéréoscopique par les mécanismes de stéréopsie fine du cortex visuel primaire.

Chez le chat Siamois, les cellules binoculaires sont extrêmement rares dans les aires 17/18 et dans l'aire 19. Ceci se reflète directement par l'absence de stéréopsie fine observée chez ces chats. Les cellules binoculaires de l'aire PMLS et du collicule supérieur sont plus nombreuses et jouent probablement les mêmes rôles que chez le chat normal en terme de contrôle de la fovéation, de la vergence et de l'accommodation. Il est probable que ces cellules remplissent aussi un rôle palliatif dans la perception stéréoscopique de la profondeur et de la troisième dimension, permettant ainsi au

chat Siamois de percevoir un certain degré de stéréopsie grossière similaire à ce qui est observé chez l'humain albinos

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ALLS: Aire antéro-latérale de la fissure suprasylvienne latérale

AMLS: Aire antéro-médiale de la fissure suprasylvienne latérale

c/deg.: cycles par degré

CGL: Corps genouillé latéral

CGLd: Corps genouillé latéral dorsal

CR: Champ récepteur

DLS: Aire dorsale de la fissure suprasyvienne latérale

LP: Noyau latéro-postérieur du thalamus

LPl: Partie latérale du noyau latéro-postérieur

LPm: Partie médiame du noyau latéro-postérieur

NIM: Noyau intralaminaire médian

PMLS: Aire postéro-médiale de la fissure suprasylvienne latérale

PLLS: Aire postéro-latérale de la fissure suprasylvienne latérale

VLS: Aire ventrale de la fissure suprasylvienne latérale

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CHAPITRE 1

Introduction générale

Depuis plus de vingt-cinq siècles, l'être humain tente de comprendre les lois optiques et les mécanismes physiologiques qui lui permettent de voir le monde qui l'entoure. En effet, les philosophes de la Grèce antique furent, comme dans bien d'autres domaines, les premiers à s'intéresser à ces questions. Empédocle (490-435 av. J.-C.), Platon (427-347 av. J.-C.), et même Ptolémée (100-170), croient que l'oeil émet un cône de lumière qui lui permettait de "sentir" les objets et ainsi de les percevoir. À l'inverse, Démocrite (460-370 av. J.-C.), puis Aristote (384-322 av. J.-C.), prétendent que les objets envoyaient vers l'oeil des images d'eux-même (simulacra) qui sont d'abord reçues par le cristallin puis relayées vers le cerveau. Près de 1500 ans plus tard, le savant arabe Abu Ali Al-Hazan (Alhazen, 965-1040) proposa avec justesse que les objets réfractaient de la lumière vers l'oeil, ce qui permettait la formation, dans l'oeil, d'une image de la scène visuelle. Ce n'est par contre que beaucoup plus tard que Johannes Kepler (1571-1630) fut en mesure de décrire en détail les phénomènes optiques sous-tendant la formation des images rétiniennes (Howard et Rogers, 1995).

Ces images rétiniennes sont minuscules, inversées, tordues et bidimensionnelles. Pourtant, de ces images, nous extrayons une scène visuelle riche et tridimensionnelle.

> "...the immediate cause of our vision of any object is just such a mosaic of stimulation as that of the photographic plate. And that raises at once the problem: how the enormous richness and variety of our visual behavioral environement can be aroused by such a mere mosaic of light and shade and color. I think, when formulated in these terms, the problem must appear thrilling by the very paradox which it seems to involve. How can such rich effects arise out of such poor causes, for clearly the "dimensions" of our environemental fields are far more numerous than those of the mosaic of stimulation." (Koffka, 1935)

Dans la même veine, Gregory (1978) déclare "From the pattern of stimulation in the retinas, we perceive the world of objects, and this is nothing short of a miracle."

La reconstruction tridimensionnelle de la scène visuelle à partir d'images bidimensionnelles est particulièrement stupéfiante. Néanmoins, les oeuvres de peintres tels que Giotto di Bondone (1266-1337), Botticelli (1445-1510) et Leonardo da Vinci (1452-1519) démontrent qu'il est possible d'obtenir une impression marquée de profondeur à partir d'un stimulus bidimensionnel. Ces grands maîtres, par l'étonnante tridimensionnalité de leurs toiles, démontrent la force des indices de profondeur monoculaires et ont ainsi, en un certain sens, contribué à masquer l'importance des indices binoculaires. En effet, le rôle crucial des indices binoculaires dans la perception de la profondeur et de la troisième dimension n'est reconnu d'emblée que depuis environ 160 ans.

Pourtant, les bases de la vision stéréoscopique sont connues depuis plus de deux mille ans. En effet, Euclide (3ième s. av. J.-C.) mentionne que les deux yeux perçoivent un même objet d'une perspective légèrement différente. Aristote note pour sa part qu'une pression du doigt sur un globe oculaire provoque une perception diplopique (Howard et Rogers, 1995). Galien (131-201) a même compris que les images venant à chaque oeil sont combinées pour former une perception unifiée de la scène visuelle (Pettigrew, 1972). Plus tard, Alhazen compris qu'un objet réfléchi sur des coordonnées correspondantes dans les deux yeux était perçu comme étant unique, alors qu'un objet réfléchi sur des coordonnées non-correspondantes était vu en double. Il avait aussi remarqué que de petites disparités d'angle visuel, et ainsi de coordonnées spatiales, pouvaient être tolérées et générer une perception unifiée. Alhazen ne réalisa toutefois pas l'importance de ces disparités (Howard, 1996).

Bien que Leonardo da Vinci nota l'effet de la parallaxe binoculaire sur la perception de la profondeur, c'est François d'Aiguillon (1546-1617) qui reconnut l'importance de la

vision binoculaire dans la perception de la profondeur. Ce dernier a même compris que les objets situés devant le point de fixation créent des disparités de type croisées alors que les objets derrière le point de fixation créent des disparités de type homonymes. Bien plus tard, Charles C. Wheatstone (1838) applique les principes énoncés par d'Aiguillon, Smith (1738) et Harris (1775) et démontre expérimentalement l'importance fondamentale de la disparité binoculaire dans la perception de la troisième dimension.

Jusqu'au milieu du vingtième siècle, on croyait encore, comme Hermann von Helmholtz (1893), que la stéréopsie était générée par des processus cognitifs de haut niveau. Ce sont les études de Hubel et Wiesel (1959, 1962) qui démontrèrent que les inputs visuels venant des deux yeux sont combinés à un stage précoce de l'analyse visuelle, soit dans le cortex visuel primaire. Quelques années plus tard, il fut démontré que ces cellules binoculaires répondent optimalement à certaines disparités spatiales (Barlow et al., 1967; Pettigrew et al., 1968). En se basant sur cette découverte, ces chercheurs proposèrent un mécanisme de perception binoculaire de la profondeur basé sur l'encodage neuronal des indices de disparité spatiale formés par l'observation binoculaire d'une scène visuelle.

> "Different neurones require different disparities. It follows that, with fixed convergence, objects at different distances will excite different neurones. This provides a plausible basis for binocular depth discrimination and stereopsis." (Barlow et al., 1967)

Des études subséquentes ont démontré la présence de cellules binoculaires dans d'autres aires visuelles ainsi que dans certains noyaux sous-corticaux du chat et d'autres mammifères supérieurs. Il existe cependant peu de données sur la sensibilité à la disparité spatiale des cellules binoculaires situées hors du cortex visuel primaire. L'objectif général de

cette thèse est donc d'étudier l'encodage des indices de disparité spatiale le long du système visuel du chat et de proposer des implications fonctionnelles pour ces région visuelles dans la perception stéréoscopique.

Afin de situer le corps de la thèse, la suite de ce premier chapitre fait le point sur cinq différents concepts. Premièrement, les mécanismes de la perception monoculaire et binoculaire de la profondeur seront présentés. Deuxièmement, les voies neuronales qui acheminent l'information vers les centres d'analyse visuelle et les régions cérébrales impliquées dans la perception visuelle seront décrites. Troisièmement, les propriétés des cellules binoculaires des régions visuelles qui seront étudiées dans cette thèse (les aires 17/18, l'aire 19, l'aire postéro-médiale de la fissure suprasylvienne latérale (PMLS) et le collicule supérieur) seront revues. Quatrièmement, ce qui est connu sur les substrats neurophysiologiques de la perception binoculaire de la profondeur sera détaillé. Cinquièmement, l'influence de l'albinisme et du strabisme sur la perception binoculaire de la profondeur et ses substrats sera évaluée. En dernier lieu, les hypothèses spécifiques de cette thèse seront énoncés.

La perception de la profondeur et de la troisième dimension

Indices monoculaires

Bien que la vision binoculaire permette une évaluation plus précise de la profondeur et une perception plus vive de la tridimensionnalité des objets, il est possible, d'un seul oeil, d'évaluer la distance relative et absolue des objets de la scène visuelle. Il existe en effet une

multitude d'indices de profondeur monoculaires qui ne requièrent pas l'intégration des deux images rétiniennes. Les peintres de la Renaissance sont passés maîtres dans l'art d'utiliser ces indices pour donner à leurs oeuvres la spectaculaire impression de profondeur qui les caractérisent. Ces grands artistes, dont Raffaello Sanzio (1483-1520) et bien-sûr Leonardo da Vinci ont intuitivement compris que le cerveau peut reconstruire la scène visuelle tridimensionnelle en se basant exclusivement sur des indices monoculaires de profondeur et sur la concordance qui existe entre ceux-ci. Leonardo da Vinci lui-même reconnaît toutefois que ces indices monoculaires, seuls, ne peuvent rendre justice à la tridimensionnalité de la scène visuelle.

> "Une oeuvre peinte avec le plus grand art et parfaite dans ses contours, ses lumières, ses ombres et ses couleurs, ne peut jamais évoquer un relief équivalent celui des objets naturels, sauf si ces derniers sont regardés de loin et d'un seul oeil." (Leonardo da Vinci, traduit de Trattato della Pittura)

Toute scène visuelle est remplie d'indices monoculaires de profondeur. Par exemple, lorsqu'un objet recouvre partiellement un autre objet, celui paraissant couvert est perçu comme étant plus lointain. Dans la même veine, la clarté ou netteté des objets perçus est aussi un indice de distance, puisque la lumière réfléchie de plus loin est soumise à une plus grande diffusion sur des petites particules en suspension dans l'air, ce qui donne aux objets lointains une définition plus floue. La taille d'objets familiers, la taille relative des objets et l'élévation de ceux-ci dans le champ visuel permettent aussi d'évaluer leur distance. Les jeux d'ombres et de lumières sur différentes surfaces peuvent aussi produire, comme le montrent les toiles de Rembrandt van Rijn (1606-1669) et Johannes Vermeer de Delft (1632-1675), une puissante impression de profondeur et de tridimensionnalité.

En 1950, J.J. Gibson souleva l'importance des gradients de texture dans la perception de la distance et de la profondeur. La plupart des surfaces possèdent en effet une texture particulière et relativement uniforme. Or, les éléments d'une texture deviennent plus denses lorsque la distance s'accroît, puisque la taille des éléments et la distance qui les sépare varient d'une manière inversement proportionnelle à l'éloignement. Ce concept rejoint la méthode graphique de la perspective linéaire, utilisée dès le quinzième siècle par Filippo Brunelleschi (1377-1446) et Leon Battista Alberti (1404-1472). Ce système géométrique permet de varier systématiquement, en proportion de leur éloignement, la taille des objets représentés en deux dimensions.

Gibson (1950, 1966, 1979) a aussi mis l'emphase sur le concept de l'observateur actif et a ainsi démontré l'importance de la parallaxe de mouvement et du flux optique dans la perception de la distance et de la profondeur. En effet, lorsqu'un observateur balaie du regard une scène visuelle, les objets situés près de l'observateur semblent se déplacer plus rapidement que ceux situés plus loin. Aussi, la direction du mouvement apparent des objets varie puisque les objets situés devant le point de fixation et les objets situés derrière le point de fixation semblent se diriger dans des direction opposées. Un phénomène semblable se produit lorsque l'observateur se déplace dans la scène visuelle et est ainsi exposé au flux optique. En effet, la vélocité et la direction du mouvement apparent des objets varient alors continuellement en fonction de la position d'où ils sont vus.

Donc, le mythique cyclope d'Homère aurait perçu la troisième dimension. Par contre, sa perception de la tridimensionnalité des objets aurait été moins saisissante et ses jugements de profondeurs auraient été moins précis que ceux de l'humain, particulièrement à courte

distance. En effet, la perception précise du fin détail tridimensionnel, particulièrement lorsque les objets sont à moins de quelques mètres de l'observateur, est fortement dépendante des indices binoculaires obtenus par la fusion des deux images rétiniennes.

Indices binoculaires: La disparité rétinienne ou disparité spatiale

Dès les premiers stades du développement embryonnaire des organismes complexes, juste après la neurulation, deux groupes de cellules de la partie rostrale du tube neural migrent latéralement. Ces cellules se différencient par la suite pour former deux rétines et deux cristallins (Cowan, 1979; Keynes et Lumsden, 1990). Ainsi, grâce à cette double migration cellulaire, ces organismes bénéficient de deux yeux, situés soit très latéralement comme chez le lapin ou la chèvre, ou plutôt frontalement comme chez le chat, le singe ou l'humain.

Tous les organismes dotés de deux globes oculaires perçoivent simultanément deux versions de la scène visuelle. En effet, l'espacement interoculaire engendre un décalage horizontal entre les images rétiniennes. Chez les espèces aux yeux situés latéralement, ce décalage est trop grand et les images rétiniennes sont trop différentes pour que des indices efficaces de perception de la profondeur soient engendrés. Par contre, le décalage horizontal entre les images rétiniennes des espèces aux yeux frontalement disposés crée des indices de disparité spatiale qui sont à la base de la perception binoculaire de la profondeur.

La formation et la détection de ces disparités spatiales reposent sur le principe de la correspondance des coordonnées rétiniennes. Lorsqu'un organisme aux yeux frontalement disposés fixe une petite cible visuelle, l'image de cette cible va se former sur la fovéa de

chacune des deux rétines. La cible est alors perçue comme unique, malgré la formation de deux images rétiniennes, parce qu'elle stimule des points correspondants sur les deux rétines. En d'autre termes, si les deux rétines sont parfaitement superposées, fovéa sur fovéa, les deux images de la cible visuelle le sont aussi.

Ainsi, pour chaque degré de convergence binoculaire, il existe une série de coordonnées spatiales qui se projettent sur des coordonnées rétiniennes correspondantes. Ces séries de coordonnées spatiales sont appelées horoptères (Figure 1). Plus un objet de la scène visuelle est éloigné de l'horoptère, plus la disparité entre les images rétiniennes est grande. Ainsi, les objets près de l'horoptère, dans l'aire de fusion de Panum (Figure 1), sont perçus comme étant uniques alors que les objets situés à l'extérieur de cette aire génèrent une perception diplopique.

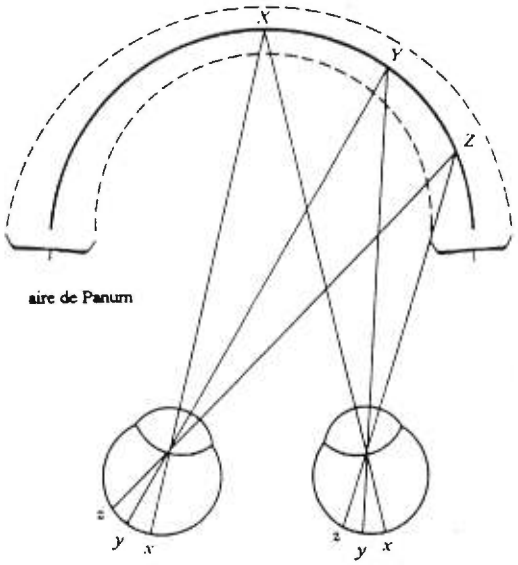

Figure 1. L'horoptère et l'aire de Panum. Les images des points X, Y et Z tombent sur des coordonnées rétiniennes correspondantes et ces points sont perçus comme étant uniques. Les points qui ne sont pas sur l'horoptère produisent une perception diplopique, à l'exception des points qui se trouvent dans la bande horizontale autour de l'horoptère, l'aire fusionnelle de Panum (adapté de Schiffman, 1990).

Tel qu'illustré dans la Figure 2, il existe deux types de disparités spatiales: les disparités croisées et non-croisées. Les images rétiniennes d'un objet situé devant le point de fixation se forment sur les hémirétines temporales. Chaque oeil perçoit donc un tel objet dans son hémichamp controlatéral. Ainsi, les perceptions monoculaires de cet objet se croisent et les disparités qui sous-tendent ces perceptions sont appelées croisées. Les images rétiniennes d'un objet situé derrière le point de fixation se forment sur les hémirétines nasales. Chaque oeil perçoit donc un tel objet dans son hémichamp ipsilatéral. Ainsi, les perceptions monoculaires de cet objet ne se croisent pas et les disparités qui engendrent ces perceptions sont appelées non-croisées ou homonymes.

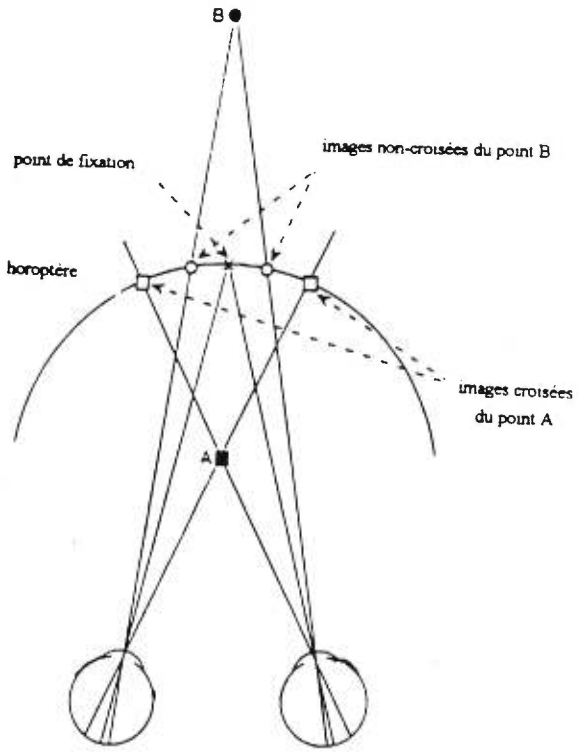

Figure 2. Les disparités spatiales croisées et non-croisées. Les images du point A sont croisées parce que les ligne de vision des deux yeux se croisent avant l'horoptère. Les images du point B sont non-croisées parce que les ligne de vision des deux yeux ne se rencontrent qu'après l'horoptère (adapté de Howard et Rogers, 1995).

De ces disparités spatiales horizontales émerge la stéréopsie, c'est à dire la perception claire et précise de la profondeur et l'impression saisissante de la tridimensionnalité des objets. L'importance des indices de disparité spatiale dans la perception de la troisième dimension fut démontrée par les expériences stéréoscopiques de Wheatstone. Ce dernier créa le stéréoscope (Figure 3) et énonça le principe sous-tendant l'utilisation de cet appareil.

> "It thus being established that the mind perceives an object of three dimensions by means of the two dissimilar pictures projected by it on the two retinas, the following question occurs. What would be the visual effect of simultaneously presenting to each eye, instead of the object itself, its projection on a plane surface as it appears to that eye? To pursue this inquiry it is necessary that means should be contrived to make the two pictures, which must necessarily occupy different places, fall on similar parts of both eyes." (Wheatstone, 1838)

Ainsi, la spectaculaire fusion tridimensionnelle des deux images bidimensionnelles légèrement disparates démontre l'importante relation entre la disparité spatiale des images rétiniennes et la perception de la profondeur et de la troisième dimension.

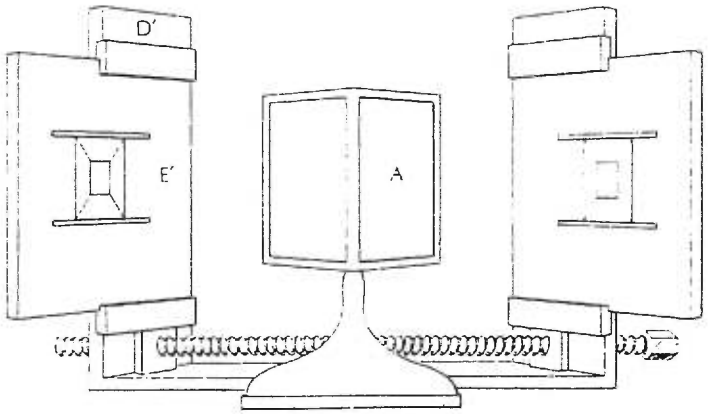

Figure 3. Le premier stéréoscope à miroir de Wheatstone (Wheatstone, 1838).

Le stéréoscope permet aussi de démontrer que l'augmentation de la disparité entre les images augmente aussi l'impression de tridimensionnalité, mais seulement dans une certaine limite. En effet, lorsque le décalage devient trop grand ou lorsque les images présentées à chaque oeil sont trop différentes, une seule des images est perçue à la fois alors que l'autre est supprimée (Engel, 1958). L'organisme évite ainsi de percevoir en double tous les objets situés à l'extérieur de l'aire de Panum.

Pour leurs démonstrations stéréoscopiques, Wheatstone et ceux qui suivirent ses traces (Wheatstone, 1838, 1853; Shaw, 1861) utilisaient toujours des images d'objets concrets. La perception stéréoscopique fut ainsi longtemps considérée dépendante de la perception de la forme. Dans les années soixante, Bela Julesz introduisit le stéréogramme de points aléatoires qui créait une impression puissante de profondeur sans indices monoculaires et sans objets discernables en présentation monoculaire. Julesz (1964, 1971) démontra ainsi que la perception de la forme n'est pas un pré-requis pour la stéréopsie. En effet, dans le cas des stéréogrammes de points aléatoires, c'est l'inverse qui se produit. Gulick et Lawson (1976), sur ce phénomène, déclarèrent "...instead of contours giving rise to depth, it is rather depth that gives rise to contours."

Les expériences de Julesz avec les stéréogrammes de points aléatoires introduisent les notions de stéréopsie locale et de stéréopsie globale (Julesz, 1971). En effet, la profondeur d'un tel stéréogramme ne peut être perçue suite à une analyse point-par-point (stéréopsie locale), puisque chaque point qui se projette sur la rétine d'un oeil peut être associé à une pléiade de points qui se projettent sur la rétine de l'autre oeil. Un processus de détection du

"pattern" de disparité (stéréopsie globale) est alors nécessaire pour percevoir le stéréogramme en trois dimensions.

À la même époque, Bishop et Henry (1971) proposèrent que la discrimination stéréoscopique repose sur un double processus de détection de la disparité spatiale. Un premier processus, la stéréopsie fine, permet l'estimation précise de la profondeur à partir de la fusion des deux représentations rétiniennes d'un objet. La stéréopsie fine est basée sur les petites disparités spatiales, de 15 minutes à deux degrés (Mitchell, 1966; Fender et Julesz, 1967) engendrées par des objets situés près de l'horoptère. Ce processus permet de détecter une différence de profondeur entre deux objets sur la base d'une disparité rétinienne d'un micron, ce qui est plus petit que le diamètre du photorécepteur moyen (Yellot, 1981). Un second processus, la stéréopsie grossière, se base sur des grandes disparités qui créent une perception diplopique. Des disparités spatiales aussi grandes que 7 à 12 degrés (Westheimer et Tanzman, 1956; Blakemore, 1970) permettent en effet de déterminer si un objet est situé devant ou derrière le plan de fixation.

Dans la perspective de cette thèse, il est important de noter qu'outre l'humain, les mammifères supérieurs tels que le singe (Bough, 1970; Cowey et al., 1975; Sarmiento, 1975; Harwerth et Boltz, 1979a, 1979b) et le chat (Fox, 1981; Lepore et al., 1986; Ptito et al., 1986), de même que plusieurs insectes, amphibiens, reptiles et oiseaux (Howard et Rogers, 1995) possèdent aussi une vision stéréoscopique. Tous ces organismes possèdent, à différents degrés, plusieurs voies rétinofuges parallèles.

Les principales voies visuelles et régions cérébrales visuelles du chat

Un grand nombre d'études anatomiques, physiologiques et comportementales suggèrent qu'il existe de nombreuses voies rétinofuges parallèles. Chez le chat (Boycott et Wässle, 1974), ces voies sont formées de trois types de cellules ganglionnaires ayant chacune des structures et des propriétés distinctes: les cellules de type X, Y et W.

Les cellules X qui représentent environ 40% des cellules ganglionnaires sont surtout situés dans l'area centralis (Cleland et Levick, 1974; Fukuda et Stone, 1974; Rowe et Stone, 1976; Stone, 1983), ont de petits champs récepteurs (CR), une vitesse de conduction moyenne (17-23 m/s) et répondent de manière tonique aux stimuli visuels (Enroth-Cugell et Robson, 1966). Les cellules X montrent une très haute résolution spatiale, à un haut seuil de contraste, et sont généralement associées à la perception du détail de la scène visuelle (Enroth-Cugell et Robson, 1966; Cleland et al., 1973; Fukuda et Stone, 1974; Stone, 1978, 1983).

Les cellules Y qui ne représentent que 5% à 10% des cellules ganglionnaires (Cleland and Levick, 1974; Fukuda et Stone, 1974; Rowe and Stone, 1976; Stone, 1983) sont surtout situées en périphérie de la rétine, et ont des CR plus grands et une vitesse de conduction (30-40 m/s) plus élevée (Enroth-Cugell et Robson, 1966). Ces cellules répondent de manière phasique aux stimuli visuels (Fukuda et Stone, 1974; Rowe et Stone, 1976; Stone, 1978) et montrent une grande sensibilité au contraste (Enroth-Cugell et Robson, 1966; Stone, 1983). Les cellules Y sont généralement associées à la détection de stimuli mobiles faiblement contrastés (Stone, 1983).

Les cellules de type W représentent environ 50% des cellules ganglionnaires (Cleland and Levick, 1974; Fukuda et Stone, 1974; Rowe and Stone, 1976; Stone, 1983) et se retrouvent autant dans les régions rétiniennes centrales que périphériques. Ces cellules de petite taille sont caractérisées par une vitesse de conduction très lente (7-12 m/s) et un taux de décharge instable en réponse à la stimulation visuelle (Bishop et al., 1969; Stone et Hoffmann, 1972; Stone et Fukuda, 1974; Cleland et Levick, 1974) . Leurs rôles dans la vision, tel que la vision ambiante, sont encore mal définis.

Ces trois types de cellules ganglionnaires (X, Y et W) se projettent vers plusieurs noyaux mésencéphaliques et diencéphaliques. On distingue toutefois deux grandes voies visuelles: les voies rétino-géniculo-corticales, qui chez les mammifères supérieurs est aussi appelée la voie visuelle primaire, et la voie rétino-tectale qui est phylogénétiquement plus ancienne et est considérée secondaire chez les mammifères supérieurs..

Les voies rétino-géniculo-corticales et les aires visuelles corticales

La voie rétino-géniculée achemine l'information visuelle vers la partie dorsale du corps genouillé latéral (CGLd). Cette structure laminaire est composée, chez le chat, des couches A, A1 et C, cette dernière couche étant en fait elle-même composée de la couche magnocellulaire C et des couches parvocellulaire C1, C2 et C3. Les couches A, C et C2 reçoivent des projections en provenance de l'oeil controlatéral alors que les couches A1 et C1 reçoivent des afférences rétiniennes ipsilatérales. La couche C3 ne semble pas recevoir de projections rétiniennes directes (Guillery et al., 1980). Deux structures adjacentes aux couches du CGLd sont aussi considérées parties intégrantes de cette structure: le noyau

interlaminaire médian (NIM) et l'aileron du corps genouillé. Ces structures reçoivent des afférences de type Y et W (Szentagothai, 1973; Jones, 1985; Guillery, 1995; Sherman and Guillery, 1996). Toutes les cellules de relais du CGLd font synapse avec un seul type de cellule ganglionnaire de la rétine. Ceci permet de maintenir la ségrégation des trois voies rétino-thalamiques distinctes, chacune acheminant des informations visuelles distinctes vers le cortex (Sherman, 1979, 1985; Stone et al., 1979; Stone, 1983). Ce parallélisme des voies visuelles est conservé lorsque l'information visuelle est acheminée du CGLd vers le cortex visuel.

Le cortex visuel, chez le chat, est divisé en un nombre impressionnant d'aires corticales distinctes (voir Figure 4). Chacune de ces aires est organisée de manière rétinotopique (Palmer et al., 1978; Tusa et al., 1978, 1979; Tusa et Palmer, 1980).

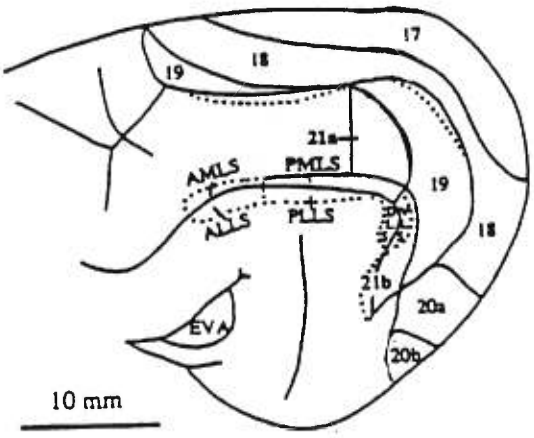

Figure 4. Positions relatives des aires visuelles du cortex cérébral du chat (adapté de Dreher, 1996).

L'aire 17, qui occupe la partie caudo-médiale des deux hémisphères est la plus vaste parce que chaque cellule de cette aire ne couvre qu'une petite partie du champ visuel et que le facteur de magnification de la région centrale du champ visuel y est maximal. Les aires 18 et 19, aussi appelées les aires péristriées, sont situées plus latéralement. Chez le chat, il est généralement admis que les aires 17 et 18 forment le cortex visuel primaire. L'aire visuelle Clare-Bishop, ou suprasylvienne, est située à l'intérieur de la fissure suprasylvienne. Cette aire peut être subdivisée en six aires rétinotopiques distinctes: les aires postéro-latérale (PLLS) et postéro-médiale (PMLS), les aires antéro-latérales (ALLS) et antéro-médiales (AMLS) ainsi que les aires ventrale (VLS) et dorsale (DLS) de la fissure suprasylvienne latérale. Quatre autres aires ont été cartographiées électrophysiologiquement: les aires 20a, 20b, 21a et 21b (Tusa et Palmer, 1980). Ces aires représentent principalement le champ visuel supérieur et leur organisation rétinotopique est complexe. Le cortex ectosylvien, situé plus antérieurement, contient aussi des cellules répondant à la stimulation visuelle, en plus de répondre aux stimulations auditives et somesthésiques. Ces cellules aux propriétés complexes laissent croire que le cortex ectosylvien est impliqué dans l'intégration multisensorielle.

De nombreuses études anatomiques ont permis de définir les différentes voies géniculo-corticales (Wilson et Cragg, 1967; Garey et Powell, 1967, 1971; Hubel et Wiesel, 1972; Rosenquist et al., 1974; Gilbert et Kelly, 1975; Maciewicz, 1975; LeVay et Gilbert, 1976; Garey et Blakemore, 1977; Holländer et Vanegas, 1977; LeVay et Ferster, 1977; Ferster et LeVay, 1978; Leventhal, 1979; Geisert, 1980). Ces études soutiennent le concept du parallélisme des voies visuelles de la rétine vers le cortex puisque les fibres géniculées se projettent vers les aires 17, 18, 19 et vers la fissure suprasylvienne latérale. Les cellules X de la couche A du CGLd projettent massivement vers l'aire 17. Un nombre restreint de cellules

X des couches A1 et C semblent projeter vers les aires 18 et 19, mais il est généralement admis que l'influence des cellules ganglionnaires de type X se limite au cortex visuel primaire. Les cellules Y des couches A, A1 et C projettent aussi vers le cortex visuel primaire, alors que les cellules Y du NIM projettent vers les aires 18 et 19. Quand aux cellules W, elles projettent particulièrement vers l'aire 19, bien qu'un nombre limité de projections W se retrouvent dans la plupart des aires visuelles.

Il est important de noter que les aires extrastriées reçoivent la majorité de leurs afférences sous-corticales en provenance de structures extragéniculées (Raczkowski et Rosenquist, 1983; Dreher, 1986). En effet, la majorité des afférences extrastriées proviennent du complexe LP-pulvinar, qui peut être subdivisé en trois grandes parties: les parties latérale (Lpl) et médiane (Lpm) du noyau LP et le pulvinar. Ces régions ne reçoivent pas de projections rétiniennes directes, mais sont plutôt innervées par des afférences venant du pretectum, du collicule supérieur et du cortex visuel lui-même (Updyke, 1977; Berson et Graybiel, 1978). Ces projections extragéniculées sont essentiellement formées de cellules de type Y et W (Raczkowski et Rosenquist, 1983).

La voie rétino-tectale et le collicule supérieur

Le collicule supérieur, ou tectum optique, est une structure mésencéphalique formée de couches de cellules et de couches de fibres qui forment un arrangement laminaire. Kanaseki et Sprague (1974) ont démontré que cette structure est anatomiquement divisée en trois parties, chacune de ces parties étant subdivisées en couches. Ainsi, la partie superficielle du collicule supérieur contient la *stratum zonale*, la *stratum griseum superficiale* et la *stratum*

opticum, également appelées couches I, II et III. La partie intermédiaire contient la *stratum griseum intermediale* et la *stratum albium intermediale*, aussi appelées couches IV et V. Finalement, la partie profonde contient les couches VI et VII, soit la *stratum griseum profundum* et la *stratum albium profundum*. Le terme *griseum* réfère à la couleur grise des corps cellulaires qui constituent les couches II, IV et VI. Les autres couches, plus pâles, sont ainsi composées de fibres. Au niveau fonctionnel, le collicule supérieur est généralement divisé en deux parties seulement, soit les couches superficielles (I, II, III) et les couches profondes (IV, V, VI, VII).

Les couches superficielles, et particulièrement la *stratum griseum superficiale*, reçoivent des afférences rétiniennes massives en provenance des deux yeux. Ces projections rétino-tectales sont organisées de manière rétinotopique (Kanaseki et Sprague, 1974). La majorité des afférences rétiniennes proviennent de cellules de type W (Berson, 1988b). Néanmoins, environ 10% des cellules colliculaires sont activées par des cellules de type Y (Wässle et Illing, 1980). Les expériences anatomiques de Wässle et Illing (1980) montrent aussi qu'environ 10% des cellules ganglionnaires X de la rétine envoient des collatérales au collicule supérieur; cependant, l'activation de cellules colliculaires par des afférences de type X n'a pu être démontrée (Berson, 1988a, 1988b).

Les couches superficielles du collicule supérieur reçoivent aussi des afférences corticales massives. En effet, Harting et al. (1992) ont relevé 17 aires corticales qui projettent vers cette structure. Les projections les plus importantes vers les couches superficielles proviennent des aires 17, 18 et 19 ainsi que des aires suprasylviennes. Ces projections corticales sont en correspondance rétinotopique avec les afférences ganglionnaires rétiniennes

(McIlwain, 1973). Les couches superficielles du collicule supérieur reçoivent également des afférences de structures sous-corticales, incluant le pulvinar, le prétectum, le CGL et le noyau parabigéminal (Huerta et Harting, 1984; Stein et Meredith, 1993). Les afférences des couches superficielles sont donc en grande majorité d'origine visuelle.

À l'opposé, les afférences des couches profondes sont extrêmement hétérogènes. Ces couches reçoivent des projections visuelles en provenance de la rétine, de divers noyaux sous-corticaux et de plusieurs aires extrastriées. Les couches profondes reçoivent aussi des afférences sensorielles de nature somesthésiques, nociceptives et auditives ainsi que des afférences motrices provenant principalement des ganglions de la base et du cervelet (Huerta et Harting, 1984; Stein et Meredith, 1993). Par ailleurs, les cellules des couches superficielles établissent des contacts synaptiques avec les cellules des couches profondes et l'organisation de ces projections présente une certaine rétinotopie (Behan et Appell, 1992; Behan et Kime, 1996).

En ce qui a trait aux efférences colliculaires, les couches superficielles projettent surtout vers le CGL et les noyaux postérieurs du thalamus ipsilatéral. Les efférences au CGL proviennent des cellules ganglionnaires de type W alors que les efférences vers les noyaux postérieurs proviennent des cellules de type Y et W (Stein et Meredith, 1993). Les couches superficielles envoient aussi des fibres vers le pretectum, le pulvinar, le noyau parabigéminal, la substance grise périaqueductale et quelques noyaux de la formation réticulée (Stein et Meredith, 1993). Les couches profondes envoient des projections ascendantes vers le thalamus et des projections descendantes vers le pons, plusieurs noyaux de la formation

réticulée, le complexe olivaire inférieur, divers noyaux mésencéphaliques et vers les segments cervicaux de la moelle épinière.

Bref, les couches superficielles du collicule supérieur entretiennent des relations étroites avec des aires corticales et des noyaux sous-corticaux appartenant au système visuel. À l'opposé, les couches profondes communiquent avec plusieurs structures impliquées dans les différents systèmes sensoriels et moteurs.

Les propriétés des CR des cellules des régions visuelles étudiées

Les propriétés des CR des cellules visuelles sont habituellement étudiées à l'aide de deux méthodes. Les aspects campimétriques des CR, tel que la taille et la position spatiale sont généralement évaluées à l'aide de barres noires et lumineuses (Hubel et Wiesel, 1962, 1965). Ces barres sont généralement mobiles, leur orientation étant orthogonale à la direction de leur déplacement. La dominance oculaire, la sélectivité à la vitesse et la sélectivité à la direction des cellules peuvent aussi être évaluées à l'aide de barres, de même que la sensibilité au contraste et certaines propriétés spatio-temporelles. D'autre part, ces mêmes caractéristiques cellulaires, et particulièrement les propriétés spatio-temporelles (fréquences spatiales et temporelles optimales, sélectivité aux fréquences spatiales et temporelles, résolution spatiale et temporelle) peuvent aussi être évaluées à l'aide de réseaux de fréquences spatiales mobiles modulés sinusoïdalement (Enroth-Cugell et Robson, 1966).

Les CR des cellules visuelles du chat et des autres mammifères supérieurs sont caractérisés par des régions excitatrices (ON) ou la lumière provoque une réponse cellulaire,

et des régions inhibitrices (OFF) ou la lumière provoque une suppression de la réponse cellulaire. Les cellules ganglionnaires de la rétine, qui sont monoculaires, possèdent un CR plutôt circulaire, caractérisé par une organisation concentrique et antagoniste de type ON/OFF entre le centre du CR et son pourtour (Kuffler, 1953; Enroth-Cugell et Robson, 1966). Les cellules du CGLd possèdent des CR similaires à ceux des cellules ganglionnaires qui se projettent vers eux (Shapley et Hochstein, 1975).

Les CR des cellules corticales ont une forme plus oblongue et sont souvent binoculaires. Ceux-ci peuvent être sensibles à certains paramètres de la stimulation visuelle tel que l'orientation, la direction et la vitesse, en plus d'être sélectifs aux propriétés spatio-temporelles des stimuli. On distingue deux types de CR corticaux: les simples et les complexes (Hubel et Wiesel, 1959, 1962; Henry, 1977; DeAngelis et al., 1993, 1995). Les CR des cellules simples sont composés de régions allongées ON/OFF, adjacentes et antagonistes. Lorsque ces CR sont stimulés à l'aide de réseaux de fréquences spatiales mobiles, ces régions adjacentes engendrent une réponse cellulaire modulée à la fréquence temporelle du balayage. Dans les CR des cellules complexes, les régions ON/OFF ne sont pas adjacentes, mais plutôt superposées. Ainsi, lorsque ces CR sont stimulés à l'aide de réseaux de fréquences spatiales mobiles, l'élévation générale du taux de réponse de ces cellules ne présente aucune modulation. Par ailleurs, les CR de certaines cellules sont flanqués de régions inhibitrices, de sorte que ces cellules réduisent leur taux de décharge lorsqu'un stimulus adéquatement orienté atteint une longueur donnée. Ces cellules, parfois appelées hypercomplexes, peuvent posséder des propriétés semblables aux cellules simples ou complexes (Hubel et Wiesel, 1965; Henry, 1977).

Les CR des cellules du cortex visuel primaire (aires 17/18)

Les CR du cortex visuel primaire sont très petits, particulièrement dans l'aire 17, et sont en grande majorité binoculaires. Ces cellules, qui sont surtout de type simple ou complexe, sont aussi, très sensibles à l'orientation du stimulus (Hubel et Wiesel, 1962, 1965; Ikeda et Wright, 1975; Movshon et al., 1978a, 1978b, 1978c).

Les cellules du cortex visuel primaire, particulièrement celles situées dans l'aire 17, montrent une très haute résolution spatiale (Maffei et Fiorentini, 1973; Movshon et al., 1978c; Tolhurst et Thompson, 1981), pouvant atteindre six cycles par degré (c/deg.). La fréquence spatiale optimale moyenne, qui fournit un bonne indication des préférences spatiales des cellules, est de 0.77 c/deg. pour les cellules de l'aire 17 et de 0.22 c/deg. pour les cellules de l'aire 18 (Movshon et al., 1978c).

Les cellules du cortex visuel primaire semblent montrer une résolution temporelle intermédiaire (Saul et Humphreys, 1992). La fréquence temporelle optimale moyenne, qui fournit une bonne indication des préférences temporelles de la cellule, est de 2.9 Hz pour les cellules de l'aire 17 et de 3.2 Hz pour les cellules de l'aire 18 (Saul et Humphreys, 1992). Movshon et al. (1978c), bien qu'ils n'aient pas calculé les fréquences temporelles optimales des cellules des aires 17 et 18, montrent des courbes où les fréquences temporelles optimales des cellules de l'aire 18 semblent supérieures à ce qui est montré par Saul et Humphreys (1992).

Les propriétés des cellules de l'aire 17 reflètent fortement l'apport massif des cellules de type X vers le cortex visuel primaire, puisque ces cellules ganglionnaires montrent aussi de petits CR, une résolution temporelle moyenne et une haute résolution spatiale. Les propriétés spatio-temporelles des cellules de l'aire 18, telles que la résolution spatiale plus basse et la résolution temporelle plus haute, reflètent plutôt l'apport des cellules de type Y vers cette aire (Lehmkule et al., 1980; Frishman et al., 1983; Stone, 1983; Sur et Sherman, 1984; Sherman, 1985).

Les CR des cellules de l'aire 19

En ce qui à trait à leur taille, les CR des cellules de l'aire 19 (Hubel et Wiesel, 1965; Duysens et al., 1982a, 1982b; Tanaka et al., 1987; Tardif et al., 1997) sont presque aussi petits que ceux des cellules de l'aire 17 (Hubel et Wiesel, 1962; Ikeda et Wright, 1975), et nettement plus petits que dans toute autre aire extrastriée (Hubel et Wiesel, 1969; von Grünau et al., 1987; Wimborne et Henry, 1992; Tardif et al., 1996). La majorité des CR de cette aire montre des régions excitatrices et inhibitrices superposées qui caractérisent les cellules complexes, mais environ 10% des cellules de cette aire sont de type simple (Tardif et al., 1997). De plus, une importante proportion, allant de 40% (Tardif et al., 1997) à 66% (Tanaka et al., 1987) à la presque totalité (Hubel et Wiesel, 1965), des cellules diminuent leur taux de décharge lorsque le stimulus est allongé au-delà des limites du CR. C'est en effet dans l'aire 19 que cette propriété est le plus souvent observée (Orban, 1991). La plupart des cellules de cette aire sont binoculaires et sont sensibles à l'orientation (Orban, 1984, 1991), mais peu sont sélectives à la direction du stimulus (Hubel et Wiesel, 1965; Tanaka et al., 1987; Tardif et al., 1997).

Les fréquences spatiales optimales pour les cellules de l'aire 19 sont inférieures (Tanaka et al., 1987 (0.4 c/deg.); Bergeron et al., 1998 (0.17 c/deg.)) à celles des cellules de l'aire 17 (Movshon et al., 1978c), mais comparables à celles de l'aire 18 (Movshon et al., 1978c). Les cellules de l'aire 19 répondent optimalement à des fréquences temporelles autour de 3 Hz (Tanaka et al., 1987; Bergeron et al., 1998), ce qui est similaire aux cellules de l'aire 17, mais inférieur à ce que l'on retrouve dans l'aire 18 (Saul et Humphreys, 1992).

Ces propriétés spatio-temporelles peuvent sembler fines pour une aire recevant surtout des projections genouillées de type W. Certaines de ces propriétés, particulièrement au niveau spatial, peuvent possiblement être attribuées aux projections sérielles en provenance du cortex visuel primaire.

Les CR des cellules de l'aire PMLS

Les CR des neurones de l'aire PMLS sont considérablement plus grands que ceux du cortex visuel primaire et de l'aire 19, et peuvent atteindre 45 degrés de diamètre en périphérie (Hubel et Wiesel, 1969; Spear et Baumann, 1975; Camarda et Rizzolatti, 1976). Par contre, des études plus récentes centrées exclusivement sur la représentation centrale du champ visuel de l'aire PMLS ont montré que les CR de cette région peuvent avoir un diamètre aussi petit que deux degrés (Rauschecker et al., 1987; von Grünau et al., 1987). Ces CR sont de type complexe, et environ un tiers de ceux-ci sont flanqués de régions inhibitrices (Spear et Baumann, 1975, Camarda et Rizzolatti, 1976; von Grünau et Frost, 1983). Bien que près du tiers des CR périphériques soient monoculaires (Spear et Baumann, 1975; Spear et al., 1985; McCall et al., 1988), la presque totalité des CR situés dans la région centrale du champ visuel

sont binoculaires (Rauschecker et al., 1987; von Grünau et al., 1987). La plupart des cellules de l'aire PMLS répondent optimalement à des stimuli mobiles et sont sélectives à la direction du stimulus (Hubel and Wiesel, 1969; Wright, 1969; Spear and Baumann, 1975; Turlejski, 1975; Camarda et Rizzolatti, 1976; Blakemore and Zumbroich, 1986; Rauschecker et al., 1987; von Grünau et al., 1987; Gizzi et al., 1990).

Les cellules de cette aire répondent en moyenne à une fréquence spatiale optimale de 0.16 c/deg. (Zumbroich et Blakemore, 1987) et à une fréquence temporelle optimale de 5 Hz (Morrone et al., 1986). Les cellules de l'aire PMLS montrent des propriétés spatiales inférieures et des propriétés temporelles supérieures aux cellules des aires 17, 18 (Movshon et al., 1978c; Saul et Humphreys, 1992) et 19 (Tanaka et al., 1987; Bergeron et al., 1998).

Ainsi, on peut avancer que les cellules de l'aire PMLS montrent des propriétés spatio-temporelles semblables à celles de deux structures sous-corticales qui projettent massivement vers les aires suprasylviennes (Rosenquist, 1985; Spear, 1985; Dreher, 1986): le LP (Casanova et al., 1989) et les couches superficielles du collicule supérieur (Bisti et Sireteanu, 1976, Pinter et Harris, 1981). Il a toutefois été démontré que la sensibilité aux fréquences spatiales des cellules de l'aire PMLS ne semble toutefois pas dépendre des projections du complexe LP-Pulvinar (Minville et Casanova, 1997).

Les CR *des cellules des couches superficielles du collicule supérieur*

Les CR des cellules du collicule supérieur sont généralement plus grands que les CR des cellules corticales, bien qu'ils peuvent être aussi petits que 2 degrés dans la représentation

centrale du champ visuel (Sterling et Wickelgren, 1969; Berman et Cynader, 1972). Ces CR sont de type complexe et une grande proportion de ces CR sont flanqués de régions inhibitrices (Berman et Cynader, 1972), ce qui a pour effet de décroître le taux de réponse de la cellule lorsqu'un stimulus adéquatement orienté est allongé au-delà des limites du CR. La majorité des cellules des couches superficielles du collicule supérieur, particulièrement dans la région représentant le centre du champ visuel sont binoculaires (Sterling et Wickelgren, 1969; Berman et Cynader, 1972) et environ les deux tiers de ces cellules montrent une sélectivité à la direction du stimulus.

Comme c'est le cas dans l'aire PMLS, les cellules des couches superficielles du collicule supérieur montrent de piètres propriétés spatiales et d'excellentes propriétés temporelles. Les cellules du collicule préfèrent en moyenne des fréquences spatiales entre 0.05 et 0.1 c/deg. (Pinter et Harris, 1981), bien que Bisti et Sireteanu (1976) ont demontré que quelques cellules colliculaires préfèrent des fréquences spatiales plus élevées (jusqu'à 0.6 c/deg.). Les cellules colliculaires préfèrent nettement les hautes fréquences temporelles, supérieures à 5 Hz (Pinter et Harris, 1981).

Les propriétés spatiales des cellules colliculaires semblent refléter l'input massif des cellules de type W vers cette structure. La préférence des cellules colliculaires pour les fréquences temporelles élevées est attribuable aux cellules ganglionnaires de type Y qui se projettent vers les couches superficielles du collicule. En général, les propriétés spatio-temporelles des cellules colliculaires sont similaires à celles des cellules de l'aire PMLS, ce qui reflète l'importance des connections réciproques qui unissent ces deux régions visuelles.

Les substrats neurophysiologiques de la perception binoculaire de la profondeur

Le grand histologiste Santiago Ramon y Cajal (1911) fut le premier à suggérer, théoriquement, qu'un input visuel tombant sur des coordonnées rétiniennes correspondantes serait combiné sur une seule et même cellule corticale. Près de 50 ans plus tard, Hubel et Wiesel (1959, 1962), en utilisant la méthode électrophysiologique de Kuffler (1953), démontrèrent expérimentalement que Cajal avait raison. Ils observèrent en effet que la plupart des cellules du cortex visuel du chat répondent à la stimulation monoculaire de chaque oeil et que les CR binoculaires de ces cellules occupent des coordonnées spatiales similaires. Les CR binoculaires de plusieurs cellules ne sont toutefois pas parfaitement superposés, mais légèrement décalés, particulièrement sur le plan horizontal (Hubel et Wiesel, 1968; Schiller et al, 1976a, 1976b; Mullikin et al., 1984a, 1984b; Camarda et al., 1985; Maske et al., 1984, 1986; Emerson et al., 1987).

Horace B. Barlow, John D. Pettigrew et leurs collaborateurs démontrèrent que plusieurs de ces cellules binoculaires répondent optimalement lorsqu'un stimulus projette son image sur des coordonnées rétiniennes légèrement non-correspondantes (Barlow et al., 1967; Nikara et al., 1968; Pettigrew et al., 1968). Ainsi, il est présumé que des cellules binoculaires ayant des CR parfaitement superposés préfèrent les stimuli projetant des images rétiniennes correspondantes alors que les cellules dont les CR sont légèrement décalés préfèrent des stimuli positionnés de sorte que leurs images rétiniennes soient disparates.

Il a toutefois été proposé que la sensibilité à la disparité binoculaire de certaines cellules visuelles dépend d'un décalage dans l'organisation interne des CR plutôt que dans la

position spatiale de ceux-ci (Ohzawa et Freeman, 1986a, 1986b; Freeman et Ohzawa, 1990; Ohzawa et al., 1990; Hammond, 1991; Smith et al., 1997). Ces chercheurs soutiennent que le décalage intra-CR génère la perception stéréoscopique de la profondeur en permettant l'encodage de la phase relative des stimuli visuels (De Angelis et al., 1991; Ohzawa et al., 1997; Anzai et al., 1997). L'importance relative du décalage inter-CR et intra-CR ainsi que les interactions entre ces deux phénomènes seront analysés en détail dans la discussion générale de cette thèse.

À la recherche de cellules sensibles à la disparité spatiale

Des cellules binoculaires montrant un décalage inter-CR ou de la sensibilité à la disparité rétinienne ont été retrouvées chez de nombreuses espèces, incluant le mouton (Clark et al., 1976), le hibou (Pettigrew et Konishi, 1976; Pettigrew, 1979), la grenouille (Gaillard, 1985) et l'opossum (Dias et al., 1991). Les bases neurophysiologiques de la perception stéréoscopique ont toutefois été surtout étudiées chez deux espèces: le singe et le chat.

Quelques années après que Barlow et al. (1967) eurent trouvé des cellules sensibles à la disparité spatiale chez le chat, Hubel et Wiesel (1970) confirmèrent leur présence chez le singe. Les travaux de Peter O. Bishop et ses collaborateurs ont par la suite fourni une quantification plus détaillée de ces mécanismes neuraux (Joshua et Bishop, 1970; Bishop et al., 1971) et ont ainsi permis l'élaboration d'une théorie plus étoffée des bases neuronales de la stéréopsie (Bishop et Henry, 1971; Bishop, 1973). Ce furent toutefois Poggio et Fisher (1977) qui définirent, chez le singe éveillé, les quatre types de détecteurs de disparité spatiale sur lesquels toutes les études subséquentes sont basées. Les cellules excitatrices répondent

à une disparité spatiale autour de zéro avec un taux de décharge supérieur à la plus forte réponse monoculaire (sommation) ou supérieur à la somme de réponses monoculaires (facilitation). Les cellules inhibitrices répondent à une telle disparité en réduisant leur taux de décharge en-deçà de la plus faible réponse monoculaire. D'autre part, certaines cellules semblent préférer les stimuli paraissant devant (cellules à disparités croisées) ou derrière (cellules à disparités non-croisées ou homonymes) le plan de fixation. Ces cellules augmentent ainsi leur taux de décharge lors de la présentation de disparités spatiales croisées et non-croisées respectivement et diminuent leur taux de décharge lors de la présentation des disparités inverses. Le reste des cellules présentent des interactions complexes et inclassifiables ou sont simplement insensibles à la disparité spatiale (Poggio and Fisher, 1977; Poggio et Poggio, 1984).

Chez le singe, ces détecteurs de disparité spatiale se retrouvent dans l'aire V1 (Poggio et Fisher, 1977); ils se retrouvent en plus grande proportion dans les aires extrastriées, dont V2 (Poggio, 1984 (70%)), V3 (Felleman et Van Essen, 1987 (45%)), VP (Burkhalter et Van Essen, 1986 (65%)), MT (Maunsell et Van Essen, 1983 (66%)), MST (Roy et al., 1992 (plus de 90%)) et LiP (Gnadt et Mays, 1995 (100%)). Alors que les quatre types de détecteurs de disparités se retrouvent à des niveaux similaires dans la plupart de ces aires, l'aire MST contient presqu'exclusivement des cellules préférant les stimuli situés devant ou derrière le point de fixation. Gian F. Poggio et ses collaborateurs (Poggio et Talbot, 1981; Poggio et al., 1985, 1988; Poggio, 1991) ont aussi testé les cellules binoculaires du singe éveillé avec des stéréogrammes de points aléatoires, ce qui implique une perception globale du pattern de disparité spatiale. Leurs résultats montrent que plus de la moitié des cellules sont sensibles à ces disparités et que cette proportion augmente progressivement dans les aires V2, V3 et

V3A. Ainsi, chez le singe, la sensibilité aux indices locaux et globaux de disparité spatiale augmente progressivement le long du "visual processing stream" (Van Essen, 1985).

Chez le chat, des cellules sensibles à la disparité spatiale ont d'abord été identifiées dans le cortex visuel primaire (Barlow et al., 1967). Bien que Ferster (1981) n'ait trouvé que 30% de cellules sensibles à la disparité spatiale dans les aires 17 et 18, des études plus récentes ont démontré que cette proportion est supérieure à 70% (LeVay et Voigt, 1988; Lepore et al., 1992). La plupart des cellules simples (Ohzawa et Freeman, 1986a) et environ 40% des cellules complexes (Ohzawa et Freeman, 1986b) varient aussi leur taux de réponse en fonction de la phase relative de contraste des stimuli présentés.

Contrairement à ce qui est observé chez le singe, la proportion de cellules sensibles à la disparité spatiale dans les aires extrastriées du chat n'est pas supérieure à ce qui est observé dans le cortex visuel primaire. Dans l'aire 19, Pettigrew et Dreher (1987) rapportent la présence de cellules sensibles, particulièrement à des disparités autour de zéro ou homonymes, mais ne fournissent aucune analyse globale de la sensibilité des cellules de cette aire. Guillemot et al. (1993a) montrent que 34% des cellules de l'aire 19 sont sensibles à la disparité spatiale. Dans l'aire 21a, cette proportion est de 69% (Wang et Dreher, 1996). La sélectivité à la disparité spatiale des cellules de ces aires est d'ailleurs inférieure à celle des cellules du cortex visuel primaire.

La sensibilité à la disparité spatiale n'a pas été étudiée systématiquement dans les autres régions visuelles du chat. Des interactions binoculaires ont tout de même été relevées dans le collicule supérieur (Berman et al., 1975) et les aires PLLS et PMLS (Rauschecker et

al., 1987; von Grünau et al., 1987). Certaines cellules de l'aire PMLS sont d'ailleurs spécialisées dans la détection de stimuli semblant s'approcher (28%) ou s'éloigner (13%) de l'organisme dans un axe fronto-perpendiculaire (Toyama et Kozasa, 1982; Toyama et al., 1985, 1986a). La moitié de ces cellules sont aussi sensibles à des variations de la taille du stimulus (expansion et contraction) qui simulent le mouvement dans la troisième dimension (Toyama et al., 1986b)

L'Influence de l'albinisme sur la perception binoculaire de la profondeur et sur ses substrats neurophysiologiques

L'albinisme est une pathologie d'origine génétique qui affecte la synthèse de la mélanine, ce qui provoque la dépigmentation des yeux (albinisme oculaire) ou de toute la surface du corps (albinisme oculocutané). Cette pathologie se manifeste chez plusieurs espèces, dont la souris (LaVail et al., 1978), le lapin (Sanderson, 1975), le chat (Creel, 1971; Guillery et Kaas, 1971), le singe (Gross et Hickey, 1980; Guillery et al., 1984) et l'humain (Aquaron, 1993).

Peu importe l'espèce, l'albinisme entraîne des anomalies au niveau de la structure rétinienne et de l'organisation des voies visuelles. Plus particulièrement, le système visuel de l'albinos est caractérisé par un croisement anormalement massif des fibres ganglionnaires de l'hémirétine temporale, de sorte que chaque hémisphère ne reçoit presque plus d'informations visuelles en provenance de l'oeil ipsilatéral (Guillery et al., 1974; Guillery, 1996). L'albinos souffre aussi souvent de strabisme, de nystagmus congénital et d'une réduction importante, voire même de l'absence, de la fusion binoculaire et de la stéréopsie.

Le chat albinos, ou chat Siamois, représente un excellent modèle pour étudier les troubles de vision binoculaire associés à l'albinisme. Le chat normal possède en effet une vision stéréoscopique (Packwood et Gordon, 1975; Fox, 1981; Lepore et al., 1986; Ptito et al., 1986) et les bases neurophysiologiques de celle-ci ont été souvent étudiées (Barlow et al., 1967; von der Heydt et al., 1978; Ferster, 1981; Ohzawa et Freeman, 1986a, 1986b; LeVay et Voigt, 1988; De Angelis et al., 1991; Lepore et al., 1992; Guillemot et al., 1993a; Wang et Dreher, 1996).

Chez le chat normal, 70% des cellules ganglionnaires se projettent vers l'hémisphère controlatéral. Chez le chat Siamois, l'information provenant de l'hémirétine temporale correspondant aux 20 degrés d'angle visuel contiguë au méridien vertical croise aussi du côté controlatéral, ce qui fait grimper la proportion de fibres croisées à 90% (Guillery, 1969; Guillery et Kaas, 1971). Ce croisement anormal, et le strabisme qui lui est souvent concomitant, provoque une réduction drastique du nombre de cellules binoculaires dans le cortex visuel primaire du chat Siamois (Hubel et Wiesel, 1971; Cool et Crawford, 1972; Cooper et Blasdel, 1980; Marzi et al., 1976, 1980; Antonini et al., 1981; Leventhal et Creel, 1985; Toyama et al., 1991). En effet, les cellules binoculaires sont en très faible minorité dans les aires 17/18 (de 0% à 16% selon les études), et dans l'aire 19 (Di Stefano et al., 1984 (moins de 2%); Toyama et al., 1991 (13%)). La plupart des cellules de ces aires répondent exclusivement à la stimulation de l'oeil controlatéral. La rareté des cellules binoculaires dans ces aires concorde avec l'absence de stéréopsie fine observée chez le chat Siamois (Dews et Wiesel, 1970; Packwood et Gordon, 1975).

Un plus grand nombre de cellules binoculaires ont toutefois été identifiées dans les aires suprasylviennes latérales (Marzi et al., 1980 (82%); Toyama et al., 1991 (55%)) et dans le collicule supérieur (Berman et Cynader, 1972 (16%); Antonini et al., 1981 (87%)) du chat Siamois. Le degré de binocularité retrouvé dans ces régions visuelles indique que l'information venant des deux yeux y est adéquatement fusionnée et que ces cellules pourraient permettre au chat Siamois d'avoir un certain degré de perception stéréoscopique. Aucun test de stéréopsie grossière n'a été effectué chez le chat Siamois, mais il a tout de même été démontré que l'humain albinos (Guo et al., 1989: Apkarian et Reits, 1989) ou strabique (Sireteanu. 1982; Kitaoji et Toyama, 1987; Sireteanu et Fronius, 1989) jouit d'un certain degré de stéréopsie grossière (stéréoacuité de 1.3 à 13 degrés, selon les sujets).

Les hypothèses spécifiques

Le premier objectif général de cette thèse est d'évaluer et de comparer l'encodage des indices de disparité spatiale qui est effectué le long du système visuel du chat. La sensibilité à la disparité spatiale des cellules des aires 17/18, 19, PMLS et du collicule supérieur sera évaluée et comparée en se basant sur les trois facteurs suivants:

1. Le nombre (pourcentage) de cellules sensibles à la disparité spatiale dans les régions visuelles étudiées.
2. Les types de profils de sensibilité à la disparité spatiale des cellules sensibles des régions visuelles étudiées.
3. La sélectivité à la disparité spatiale des détecteurs de disparité des différentes régions visuelles étudiées. La sélectivité est définie opérationellement comme étant

la largeur de la bande-passante à mi-hauteur des cellules excitatrices et inhibitrices et la pente à mi-hauteur des cellules préférant les disparités croisées et homonymes.

Le deuxième objectif général de cette thèse est d'étudier la sensibilité à la disparité spatiale des cellules binoculaires du chat Siamois, qui est albinos. La sensibilité des cellules des différentes régions visuelles de cette espèce seront comparées entre elles puis comparées à ce qui est observé chez le chat normal, selon les trois critères énoncés plus haut.

Sensibilité et sélectivité à la disparité spatiale dans le cortex visuel primaire du chat

La sensibilité à la disparité spatiale des cellules des aires 17 et 18 a été fréquemment étudiée (Barlow et al., 1967; Pettigrew et al., 1968; Nikara et al., 1968; Joshua et Bishop, 1970; von der Heydt et al., 1978; Ferster, 1981; LeVay et Voigt, 1988; Lepore et al., 1992). Toutefois, seules les trois dernières études ont été conduites après celle de Poggio et Fisher (1977) et tiennent ainsi compte de sa classification des types de détecteurs de disparité.

Ferster (1981) ne trouve que 30% de cellules sensibles à la disparité spatiale dans le cortex visuel primaire du chat. Ce faible pourcentage est en partie attribuable au fait que son échantillon inclut une forte proportion de cellules monoculaires et/ou dont les CR étaient situés en périphérie (jusqu'à 25 degrés d'excentricité) du champ visuel. Il rapporte néanmoins plusieurs cellules excitatrices (surtout dans l'aire 17) et plusieurs cellules des trois autres types (surtout dans l'aire 18). Il ne fournit toutefois pas d'analyse de sélectivité de ces cellules.

LeVay et Voigt (1988), qui étudièrent la représentation centrale du champ visuel, trouvent que plus de 70% des cellules 17/18 sont sensibles à la disparité spatiale. Bien qu'ils reconnaissent que plusieurs de leurs cellules ressemblent aux quatre types de détecteurs de disparité de Poggio et Fisher (1977), ils ne fournissent pas de classification de leurs cellules en terme de classes de détecteurs de disparité. Ces auteurs fournissent par contre une analyse de la sélectivité de leurs cellules. Ainsi, ils rapportent que la largeur moyenne de la bande-passante à mi-hauteur des 94 cellules montrant une pointe excitatrice est de 1.70 degrés. Ils indiquent aussi que la pente à mi-hauteur des 196 cellules ayant une pente mesurable (incluant les cellules qui montrent une pointe excitatrice) est de 38 (38% de la réponse maximale par degré de disparité). Comme ces auteurs ont testé la sensibilité aux différentes disparités spatiales par intervalles plutôt larges (0.5 et 1 degrés), il est possible que ces chiffres ne rendent pas justice à la sélectivité des cellules du cortex visuel primaire.

Lepore et al. (1992) montrent que 70% des cellules binoculaires situées à la bordure des aires 17 et 18 sont sensibles à la disparité spatiale. Ils trouvent plusieurs détecteurs de disparité des quatre types, et montrent une distribution plutôt équitable des cellules sensibles dans ces quatre catégories. Ils testèrent la sensibilité des cellules aux différentes disparités spatiales par pas de 0.2 degré, mais ne fournissent pas d'analyse de la sélectivité des cellules.

Les résultats de Lepore et al. (1992) seront donc réanalysés pour permettre une évaluation de la sélectivité des cellules des aires 17/18. L'intervalle inter-stimuli (0.2 degré), plus petit que celui de LeVay et Voigt (1988) est plus approprié pour tester les cellules d'une aire où les propriétés spatiales sont si fines. Ainsi, les bandes-passantes seront moins larges et les pentes seront plus abruptes que celles observées par LeVay et Voigt (1988). Ces

résultats serviront de niveau de base et de point de comparaison pour la sensibilité et la sélectivité à la disparité spatiale des cellules des autres régions visuelles.

Sensibilité et sélectivité à la disparité spatiale des cellules de l'aire 19 du chat

Pettigrew et Dreher (1987) furent les premiers à étudier la sensibilité à la disparité spatiale des cellules de l'aire 19. L'objectif principal de cette étude était de mesurer et de comparer le décalage inter-CR des aires 17, 18 et 19. Ainsi, bien que ces auteurs rapportent des interactions binoculaires excitatrices et inhibitrices et montrent quelques profils de sensibilité à la disparité spatiale, ils ne fournissent aucune analyse de population des cellules de l'aire 19.

Guillemot et al. (1993a) indiquent que 34% des cellules de l'aire 19 sont sensibles à la disparité spatiale. Ils démontrent que les quatre types de détecteurs de disparité se retrouvent dans l'aire 19, et que près des deux tiers de ces détecteurs préfèrent des disparités de type croisées et homonymes. Ces auteurs ne fournissent toutefois pas d'analyse de la sélectivité de ces cellules.

Ainsi, les résultats de Guillemot et al. (1993a), comme ceux de Lepore et al. (1992), seront réanalysés afin de permettre une évaluation et une comparaison de la sélectivité des cellules de l'aire 19. Les propriétés spatiales de l'aire 19, plus grossières que dans le cortex visuel primaire, laissent supposer une sélectivité moins fine qui se traduira par des bandes passantes plus larges et des pentes moins abruptes que dans les aires 17/18.

Sensibilité et sélectivité à la disparité spatiale dans l'aire PMLS du chat

L'aire PMLS contient un grand nombre de cellules binoculaires, particulièrement dans la représentation centrale du champ visuel (Hubel et Wiesel, 1969; Spear et Baumann, 1975; Rauschecker et al., 1987; von Grünau et al., 1987). La sensibilité à la disparité spatiale de ces cellules n'a jamais été systématiquement étudiée.

Spear et Baumann (1975) furent les premiers à rapporter des interactions binoculaires dans l'aire PMLS, soit des cellules qui ne répondent qu'à la stimulation binoculaire. Von Grünau et al. (1987) étudièrent plus en détail ces interactions en stimulant simultanément les deux CR superposés (disparité zéro). Ces auteurs indiquent que plus de 80% des cellules de l'aire PMLS répondent à la stimulation binoculaire avec plus de vigueur qu'à la stimulation monoculaire de l'oeil dominant (sommation binoculaire). Ils indiquent aussi avoir observé de l'inhibition (occlusion binoculaire), mais seulement pour quelques cellules.

Keisuke Toyama et ses collaborateurs ont étudié la sensibilité des cellules de l'aire Clare-Bishop au mouvement de stimuli dans la troisième dimension (Toyama et Kozasa, 1982; Toyama et al, 1985, 1986a, 1986b). Les coordonnées où leurs enregistrements ont été conduits suggèrent que leur échantillon provient des aires AMLS et PMLS. Leur analyse de plus de 500 cellules montre que 41% de celles-ci préfèrent les stimuli se déplaçant sur l'axe fronto-perpendiculaire (28% vers l'organisme, 13% vers l'horizon). De plus, 50% de ces cellules répondent à une variation de la taille d'un stimulus fixe qui simule le mouvement sur l'axe des Z.

Ces études démontrent que les interactions binoculaires abondent dans l'aire PMLS. En effet, les cellules de cette aire intègrent très bien l'information venant des deux yeux et se servent de cette intégration pour détecter la direction d'un mouvement dans la troisième dimension. Une telle analyse, concomitante à l'implication de l'aire PMLS dans l'accommodation (Bando et al., 1988) et la vergence (Bando et al., 1996), amène à penser que plusieurs cellules de l'aire PMLS sont sensibles à la disparité spatiale. L'aire MT du singe qui est souvent considérée homologue à l'aire PMLS (Payne, 1993) contient d'ailleurs une importante proportion (66%) de cellules sensibles à la disparité spatiale (Maunsell et Van Essen, 1983).

La prédominance d'interactions binoculaires de type sommatives et l'importance de l'aire PMLS dans la fixation du regard suggèrent que la majorité des détecteurs de disparité de cette aire seront de type excitateurs. Par contre, puisque 28% des cellules de l'aire Clare-Bishop préfèrent des stimuli se dirigeant vers l'organisme, une proportion des cellules de l'aire PMLS préférera probablement les disparités croisées. En suivant le même raisonnement, une proportion moins importante mais non-négligeable de cellules de cette aire préférera les disparité homonymes.

La préférence des cellules de l'aire PMLS pour les stimuli se déplaçant à grande vitesse et leurs propriétés spatiales grossières laissent présumer que leur sélectivité à la disparité spatiale sera moins fine que dans les aires 17/18 et 19. D'ailleurs, une aire impliquée dans la détection des mouvements et la fovéation sur l'axe des Z nécessite beaucoup de sensibilité à la disparité spatiale, mais peut se contenter d'une sélectivité plus grossière que les aires impliquées dans la perception de la forme.

Sensibilité et sélectivité à la disparité spatiale dans le collicule supérieur du chat

Le collicule supérieur est une structure sous-corticale reconnue surtout pour son rôle dans le contrôle des mouvements oculaires. En effet, les couches colliculaires profondes sont impliquées dans le contrôle des saccades et de la position oculaire déterminée par une cible visuelle (Wurtz et Mohler, 1974; Robinson, 1975; Schiller et Wurtz, 1975; Sparks, 1975, 1978; Wurtz et Albano, 1980; Van Opstal et al., 1990; Guitton, 1991). Cette structure est aussi impliquée dans le contrôle de l'accommodation (Sawa et al., 1994; Sato et Ohtsuka, 1996) et joue probablement un rôle dans le contrôle des mouvements de vergence, par un circuit impliquant l'aire PMLS et les noyaux oculomoteurs du tronc cérébral (Bando et al., 1996).

Le contrôle des saccades par les cartes motrices des couches colliculaires profondes est basé sur les cartes spatiales des couches superficielles avec lesquelles elles sont rétinotopiquement connectées (Behan et Appell, 1992; Behan et Kime, 1996). De la même manière, ces cartes spatiales des couches superficielles doivent guider le contrôle moteur de l'accommodation et de la vergence. Pour ce faire, les cartes spatiales des couches superficielles doivent être tridimensionnelles et doivent donc combiner l'information des deux yeux pour en extraire les indices de disparité spatiale.

Les couches superficielles du collicule supérieur du chat contiennent de nombreuses cellules binoculaires (Sterling et Wickelgren, 1969; Berman et Cynader, 1972; Hoffmann et Sherman, 1975). Hayashi et al. (1973) furent les premiers à étudier les interactions binoculaires de ces cellules. Ils rapportent que la plupart des cellules, lorsque les CR sont

stimulés simultanément (disparité nulle), montrent de la sommation binoculaire et que quelques cellules montrent de la suppression binoculaire.

Une seule étude (Berman et al., 1975) se penche sur les interactions binoculaires produites dans le collicule supérieur du chat par des stimuli dont la disparité spatiale est systématiquement variée. Ces auteurs montrent des profils de sensibilité de cellules qui sont clairement des détecteurs de disparité de type excitateurs. Ils rapportent aussi des effets d'occlusion binoculaire mais ne montrent pas de profils de cellules inhibitrices. Ces auteurs ne montrent pas non plus de cellules qui préfèrent les disparités de type croisées ou homonymes. D'ailleurs, puisque cette étude précède celle de Poggio et Fisher (1977), aucune classification des cellules en terme de profils de sensibilité à la disparité spatiale n'est fournie. Aucune analyse de la sélectivité des cellules n'est effectuée, mais il est possible de voir sur les courbes de réponse des cellules excitatrices que la sélectivité est grossière (largeur de la bande-passante à mi-hauteur entre 2 et 4 degrés).

Des cellules montrant un décalage inter-CR ont aussi été identifiées dans le tectum optique de la grenouille (Gaillard, 1985). Comme les réponses de ces cellules à des stimuli simulant différentes disparités spatiales n'ont pas été évaluées, il est malheureusement impossible d'affirmer que ces cellules sont sélectives aux disparités spatiales. Ces résultats suggèrent toutefois que la vision stéréoscopique que la grenouille utilise pour localiser ses proies avec précision (Fite et Scalia, 1976; Collett, 1977) est ancrée dans des bases neurologiques tectales. En ce sens, les collicules supérieurs de la grenouille et des espèces phylogénétiquement plus évoluées, comme le chat et le singe, semblent remplir des fonctions similaires de localisation et de fovéation.

Plus récemment, Dias et al. (1991) ont étudié la sensibilité à la disparité spatiale des cellules du collicule supérieur de l'opossum. La plupart des cellules colliculaires de cette espèce sont binoculaires et 66% de ces cellules montrent de la sommation ou de la facilitation binoculaire. Ces auteurs rapportent 26 cellules (19%) clairement de type excitatrices et quelques cellules dont les profils de réponse s'apparentent aux cellules préférant les disparités croisées. Ces auteurs ne rapportent pas de cellules inhibitrices ni de cellules préférant les disparité homonymes. Ils attribuent l'absence de ce dernier type de détecteur de disparité à la myopie chronique (Picanço-Diniz et al., 1983) de l'opossum. La sélectivité des cellules excitatrices de cette étude est excessivement grossière (largeur de la bande passante à mi-hauteur de 6 à 18 degrés). Ceci reflète la grande taille (de 8 à 26 degrés de diamètre) et le décalage horizontal important (jusqu'à 19 degrés) des CR des cellules binoculaires du collicule supérieur de l'opossum. Cet animal a d'ailleurs les yeux situés très latéralement et aucune étude ne démontre qu'il possède une vision stéréoscopique.

Ces études, particulièrement celle de Berman et al. (1975), ne laissent aucun doute quant à la présence de détecteurs de disparité spatiale dans le collicule supérieur du chat. La proportion de cellules sensibles à la disparité sera sans aucun doute supérieure à ce qui a été observé chez l'opossum, puisque le chat à les yeux disposés frontalement et qu'il possède une vision stéréoscopique (Fox et al., 1981; Lepore et al., 1986).

Les études de Berman et al. (1975) et de Dias et al. (1991) suggèrent que ces cellulles seront pour la plupart des excitatrices. Par contre, l'occlusion binoculaire (Berman et al., 1975) et les cellules préférant les disparités de type croisées (Dias et al., 1991) laissent croire que les autres types de détecteurs de disparité seront aussi présents, en moins grand nombre,

dans le collicule supérieur du chat. Les fonctions colliculaires de fovéation dépendraient ainsi des cellules excitatrices et inhibitrices alors que les fonctions de convergence et de divergence dépendraient des cellules préférant les disparités spatiales croisées et homonymes respectivement.

La sélectivité à la disparité spatiale des cellules colliculaires sera plus grossière encore que dans les aires extrastriées telles que l'aire 19 et l'aire PMLS. Les CR des cellules colliculaires sont en effet plus grands et leurs propriétés spatiales sont plus grossières. De plus, un système impliqué dans le contrôle des mouvements oculaires ne requiert pas la sélectivité fine qui permet l'analyse de la forme, mais seulement la sélectivité grossière qui permet la détection et la localisation des stimuli.

Sensibilité et sélectivité à la disparité spatiale chez le chat Siamois

Le système visuel des organismes albinos, tel que le chat Siamois, est caractérisé par une décussation anormalement massive des cellules ganglionnaires vers l'hémisphère controlatéral (Creel, 1971; Guillery et al., 1971; Guillery, 1996). Cette décussation et le strabisme qui souvent l'accompagne entraînent une forte réduction de la binocularité corticale du Siamois. En effet, les cellules des aires 17/18 (Hubel et Wiesel, 1971; Cool et Crawford, 1972; Cooper et Blasdel, 1980; Marzi et al., 1976, 1980; Antonini et al., 1981; Leventhal et Creel, 1985; Toyama et al., 1991) et 19 (Di Stefano et al., 1984; Toyama et al., 1991) du chat Siamois sont en grande majorité (certaines études parlent de totalité) monoculaires. Tout porte à croire que bien peu de cellules binoculaires seront identifiées dans ces aires.

Il a été démontré que les cellules binoculaires sont plus abondantes dans les aires suprasylviennes latérales (Marzi et al., 1980; Toyama et al., 1991) et dans le collicule supérieur (Berman et Cynader, 1972; Antonini et al., 1981) du chat Siamois. Par contre, aucune étude ne s'est penchée sur la sensibilité à la disparité spatiale de ces cellules. Toyama et al. (1991) ont évalué la réponse de ces cellules à des stimuli se déplaçant dans la troisième dimension, comme ils l'avaient fait chez le chat normal. Ils indiquent que 18% des cellules répondent à des stimuli s'approchant de l'organisme et que 3% de ces cellules préfèrent des stimuli s'éloignant de l'organisme.

Ces études laissent entrevoir la possibilité qu'une proportion des cellules binoculaires de l'aire PMLS et du collicule supérieur du chat Siamois soient sensibles à la disparité spatiale. Les grands CR et les fortes projections calleuses qui créent la binocularité des cellules de cette aire (Marzi et al., 1980) permettent la fusion des informations visuelles venant des deux yeux et possiblement la détection de leur décalage spatial. Les détecteurs de disparité de ces deux régions visuelles seront, comme chez le chat normal et pour les mêmes raisons, en majorité de type excitateurs. Les déficits d'acuité visuelle et le strabisme que montrent certains Siamois laissent entrevoir que la sélectivité des détecteurs de disparité sera encore plus grossière que ce qui est observé dans les mêmes régions visuelles chez le chat normal.

L'albinisme entraîne des déficits importants au niveau de la fusion binoculaire et de la stéréopsie. Il a toutefois été démontré chez l'humain que cette pathologie épargne un certain degré de stéréopsie grossière (Guo et al., 1989; Apkarian et Reits, 1989). Le chat Siamois est albinos et il a été démontré qu'il ne possède pas de stéréopsie fine (Packwood et

Gordon, 1975). Aucun test de stéréopsie grossière n'a été effectué chez le chat Siamois, mais il est plus que probable que cette capacité soit conservée, du moins jusqu'à un certain degré. Si tel est le cas, cette stéréopsie grossière dépend probablement de l'encodage de la disparité spatiale effectué par les cellules binoculaires de l'aire PMLS (Marzi et al., 1980; Toyama et al., 1991) et du collicule supérieur (Berman et Cynader, 1972; Antonini et al., 1981).

CHAPITRE 2

Article 1:

Striate, extrastriate and collicular processing of spatial disparity cues

Sous-presse: Archives of physiology and biochemistry

STRIATE, EXTRASTRIATE AND COLLICULAR PROCESSING OF SPATIAL DISPARITY CUES

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Running title: ***Spatial disparity processing in the cat***

ABSTRACT

The spatial disparity sensitivity of single units in the primary visual cortex (17-18 border), in extrastriate area 19 and in the superficial layers of the superior colliculus of the cat brain were compared in the present study. Unit recordings were performed in paralyzed and anesthetized animals. Centrally located receptive fields were mapped, separated using prisms and then stimulated simultaneously using two luminous bars optimally adjusted to the size of the excitatory receptive fields. In the three regions studied, cells selective to spatial disparity were found and four classes of disparity sensitivity profiles emerged. Although the disparity sensitivity profiles of the cells in the three regions appeared to have the same general shape, selectivity was clearly different. Cells at the 17-18 border were sharply tuned, those of area 19 were not only less numerous but also less well tuned and collicular cells exhibited coarse selectivity. These differences in selectivity appear to be linked to the projection pattern of the X, Y and W systems to these regions and the roles that these cells might play in vision.

KEY WORDS

Area 19, Areas 17-18, Cat, Disparity selectivity, Spatial disparity, Stereopsis, Superior colliculus.

INTRODUCTION

Wheatstone (1838) was the first to demonstrate that the spatial disparities between the two-dimensional images cast upon the retina by objects in the visual scene are used to estimate the depth of these objects and generate a vivid perception of the third dimension. It has been demonstrated several times that higher mammals, such as the cat (Fox, 1981; Lepore et al., 1986; Ptito et al., 1986) and monkey (Bough, 1970) are also endowed with such stereoscopic vision.

The organization of higher visual systems allows for the convergence of corresponding inputs from both retinae upon a single cell. Such binocular cells, first identified in area 17 of the cat (Hubel and Wiesel, 1959, 1962), are presumed to form the neural substrate of stereopsis. Indeed, a large proportion of these cells in the striate cortex of the cat (Barlow et al., 1967; LeVay and Voigt, 1988; Lepore et al, 1992) and monkey (Poggio and Fisher, 1977) respond differentially to specific spatial disparities. Some of those cells seem to prefer stimuli located within panum's fusional area and respond with an increase (tuned excitatory) or decrease (tuned inhibitory) in their response rate to spatial disparities at or around zero. Others increase their response rate to a broad range of disparities in the crossed range and decrease their response to a broad range of disparities in the uncrossed range (near cells) or vice-versa (far cells), hence appearing to be respectively coding for stimuli lying in front of or behind the fixation point.

Such disparity sensitive cells have been identified in most higher order visual areas of the cat, such as area 19 (Pettigrew and Dreher, 1987; Guillemot et al., 1993) and 21a (Wang and Dreher, 1996). Recent studies conducted in our laboratory also demonstrated the existence of disparity sensitive cells in the superior colliculus of the

cat (Lepore et al., 1996).

The present report aims at comparing and contrasting disparity selectivity of cells in the striate cortex (17-18 border), in extrastriate area 19 and in the superior colliculus of the cat. The study of these cortical and tectal regions, tested under identical stimulation procedure, should demonstrate whether similar disparity sensitivity profiles are present in all three and whether there are differences in the degree of selectivity tuning among them. Indeed, it would be expected that, if spatial receptive field properties of the cells were taken into consideration, the finest disparity tuning would be found in the striate cortex and the coarsest selectivity would occur in the superior colliculus. An attempt will be made to link differences in selectivity to anatomical observations, particularly the pattern of projection of the X, Y and W sub-systems, and to the functions that these cells might play in depth perception and stereopsis.

MATERIALS AND METHODS

All surgical interventions, manipulations and husbandry were carried out within the guidelines of the Canadian Council on Animal Care (CCAC) and of the National Institute of Health (NIH) concerning the preparation and maintenance of higher animals during visual neuroscience experiments. Moreover, the experimental protocols were approved by the University Animal Care Committee before the beginning of experimentation.

The techniques of animal preparation and care, anesthesia, surgery, optical preparation, recording and histology have been fully described in previous articles (Lepore et al., 1992; Guillemot et al., 1993) and will only be briefly summarized herein. The animal was anesthetized using a face mask with a gaseous mixture of nitrous oxide, oxygen (N_2O:O_2, 70:30) and Fluothane (5%). Throughout the surgery, the fluothane level was kept between 1 and 2%. Unit recordings were then performed in the central visual field representation of the 17-18 border, of area 19 and of the superior colliculus of the cat using glass microelectrodes filled with 3M NaCl. Throughout recording, the animal was maintined under light anesthesia (N_2O:O_2, 70:30; fluothane, 0.5% of gaseous mixture), the expired CO_2 level was maintained at 4% and ECG was constantly monitored to insure stable heart rate. The absence of reflexes and changes of heart rate to stimulation as well as a synchronized slow-wave EEG insured that the anesthesia level was sufficient. At the end of surgery and under these conditions, a solution of gallamine triethiodide (Flaxedil: 200 mg) and d-tubocurarine (Tubarine, 15 mg) dissolved in 30 ml lactated ringer solution with dextrose (5%) was infused through the saphenous vein to maintain paralysis of the extra-ocular muscles. EEG and ECG were monitored intermittently yet regularly throughout the recording session to ensure stable anesthetic

levels.

To prevent eye dehydration and to improve image resolution, a neutral contact lens with a 3 mm artificial pupil was placed on each eye. The optic quality of the eyes was routinely checked during the recording session and the image on the retina was focused on a tangent screen by the use of appropriate dioptric lenses.

The stimulation procedure was adapted from Henry et al. (1967). The optic axis of one of the eyes was deviated using prisms so that the receptive fields (RFs) of the two eyes would be located on widely separated coordinates on the tangent screen. When recording was performed in cortical areas, the tangent screen was placed 171 cm from the animal, such that 3 cm of space corresponded to 1 degree of visual angle. Due to the larger receptive fields of collicular cells, the screen was placed 57 cm from the animal when recording was performed in this structure. Two projectors, placed behind the backward projection screen allowed the independent stimulation of each eye with two light bars equated in luminance and contrast. A dual optic bench system, controlled through a PC computer, ensured the independent and precise definition of the other stimuli parameters: length, width, direction, velocity, position in space, stimulus onset, as well as sweep duration and amplitude.

Upon isolating a binocular cell, the following initial protocol was followed. The RF of each eye was precisely mapped using light and dark bars. During this phase, the best stimulus parameters, defined as the stimulus configuration which produced the greatest cellular response, were determined for both RFs. Quantitative evaluation was then performed. Stimulation was carried out using the dual optic bench system: two light bars having the best estimated dimensions were swept at optimal velocity and direction across each RF. When recording cortical cells, stimulus velocity varied between 0.67

deg/s and 7.41 deg/s, each sweep covering 6.67 degrees. Recording of collicular cells was performed with stimulus velocity varying from 1 deg/s to 20 deg/s, each sweep covering 20 degrees. Each eye was first stimulated separately to determine the monocular response. Binocular interactions were tested through simultaneous stimulation of both RFs at different spatial disparities.

The two light bars were positioned exactly equidistant from the center of each RF. When the two bars started moving at the same time, they crossed the centers of the RFs simultaneously, and disparity was null. However, if the initiation of the sweep of one bar was delayed with respect to the other, the two bars would at any particular time be situated at non corresponding points in each RF. The introduction of such a delay hence allowed the creation of crossed and uncrossed disparities. In addition to the null condition, several spatial disparity conditions were tested. In the striate cortex, disparities ranging from 1 degree crossed to 1 degree uncrossed were tested, in 0.2 degrees steps. In area 19, the disparities tested varied from 3 degrees crossed to 3 degrees uncrossed, in 0.2, 0.5, or 1 degrees steps. Collicular cells were tested using disparities from 3 degrees crossed to 3 degrees uncrossed, in 0.5 or 1 degrees steps. Disparity, therefore, was defined relative to the RFs. These in turn were defined in terms of the coordinate reference points of the eyes. Although spatial disparity cannot be considered in absolute terms, it is nonetheless a very close approximation limited only by the accuracy of the definition of retinal landmarks. Their location were in fact quite easy to determine and to reproduce. It should moreover be added that obtaining the information in terms of absolute disparity is not critical as the present report, like others of similar nature (LeVay and Voigt, 1988; Freeman and Ohzawa, 1992) is principally interested in the degree or range of disparity selectivity.

Cellular action potentials were conventionally amplified, displayed on an oscilloscope, filtered through a time/amplitude discriminator and transferred to an audio monitor. They were also transformed into square pulses and fed to a generic brand PC-486 computer for on line and a posteriori analysis. All conditions, each tested a total of 10 times, were interleaved with each other in a pseudo-random fashion. The time interval between each sweep was 10-20 seconds to avoid habituation. For each condition, a peri-stimulus time histogram (PSTH) was built from the cellular responses. These PSTHs were divided into 500 bins, each having a binwidth of 1-40 ms, depending upon the duration of the sweep. For each condition, a second PSTH, of equal duration, was derived prior to each sweep when no stimulation was present to establish a baseline level. Each point on the response profiles of a cell was obtained in the following manner. For each condition, the average number of spikes elicited without stimulation (baseline PSTH) was subtracted from the average number of spikes elicited during the stimulation PSTH.

Eye stability control was insured by the pre- and post-recording quantitative mapping of the RFs. Any measurable displacement in the location of either field resulted in the data being discarded. The stability of the eyes throughout the recording session was also monitored through the frequent mapping of the optic disks and major blood vessels. Fairly stable eye positions were maintained throughout the recording session, and failure to maintain stability also resulted in the data being discarded.

At the end of the experiment, the brain was removed and sliced (40 μm) along the coronal plane. Every second slice from the block containing the recorded structure was kept and stained using the cresyl violet or Kluver-Barrera methods and only cells clearly located in the desired region were included in the results.

RESULTS

Disparity sensitivity was evaluated in 78 cells from the primary visual cortex (17-18 border), in 65 cells from area 19 and in 172 cells from the superficial layers of the superior colliculus. These cells were regrouped according to the disparity profiles first proposed by Poggio and Fisher (1977) and briefly defined herein. Tuned excitatory cells significantly increased their discharge rate in response to a narrow range of spatial disparities around null (see Figure 1 and upper part of Figure 2). Tuned inhibitory cells decrease their rate of firing clearly below the lowest monocular response when presented with a stimulus appearing on the fixation plane (see lower part of Figure 2). Near cells and far cells respectively increase their rate of firing to a wide array of spatial disparities located in the crossed or uncrossed disparity range (see Figure 3). These four classic subsets of disparity detectors were found in the three visual regions studied. It must be noted that insensitive cells, which keep a constant rate of firing regardless of the disparities presented and unclassifiable cells, which present complex patterns of disparity sensitivity were also encountered both at the cortical and tectal levels.

Insert Figures 1, 2 and 3 approximately here

Distribution of these cells across the classes of disparity sensitivity profiles can be seen in Table 1. It must be noted that whereas 70% of cells at the 17-18 border and 65% of collicular cells were sensitive to spatial disparity, only 31% of cells recorded in area 19 exhibited disparity sensitivity. As the proportion of unclassifiable cells was rather constant across the three regions under investigation, the low proportion of disparity sensitive cells in area 19 was directly imputable to the abundance of insensitive cells.

Insert Table 1 approximately here

The main objective of this report was to compare and contrast the tuning of disparity sensitivity profiles of striate, extrastriate and collicular regions. Therefore, only cells exhibiting sensitivity to spatial disparity were included in the selectivity analysis that follows.

Bandwidths of the tuned cells

Full-widths at half-height were computed for both the tuned excitatory and tuned inhibitory cells of the three visual regions studied. The average bandwidths, in degrees, of these cells are summarized in table 2.

Insert Table 2 approximately here

A one-factor ANOVA was conducted to compare the bandwidths of tuned excitatory cells in the three regions studied and a significant group effect was found ($F_{2,83} = 47.9$, $p<0.0001$). The bandwidths of collicular cells were significantly larger than those of cells in area 19, which were in turn larger than the bandwidth of cells recorded at the 17-18 border ($p<0.01$, Student-Neuman-Keuls). Another one-factor ANOVA was conducted to assess the difference between the bandwidths of tuned inhibitory cells recorded at the 17-18 border and in the superior colliculus. As only two cells in area 19 were of the tuned inhibitory type, these could not be included in the statistical analysis. There was a significant group effect ($F_{1,22} = 14.18$, $p<0.01$). These differences in bandwidths of both tuned excitatory and tuned inhibitory cells can clearly be seen in

Figure 2, where representative examples of disparity sensitivity profiles recorded at the 17-18 border, in area 19 and in the superior colliculus are shown on the same scale.

Slopes of the near and far cells

Slopes at 50% of the tuning function were computed for both the near and far cells recorded in the three visual regions studied. The average slopes of these cells are summarized in Table 3.

Insert Table 3 approximately here

A one-factor ANOVA was conducted to compare the slopes of near cells in the three regions under investigation and a significant group effect was found ($F_{2,37} = 63.00$, $p<0.0001$). The slopes of near cells recorded in the superior colliculus were significantly less steep than slopes of near cells at the 17-18 border and in area 19 ($p<0.01$, Student-Neuman-Keuls). However, the slopes of cells in area 19 were not significantly different from those of cells recorded at the 17-18 border. The same procedure was used to compare the slopes of far cells and a significant group effect was also found ($F_{2,31} = 41.81$, $p<0.0001$). The slopes of far cells in the superior colliculus were less steep than those of far cells in area 19 ($p<0.05$, Student-Neuman-Keuls), which in turn were less steep than those of near cells at the 17-18 border ($p<0.01$, Student-Neuman-Keuls). These differences in slopes of both the near and the far cells can clearly be seen in Figure 3, where representative examples of disparity sensitivity profiles recorded at the 17-18 border, in area 19 and in the superior colliculus are shown on the same scale.

DISCUSSION

The present report aimed at comparing and contrasting the disparity selectivity of binocular units at three level of the visual system, namely the primary visual cortex, an extrastriate area and a sub-cortical visual structure. Results indicate that the manner in which horizontal spatial disparity is coded at those three level appears to be similar, as binocular cells recorded at the 17-18 border, in area 19 and in the superior colliculus show disparity sensitivity profiles of comparable shapes. However, closer examination of the profiles reveals that selectivity at these three levels is different, ranging from extremely fine in the striate cortex to coarse in the superior colliculus. The question that follows from these observations is whether this reflects a genuine difference in the function of the three visual regions for the analysis of spatial disparity information and hence in the treatment of fine and coarse stereopsis (Bishop and Henry, 1971).

Anatomical considerations

Anatomical studies reveal that the border region of areas 17-18 receives most of its retinal afferents from X-type cells, which are involved in fine spatial analysis. The fine disparity selectivity of these cortical cells are thus in concordance with the nature of the input which they receive. They also agree with behavioral experiments of random-dot stereogram discrimination in cats (Lepore et al., 1986; Ptito et al., 1986; Ptito et al., 1992), where the disparities used were small, which showed that intact cats could extract the figure from the stimulus array whereas those with sub-total lesions of areas 17/18 could not.

Area 19 receives massive afferents from areas 17-18 and was expected that disparity sensitivity would be maintained along the functional stream (Van Essen, 1985). However, area 19 also receives important parallel Y and W afferents of sub-cortical

origin, especially from the C-laminae of the dorsal lateral geniculate nucleus and the lateral pulvinar complex as well as from the medial interlaminar nucleus and the geniculate wing. Whereas RFs properties of the cells in the latter two structures are poorly defined, it is known that cells of the C-laminae of the dorsal lateral geniculate nucleus and the lateral pulvinar complex have large receptive fields and coarse spatial properties (Rodieck and Brening, 1983; Stone, 1983; Rosenquist, 1985; Dreher, 1986; Casanova et al., 1989). These afferents might thus account for the rather coarse disparity selectivity of cells in area 19. It would also appear that area 19, despite the varied inputs from all these regions, including areas 17-19, is at best only marginally involved in the analysis of disparity information. This failure to maintain disparity sensitivity to the next level of the functional stream points to organizational differences between cat and monkey visual systems, since in the latter disparity sensitive units are not only found in higher order areas, but they are proportionately more abundant (Hubel et Wiesel, 1970; Poggio et al., 1988; Wang and Dreher, 1996).

The superior colliculus receives afferents directly from the retina, the primary visual cortex and most extrastriate areas, as well as from a large variety of sub-cortical structures (Stein and Meredith, 1993). However, it has been demonstrated that activation of collicular cells via X-type afferents is negligible (Stein and Berson, 1995). Indeed, most retinal ganglion projections to the superior colliculus are of the Y-type and W-type (Updyke, 1977), which could account for the coarse selectivity to spatial disparity of collicular cells.

The fine selectivity to spatial disparity of cells in the primary visual cortex and the fact that subtotal area 17/18 lesions abolish stereoscopic depth discriminations in cats (Ptito et al., 1992) point to these cells as underlying fine stereopsis (Bishop and Henry,

1971), as they also possess the highest spatial resolution. Indeed, both the high spatial acuity characterizing striate cortical cells and their fine tuning to disparity are probably mediated through the X system which massively project to this area.

The role of area 19 cells in stereoperception is more difficult to define. First, reports regarding the actual percentage of disparity sensitive cells differ greatly. Pettigrew and Dreher (1987) speculated that disparity sensitive cells might be present in greater number in area 19 than in areas 17-18 and suggested that they were particularly sensitive to uncrossed disparities. The latter proposition is not supported by the results obtained herein, which tend to indicate, if anything, a slight preference for crossed disparities. Moreover, the rather small percentage of disparity sensitive cells in area 19 and the large proportion of insensitive cells obtained in the present study appear, coupled with behavioral studies indicating that subtotal areas 17-18 lesions abolished depth discrimination using random-dots stereograms (Ptito et al., 1992), suggests that the role of area 19 in the analysis of fine spatial disparity is limited. Some disparity sensitive cells are nonetheless present in area 19 and their rather coarse selectivity might be taken as an indication of their involvement in other aspects of depth processing. The large number of binocular cells which were found to be insensitive to spatial disparity suggest that this area may be more involved in binocular fusion.

As for the cells sensitive to spatial disparity at the tectal level, their coarse selectivity might be used by organisms to encode the position of a stimulus with regard to the actual point of fixation and relay this information, via projections to deep collicular layers (Behan and Appell, 1992; Behan and Kime, 1996), to oculomotor structures which could then generate eye movements appropriate for the fixation of the stimulus and to maintain eye fixation upon this plane.

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Table 1

Number and proportion of disparity sensitive cells recorded at the 17-18 border, in area 19 and in the superior colliculus of cats.

	17-18 border		area 19		sup. colliculus	
	n	%	n	%	n	%
Tuned excitatory	15	19	5	8	66	38
Tuned inhibitory	9	12	2	3	15	9
Near cells	12	15	9	15	19	11
Far cells	19	24	3	5	12	7
Insensitive	10	13	28	45	35	20
Unclassifiable	13	17	15	24	27	15
Total	78		62		174	

Table 2

Bandwidths (in degrees) of the normalized sensitivity profiles of tuned excitatory and tuned inhibitory cells recorded at the 17-18 border, in area 19 and in the superior colliculus of cats.

	17-18 border	area 19	sup. colliculus
Tuned excitatory	0.41	1.71	2.97
Tuned inhibitory	0.57	0.75	1.53

Table 3

Slopes of the normalized disparity sensitivity profiles of near and far cells recorded at the 17-18 border, in area 19 and in the superior colliculus of cats.

	17-18 border	area 19	sup. colliculus
Near cells	-303.0	-282.8	-57.84
Far cells	254.7	120.0	48.73

FIGURE LEGENDS

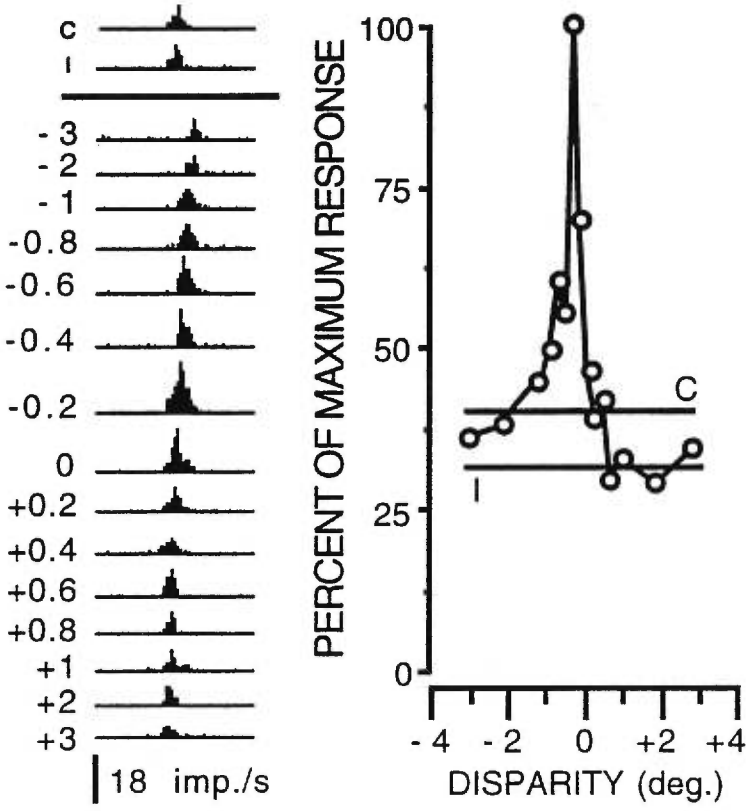
Figure 1. Example of peri-stimulus time histograms (PSTHs), indicating the response of a complex cell at each spatial disparity tested. The response to monocular contralateral (C) and ipsilateral (I) stimulation are shown at the top of the set of PSTHs and are considered baseline levels for the binocular responses. The normalized response profile of the cell, which was recorded in area 19, was derived from the PSTHs obtained under binocular stimulation at different spatial disparities.

Figure 2. Three tuned excitatory and three tuned inhibitory cells are shown on a normalized scale. The tuned excitatory cells are examples of the less finely tuned units in each region. Their respective bandwidths, from left to right, were 0.73°, 2.69° and 4.43°. The tuned inhibitory cells shown are representative of the selectivity of their respective regions. Their respective bandwidths were 0.57°, 0.96° and 1.72°. The cells recorded at the 17-18 border therefore have extremely narrow bandwidths. The cells recorded in area 19 have larger bandwidths, as their selectivity is not as fine. The collicular cells have the large bandwidths of cells exhibiting coarse disparity selectivity. The response to monocular stimulation through the contralateral and ipsilateral eye are indicated by (C) and (I) respectively.

Figure 3. Three near cells and three far cells are shown on the same scale. The slopes of the near cells presented were, from left to right, -335.0, -240.0 and -36.9. The slopes of the far cells shown, in the same order, were 255.0, 115.0 and 26.3. The cells recorded at the 17-18 border have extremely steep slopes. The cells recorded in extrastriate area 19 have less steep slopes, as their selectivity is not as fine. The collicular cells have the

attenuated slopes of cells exhibiting coarse disparity selectivity. The response to monocular stimulation through the contralateral and ipsilateral eye are indicated by (C) and (I) respectively.

FIGURE 1


c
i
- 3
- 2
- 1
-0.8
-0.6
-0.4
-0.2
0
+0.2
+0.4
+0.6
+0.8
+1
+2
+3
18 imp./s
PERCENT OF MAXIMUM RESPONSE
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75
50
25
0
C
I
- 4
- 2
0
+2
+4
DISPARITY (deg.)

FIGURE 2

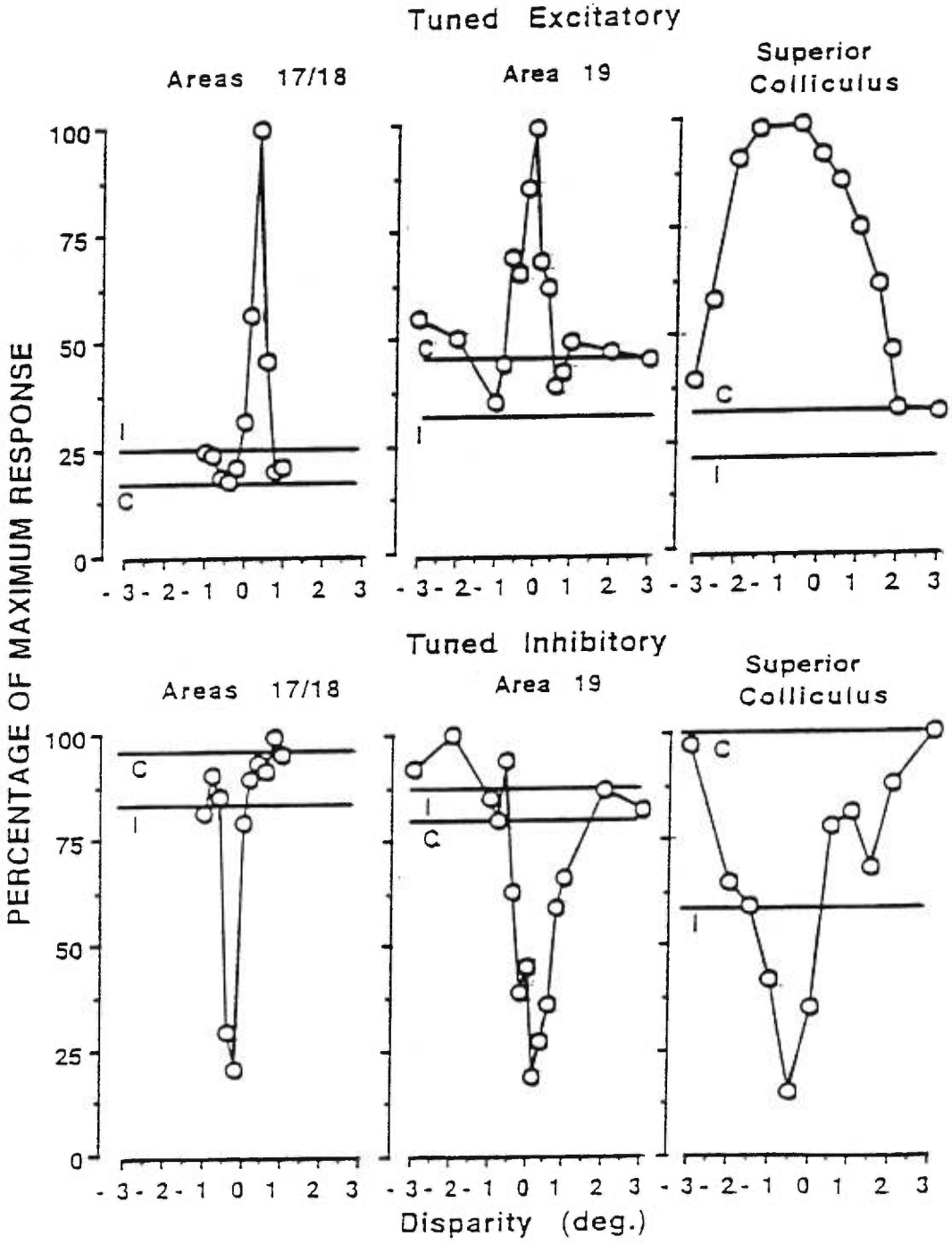
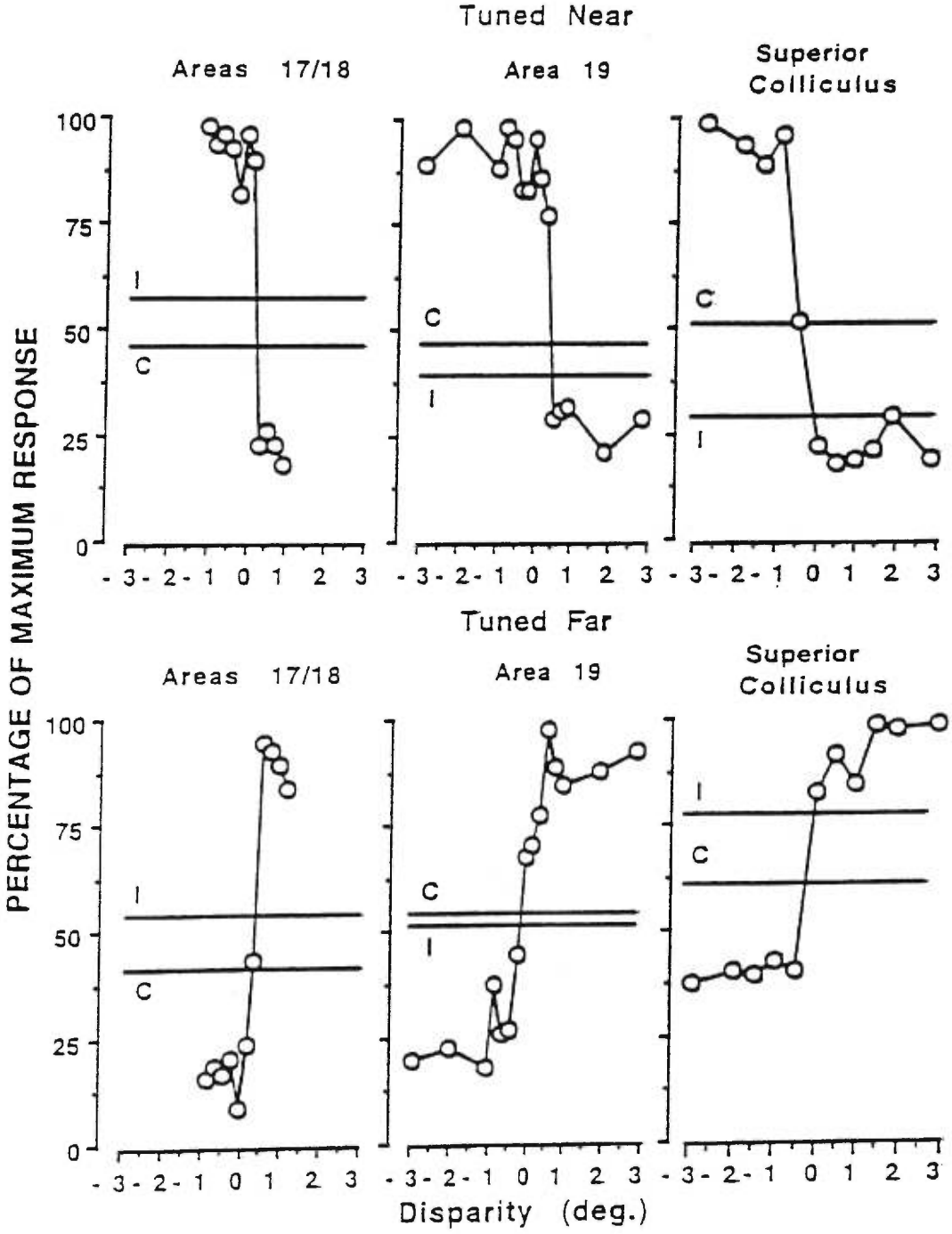

Tuned Excitatory
Areas 17/18
Area 19
Superior Colliculus
Tuned Inhibitory
Areas 17/18
Area 19
Superior Colliculus
PERCENTAGE OF MAXIMUM RESPONSE
100
75
50
25
0
C
I
- 3 - 2 - 1 0 1 2 3
Disparity (deg.)

FIGURE 3


Tuned Near
Areas 17/18
Area 19
Superior Colliculus
PERCENTAGE OF MAXIMUM RESPONSE
100
75
50
25
0
I
C
- 3 - 2 - 1 0 1 2 3
Tuned Far
Areas 17/18
Area 19
Superior Colliculus
Disparity (deg.)

CHAPITRE 3

Article 2:

Neurons in the posteromedial lateral suprasylvian (PMLS) area are sensitive to binocular positional depth cues

Soumis: **Experimental Brain Research**

NEURONS IN THE POSTEROMEDIAL LATERAL SUPRASYLVIAN (PMLS) AREA OF THE CAT ARE SENSITIVE TO BINOCULAR POSITIONAL DEPTH CUES

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Short title: Disparity sensitivity in area PMLS of the cat

38 pages, 1 table, 6 figures

ABSTRACT

Single units in the posteromedial lateral suprasylvian area of the cat are known to be very sensitive to movement. A proportion of these cells can encode movement in depth, but it is unclear whether posteromedial lateral suprasylvian cells only rely upon motion cues to evaluate stimulus depth or if they can also code for spatial cues. The present study aims at assessing the sensitivity to spatial disparity of binocular cells, in posteromedial lateral suprasylvian area, in order to determine whether these units are tuned to positional depth cues. A total of 126 single cells located in posteromedial lateral suprasylvian area of anesthetized paralyzed cats were examined. As recordings were performed in the central visual field representation, receptive fields were small. A third of the receptive fields were surrounded by an inhibitory region and almost three-quarters of the cells were direction-selective. Most cells (110/114) were binocular and a large proportion of single neurons responded to stimuli appearing on the fixation plane by increasing (tuned excitatory cells, 43%) or decreasing (tuned inhibitory cells, 14%) their response rate. A smaller proportion of cells increased their firing rate in response to crossed (near cells, 10%) or uncrossed (far cells, 6%) spatial disparities, hence demonstrating respective preference for stimuli presumably appearing in front of or behind the fixation plane. As compared to primary visual cortex, the proportion of disparity sensitive cells in posteromedial lateral suprasylvian area is similar, but selectivity is significantly coarser. As posteromedial lateral suprasylvian area can code for both spatial and temporal aspects of stimuli, this area might be involved in the spatio-temporal integration of depth cues, a process which may also participate in the control of accommodation and vergence.

Key words: Spatial disparity, binocular interactions, ocular dominance, extrastriate, vision

INTRODUCTION

Several monocularly perceived cues such as interposition, texture gradients and motion parallax can yield an appreciation of depth. However, a precise and vivid perception of tridimensional objects can only be achieved through binocular vision. Wheatstone (1838) indeed demonstrated that such stereoscopic depth perception hinged upon slight spatial disparities between the two retinal images and that these positional differences were engendered by the natural horizontal interstice separating frontally placed eyes. Behavioral experiments on animals with eyes having this disposition, such as the monkey (Bough, 1970; Cowey et al., 1975; Sarmiento, 1975; Harwerth and Boltz 1979a, 1979b) and cat (Fox, 1981; Lepore et al., 1986) have indeed confirmed that frontally placed eyes and stereoscopic depth perception were concomitant.

It was often proposed that the fusion of the bidimensional retinal images is achieved in the primary visual cortex, as inputs from the two eyes first coalesce in this area, thus forming binocular cells (Hubel and Wiesel, 1959, 1962). It was demonstrated repeatedly that the two receptive fields of such binocular cells are of similar shape and structure, yet that they are often located at slightly disparate spatial, and therefore retinal, locations (Hubel and Wiesel, 1962, 1968; Schiller et al., 1976a, 1976b; Movshon et al., 1978; Mullikin et al., 1984a, 1984b; Skottun and Freeman, 1984; Camarda et al., 1985; Maske et al., 1984, 1986; Emerson et al., 1987). These cells are thus presumed to code for binocular positional cues, or spatial disparities, and are therefore regarded as the neural substrate of stereoscopic vision. It should be noted that it has been recently proposed that retinal disparities could also be coded through differences in the internal organization (shape or phase) of the left and right receptive fields (Ohzawa and Freeman, 1986a, 1986b; Freeman and Ohzawa, 1990; Ohzawa et al., 1990; De Angelis et al., 1991; Ohzawa et al., 1997; Anzai et al., 1997).

Binocular cells responding differentially to spatial disparity cues were first found in areas 17-18 of cats (Barlow et al., 1967; Nikara et al., 1968; Pettigrew et al., 1968) but were also identified in the primary visual cortex of sheep (Clarke et al., 1976), owl (Pettigrew and Konishi, 1976; Pettigrew, 1979) and monkey (Hubel and Wiesel, 1970; Poggio and Fischer, 1977; Poggio and Poggio, 1984).

These cells sensitive to spatial disparity are usually divided into four categories, according to their response profile and, presumably, their function (Poggio and Fisher, 1977; Poggio and Poggio, 1984). Tuned excitatory cells increase their firing rate, whereas tuned inhibitory cells decrease theirs, in response to a small range of spatial disparities around zero. Other cells respond differentially to a large range of spatial disparities in the crossed (near cells) or uncrossed (far cells) range. Thus, near cells seem to prefer stimuli located in front of the fixation plane whereas far cells appear to prefer stimuli appearing behind the fixation point.

Across the visual cortex of the cat, the majority of single units in areas 17-18 are known to be very sensitive to spatial disparity, and many cells of each type could be found in this region (Ferster, 1981; LeVay and Voigt, 1988; Lepore et al., 1992). Disparity detectors of each types could also be found, albeit in lesser numbers, in areas 19 (Pettigrew and Dreher, 1987; Guillemot et al., 1993) and 21a (Wang and Dreher, 1996).

These areas receive input via the retino-geniculate pathway and are thought to be mostly involved in the perception of form. Single units which can precisely code for stimulus depth and thus provide volume, or solidity, to objects seem an invaluable asset to precise form perception. The other important subdivision of the visual system of the cat is the posteromedial lateral suprasylvian (PMLS) visual cortex. This area receives direct input from the geniculate wing, the medial intralaminar nucleus and the C layers of the dorsal lateral geniculate nucleus. It also entertains reciprocal connections with most other visual areas. More importantly, area PMLS receives an important input from the superficial layers of the superior colliculus, via the dorsal

lateral geniculate nucleus, the lateral posterior nucleus and the posterior nucleus of the thalamus (Rosenquist, 1985; Spear, 1985; Bullier 1986; Dreher, 1986). Most PMLS neurons respond to drifting sinusoidal gratings or light bars, are binocular and have well defined receptive fields (Hubel and Wiesel, 1969; Spear and Baumann, 1975; Camarda and Rizzolatti, 1976; Rauschecker et al., 1987; von Grunau et al., 1987). Receptive fields in this area tend to be larger than in areas 17-18, and can be as large as 45 degrees in periphery. However, centrally located receptive fields can be as small as 2 degrees (Hubel and Wiesel, 1969; Spear and Baumann, 1975; Zumbroich et al., 1986; Rauschecker et al., 1987; von Grunau et al., 1987). Most PMLS cells respond more vigorously to moving than to flashed stimuli and show direction selectivity (Blakemore and Zumbroich et al., 1986; Rauschecker et al., 1987; von Grunau et al., 1987). PMLS single units are therefore efficient detectors of movement.

It has been proposed that some PMLS cells are specialized in the coding of motion in three-dimensional space (Toyama and Kozaka, 1982; Toyama et al., 1985, 1986a, 1986b). Toyama and his collaborators tested PMLS neurons with actual objects moving toward or away from the animal or with two-dimensional stimuli that simulated cues of motion in depth. They demonstrated that although approximately half of the cells responded optimally to movement in the fronto-parallel plane, a non-negligible proportion of units responded best to stimuli moving in three-dimensional space. Approximately 20% of PMLS cells preferred stimuli approaching or seeming to approach (looming) toward the animal and 12% preferred stimuli receding or seeming to move away from the animal. It therefore appears that approximately one-third of single units in area PMLS can code for depth using cues such as motion and size. The question remains, however, as to whether area PMLS, which does appear to carry out precise spatial analyses at least in the central visual field representation, can also contribute to stereoscopic processing by coding binocular positional cues. The present study therefore aims at investigating the sensitivity to spatial disparity of single units with centrally located receptive fields in area PMLS of the cat.

MATERIALS AND METHODS

Animals

The experiment was carried out on 10 adult cats, each weighting between 2 to 4 kg who came from a Université de Montréal approved supplier. They were all in good health and had no obvious malformations or pathologies. All surgical interventions, manipulations and husbandry were carried out within the guidelines proposed by the Canadian Council on Animal Care. Moreover, the guidelines of the American Physiological Society and the Society for Neuroscience regarding the care and use of animals as well as the guidelines of the National Institute of Health (USA) concerning the preparation and maintenance of higher animals during visual neuroscience experiments were followed. All experimental protocols were approved by the University Animal Care Committee before the beginning of the experiment.

Surgery

On the day prior to the recording session, 2 ml/kg of dexamethasone sodium phosphate (5 mg/ml) was injected i.m. to limit inflammation during the surgical intervention. On the day of recording, the cat was injected with atropine (Atro-sol: 0.2 mg/kg; Ormond Veterinary Supply Ltd, Ancaster, Canada) to reduce bronchial secretions and induce mydriasis, after which anesthesia was induced using a face mask with a gaseous solution of nitrous oxide, oxygen (N_2O : O_2, 70 : 30) and fluothane (5% of total gaseous mixture). Once anesthetized, the cat was intubated and connected to a respiratory pump. Throughout the surgery, fluothane was kept between 1% and 2% of the total gaseous mixture so as to maintain surgical anesthesia level. The animal was then placed in the stereotaxic apparatus (Kopf Instruments, Tujunga, CA, USA). This apparatus was modified to insure that the eyes were not touched or pressed upon and to avoid obstruction of the visual field. The saphenous vein was cannulated and, throughout the surgery, the animal was administered 5% dextrose in lactated ringer at the rate of 5.6 ml/h to maintain blood pressure and hydration. The scalp was shaved and the cranial muscles and pressure points

were infiltrated with a local anesthetic (xylocaine 2%), a procedure routinely repeated throughout the recording session. A small trepanation was performed over the PMLS area (A-P: 0 - 8, L: 10 - 16) at the coordinates derived from the atlas of Reinoso-Suarez (1961). A small incision was made in the exposed dura mater to allow the penetration of the microelectrode. The latter was lowered perpendicularly to the cortex, pointed medially and deviated from the vertical by an angle of 30 degrees. The entire trepanned area was then covered and sealed with 4% agar in physiological saline to minimize pulsations and prevent dehydration.

At the end of the surgery, the fluothane level was progressively reduced (0.5% every 15 minutes), stabilized at 0.5% and kept at that level for the duration of the recording session (30 - 33 hours). Stable heart rate, constantly monitored by electrocardiogram, and the absence of reflexes insured that the anesthesia level was sufficient. From that point on, a solution of 15 ml of gallamine triethiodide (Flaxedil: 200 mg; Rhone-Poulenc, Montréal, Canada) and d-tubocurarine (Tubarine: 15 mg; Sigma Chemicals, St. Louis, MO, USA) dissolved in 30 ml lactated ringer solution with dextrose (5%) was continuously infused through the saphenous vein at the rate of 5.6 ml/h (average cat weight = 3.2 Kg) to induce and maintain paralysis of extra-ocular muscles. Respiratory rate and stroke volume were adjusted so as to maintain a constant level of expired CO_2 ($\approx$ 4%), which serves as an indirect indication of stable blood pressure. Body temperature was also kept constant (37.5° C) with the help of a heating water pad thermostatically controlled with a rectal thermoprobe. Electroencephalogram, monitored intermittently yet regularly, showed slow-wave activity throughout the recording session. Heart rate was constantly monitored throughout the recording session. These two measurements served not only to control for the general well-being of the animal but also to ensure that it felt no pain during electrode placement, as no changes in either electroencephalogram pattern or heart rate was observed when the manipulations were carried out.

Optical preparation

Mydriasis was induced by an initial i.m. injection of atropine sulfate 1% (Atro-Sol, 0.2 mg/kg) followed by topical applications, as needed, to the eyes. Nictitating membranes were retracted with topical applications of phenylephrine hydrochloride (Neo-synephrine: 0.1%; Winthrop Laboratories, Aurora, Canada). To prevent dehydration and to improve image resolution, a zero-power plastic contact lens with a 3 mm artificial pupil was placed on each eye. In order to determine the relative position of the areae centrales, retinal landmarks such as the optic disks and some major blood vessels were projected on a tangent screen situated 57 cm in front of the animal (Fernald and Chase 1971). The areae centrales were considered to be situated 16 degrees medially and 7.5 degrees below the iso-elevation line of the center of each optic disk (Bishop et al., 1962). This approximation is made necessary by the fact that it is quite impossible to precisely determine, in this preparation, the exact position of the area centralis. Retinoscopy was used to determine the appropriate value of dioptric lenses necessary to focus the eyes on the tangent screen located 57 cm in front of the eyes.

Recording and stimulation procedure

As was the case in a previous paper (Bacon et al., 1998), recording was carried out with glass microelectrodes filled with a 3M NaCl solution and having an impedance measured at 1000 Hz of 3 to 6 MΩ. The microelectrode was stereotaxically lowered into area PMLS (A-P: 2 - 7, L: 12 - 14) according to the stereotaxic coordinates of Reinoso-Suarez (1961) and Palmer et al. (1978). The target units were those having receptive fields in the center of the visual field. Cellular action potentials were conventionally amplified, displayed on an oscilloscope and transferred to an audio monitor. They were also filtered using time/amplitude criteria and transformed into square pulses and fed to a generic brand PC-486 computer for on line and *a posteriori* analysis.

Upon isolating a cell, the following protocol was followed. The receptive field (minimal response field, Barlow et al., 1967) of each eye was mapped on a fronto-parallel screen using the narrow slit of an ophtalmoscope as stimulus. The optic axis of one of the eyes was deviated using prisms so that the receptive fields of the two eyes would be located on widely separated coordinates on the tangent screen. The latter was placed at 57 cm from the animal, such that 1 cm of space corresponded to 1 degree of visual angle. The stimulation procedure was adapted from Henry et al. (1967). Two projectors, placed behind the back projection screen allowed the independent stimulation of each eye with two light bars equated for luminance and contrast. The luminance of the stimuli was maintained at 48 cd/m^2 while the luminance of the background was 0.6 cd/m^2. The contrast, kept constant throughout the experiment, was defined as $C = (L_s - L_b) / L_b$, where L_s was the luminance of the stimuli and L_b was the luminance of the background. Two optic benches, controlled independently through a computer, ensured the independent and precise definition of the other stimulus parameters: length and width, directionality, position in space, stimulus onset, velocity, as well as sweep duration and amplitude.

Upon isolating a binocular cell, the following initial protocol was followed. The receptive field of each eye was precisely mapped using the luminous slits of a manually controlled projector. During this phase, the best stimulus parameters (size, directionality and velocity) were determined for both eyes. The optimal parameters were defined as the stimulus configuration which produced the greatest number of spikes, as estimated by ear from the output of the audio monitor. The optimal width and length of the slits were closely related to receptive field size, whereas preferred velocity and direction of stimulation varied independently from other parameters. Each cell was classified according to receptive field type according to the criteria of Henry et al. (1967) and tested for direction selectivity and end-stopping. The principal inclusion criteria for the latter class was that the cell preferred a bar of optimal length, such that extending it beyond a determined limit caused a decrease in response.

This qualitative protocol was followed by a quantitative one. Stimulation was carried out using the dual optic bench system: two light bars having the best estimated dimensions were swept at optimal velocity and direction across each receptive field. Stimulus velocity varied between 1 degree/s and 20 degrees/s, each sweep covering 20 degrees. Each stimulus condition was presented 10 times and a peri-stimulus time histogram was derived from the responses to these stimulations. Each eye was stimulated separately to determine the monocular response and the binocular interactions were tested through simultaneous stimulation of both receptive fields at different spatial disparities. Since complex-like cells show little structural detail, determining absolute position disparity for these extrastriate cells is quite difficult. Thus, as was the case in previous, similar studies in our laboratory (Guillemot et al., 1993; Bacon et al., 1998) and those of others (Wang and Dreher, 1996; Vickery and Morley, 1998), relative disparities were used. These disparities were defined relative to the receptive fields which in turn were defined in terms of the coordinate reference points of the eyes. Thus, relative disparity is a precise estimation of absolute disparity, limited only by the accuracy of the definition of retinal landmarks.

The two light bars were precisely positioned so as to be equidistant from the center of each receptive field. When the two bars started moving at the same time, they crossed the centers of the receptive fields simultaneously, and relative disparity was null. However, if the initiation of the sweep of one bar was delayed with respect to the other, the two bars would at any particular time be situated at non corresponding points in each receptive field. The introduction of such a delay thus allowed the creation of crossed and uncrossed disparities. In addition to the null condition, several spatial disparity conditions were tested. These varied from 3 degrees crossed to 3 degrees uncrossed, in 0.5 degrees or 1 degree steps. If receptive fields were sufficiently large, disparities up to 4 degrees were tested to insure that cells (especially those of the near and far types) maintained their response rates to crossed and uncrossed disparities and hence insure that these were not simply cells tuned to a specific disparity in the crossed or uncrossed range.

Data processing

All conditions, each tested a total of 10 times, were interleaved with each other in a pseudo-random fashion. The time interval between each sweep was 10 - 20 s to avoid habituation. For each condition, a peri-stimulus time histogram was derived from the cellular responses. These peri-stimulus time histograms were divided into 500 bins, each having a binwidth of 2 - 40 ms, depending upon the duration of the sweep. For each condition, a second PSTH, of equal duration, was computed prior to each sweep when no stimulation was present to establish a baseline level.

Each point on the disparity sensitivity profile of a cell was obtained in the following manner. The average number of spikes elicited without stimulation was derived from the baseline peri-stimulus time histogram taken just prior to stimulation and of equal duration as the latter. The average number of spikes elicited at each spatial disparity during the entire period of stimulation was derived from the PSTH. The former average number of spikes was then subtracted from the latter.

In disparity experiments, the two bars moving in the two receptive fields mimic simulations by a single object moving in superimposed receptive fields of the awake fixating animal. When testing for large disparities, longer temporal delays must be used. In the case of cells with small receptive fields, the two bars may no longer simulate the simultaneous passage of the stimuli into the (superimposed) receptive fields but rather the successive stimulation of the two fields. This would result in the testing of binocular summation rather than binocular interaction. As only the latter is relevant as a stereoscopic cue, only disparities smaller than the width of the receptive fields were tested.

Eye stability control

It is important in this type of study to precisely control for eye position to make certain that they do not move during the recording period. This was controlled in three ways. First, recording was cautiously delayed for at least four hours after the induction of paralysis since residual eye-

drifts continue to be present for approximately one hour after the induction of paralysis, after which the eyes stabilize (Nikara et al., 1968; Wang and Dreher, 1996). Second, before undertaking each quantitative evaluation, the precise positions of both receptive fields were determined. These positions were again checked after having terminated the quantitative protocol. These positions remained remarkably stable throughout the protocol and a noticeable displacement (+/- 0.3 degrees) was found in only a few trials, which were discarded. If the response of the cell was still robust, a new quantitative assessment and consequent control were then carried out. Third, the possible drift of the eyes was estimated from the positions of the optic disks (Fernald and Chase, 1971). Since the diameter of the optic disk at this screen distance was fairly large, the major blood vessels radiating from the optic disk were also taken as reference points (Pettigrew et al. 1979). This procedure, therefore, furnished a useful index of both short and long term stability of eye position. This evaluation was carried out just before and immediately after the quantitative protocol for a particular cell and the results obtained indicated that fairly stable eye positions were maintained throughout each recording session.

Histology

At the end of the each penetration, a small electrolytic lesion (4mA, 5s, tip negative) was performed so as to allow identification of the recording sites. At the end of the recording session, the cat was deeply anesthetized with 5 % Fluothane, after which it was perfused through the heart with isotonic saline followed by formalin (4%). The brain was removed, placed in formalin (4%), soaked in sucrose and then frozen. The section containing the recording sites was sliced (40 μm) along the coronal plane. Every second slice was kept and stained using the cresyl-violet method. All the cells included in the present report were clearly located within the boundaries of the PMLS area, as defined in the maps of Palmer et al. (1978).

RESULTS

A total of 126 PMLS single units were successfully isolated from background activity. For each of these units, binocularity was assessed by the individual stimulation of each eye. Four cells appeared to be monocular and these were not submitted to the qualitative and quantitative protocols described above. There is a possibility that these cells would have shown some degree of binocular interaction (Maske et al., 1986a, 1986b), yet the nature of the present investigation demanded a precise mapping of both receptive fields which was difficult to obtain for the unresponding eye of these seemingly monocular cells. All binocular units were submitted to the spatial disparity protocol, but only those for which a complete response profile was obtained (n = 110) were included in the final data analysis.

Basic receptive field properties

The following receptive field characteristics of PMLS neurons have been extensively studied and reported (Hubel and Wiesel, 1969; Spear and Baumann, 1975; Zumbroich et al., 1986; Rauschecker et al., 1987; von Grunau et al., 1987). They were therefore mainly collected for normative purposes and will only be briefly summarized herein.

As stereoscopic depth is believed to be most precisely perceived in the central visual field, electrode penetrations were performed so as to record cells whose receptive field center of the dominant eye was located in the contralateral hemifield, extending up to a maximum of 10 degrees of eccentricity, and located between +5 degrees and -10 degrees of elevation. As a result of this intentional selection bias, the receptive fields mapped in the present study were relatively small for area PMLS, although they were still considerably larger than their counterparts in areas 17/18. The receptive fields indeed ranged from 1.5 to 8.4 degrees in width (mean = 3.9 degrees, σ = 1.45 degrees), on the axis parallel to the preferred direction of stimulation. It should be noted that whereas stimulus width and length were adjusted to the size of the receptive fields, sweep amplitude remained constant (20 degrees). As it was expected, flashed stimuli were inefficient

and drifting stimuli elicited the best response rates. Receptive fields were of the complex type (65/110), and for almost one third of the cells (35/110), elongating the stimuli beyond the boundaries of the receptive field caused a clear decrease in the firing rate of the cells. Previous investigations also reported such inhibitory surround regions in 30 - 40% of PMLS cells (Spear and Baumann, 1975; Camarda and Rizzolatti, 1976).

The selectivity to stimulus direction was tested for each binocular cell by sweeping an oriented light bar, from all directions in 15 degrees steps, across the receptive field. Almost 60% of the cells (64/110) clearly preferred stimulation from a particular direction. An additional 10 - 15% were equally responsive to two opposite directions, and thus responded to stimuli moving along a particular axis. No unit could be found with two preferred directions which were 90 degrees apart, as found by Blakemore and Zumbroich (1987). This is probably due, as proposed by Spear (1991), to differences in stimulations as Blakemore and Zumbroich (1987) presented gratings instead of bars. Due to variations in the stringency of the criteria for direction selectivity, it is difficult to precisely compare the present results with those in the literature. All studies nonetheless agree that the majority of PMLS neurons are direction-selective (Hubel and Wiesel, 1969; Spear and Baumann, 1975; Turlejski, 1975; Camarda and Rizzolatti, 1976; Blakemore and Zumbroich, 1987; Rauschecker et al., 1987; von Grunau et al., 1987).

The preferred directions of stimulations tended to be along the horizontal axis and away from the area centralis, as it was also demonstrated in previous reports (Hubel and Wiesel, 1969; Spear and Baumann, 1975; Camarda and Rizzolatti, 1976; Hamada, 1987; Rauschecker et al., 1987; von Grunau et al., 1987). Only two cells preferred stimuli moving along the vertical axis. Thus, although PMLS seem to include cells coding for all directions, a disproportionate number of units seem to code edges moving away from the center of gaze, as would be produced by objects looming toward the organism or as the animal moves through the visual scene.

The ocular dominance of each unit was also established, by quantitatively comparing the responses obtained from the independent stimulation of each receptive field. The classification of Hubel and Wiesel (1959, 1962) was used to create the ocular dominance histogram that can be seen in Figure 1. Classes 1 and 7 represent monocular cells that could respectively be driven only through stimulation of the contralateral or ipsilateral eye. In order to quantitatively assign cells to the intermediate categories 2 - 6, an ocular dominance index for each binocular cell was determined using the formula: (I / (I + C)) * 100 where I represents the response to stimulation of the ipsilateral eye and C that in response to stimulation of the contralateral eye. The ocular dominance index thus obtained allowed for classification on the following scale: 2, (1 - 20%); 3, (21 - 40%); 4, (41 - 60%); 5, (61 - 80%); 6, (81 - 99%).

Insert Figure 1 approx. here

As can be seen in Figure 1, three cells responded only to contralateral eye stimulation and a single unit could only be driven through the ipsilateral eye. The vast majority of the PMLS units recorded in this study were thus binocular (110/114). A large proportion of cells were equally well driven by stimulation of both eyes and were thus included in category 4 (45/110). As for the remaining binocular cells, almost twice as many were driven more strongly through the contralateral (41/110) than through the ipsilateral (24/110) eye. Both the proportion of binocular cell and the general shape of the histogram are very similar to what was obtained in studies investigating the central visual field representation of area PMLS (Rauschecker et al., 1987; von Grunau et al., 1987). Not surprisingly, studies investigating the entire binocular-overlap visual field, and therefore including more peripherally located receptive fields, reported a larger number of monocular cells (Spear and Baumann, 1975; Smith and Spear, 1979; Spear et al., 1985; McCall et al., 1988).

Sensitivity to spatial disparity cues

Previous studies have shown the presence of binocular interactions in area PMLS of the cat (Spear and Baumann, 1975; Rauschecker et al., 1987; von Grunau et al., 1987). However, no study systematically varied the relative retinal locations of binocular stimuli, and it is therefore still unknown whether PMLS single units are sensitive to spatial disparity. In the present study, both receptive fields were therefore stimulated independently yet simultaneously, using a wide array of stimulus disparities.

Thus, for each unit, a spatial disparity profile was obtained. A typical example of such a profile can be seen in Figure 2. The peri-stimulus time histograms at the top of the set labeled **c** and **i** were derived from the cellular response to monocular stimulation through the contralateral and ipsilateral eye respectively. These responses are regarded as baseline levels for the binocular responses. A peri-stimulus time histogram was also derived from the response of the cell to each spatial disparity tested, and these responses were plotted against spatial disparity to generate the normalized response profiles of the cells.

Insert Figure 2 approx. here

At null (zero) disparity, the cell in Figure 2 exhibited binocular facilitation, a type of interaction that both Rauschecker et al. (1987) and von Grunau et al. (1987) found to be present in over half of PMLS units. The cellular response of this unit decreased from this optimum as spatial disparity was increased, and resumed baseline level in the crossed and in the uncrossed range. This type of response profile is typical of the tuned excitatory cells first described by Poggio and Fisher (1977), whose terminology will be used throughout this report. Single units exhibiting this response profile can also be seen in Figure 3. Overall, 47/110 (42.7%) of the cells recorded in the present study showed such a tuned excitatory response profile, meaning that the

binocular response at a given disparity around null exceeded the sum of its monocular responses. The peak response of those tuned excitatory units was less than 0.5 degrees from null disparity in 25 cells out of 47. Moreover, only 6 cells had their peak response for a stimulus disparity more than one degree from null.

Insert Figure 3 approx. here

Binocular inhibitory interaction was reported to be very rare in area PMLS, as it was observed in only 3% of the cells by Rauschecker et al. (1987) and in a single cell by von Grunau et al. (1987). It was thus surprising to find 15 units (13.6%) which showed a tuned inhibitory response profile, meaning that its binocular response at a given disparity around null was clearly inferior to its monocular responses. Three of these units can be seen in Figure 4. The responses of the tuned inhibitory cells to crossed and uncrossed disparities were strong, in some case even stronger than the best monocular response (see Figure 4A). However, these cells became almost silent when a specific disparity in the middle range was presented. As was the case for tuned excitatory cells, the tuned inhibitory units appeared to be coding for the fixation plane. Indeed, the greatest binocular inhibition of the 15 tuned inhibitory cells was obtained at a spatial disparity one degree or less from null.

Insert Figure 4 approx. here

As no previous study has systematically varied spatial disparity of single units in area PMLS of the cat, no predictions could be made regarding the presence of near and far cells (Poggio and Fischer, 1977) in this cortical region. Near cells are presumed to code for a stimulus appearing in front of the fixation plane, whereas far cells prefer a stimulus located behind the fixation plane.

An example of the normalized response profiles of a far cell can be seen in Figure 5. From the peri-stimulus time histograms, it can clearly be seen that this unit responds strongly to uncrossed disparities while being inhibited by crossed disparities.

Insert Figure 5 approx. here

Cells responding to a broad range of disparities in the crossed or uncrossed range are therefore present in area PMLS of the cat. Neurons were classified as near cells if crossed disparities elicited a greater response than the best monocular response and uncrossed disparities elicited a smaller response than the lesser monocular response. On the other hand, neurons were classified as far cells if their response profiles were the converse of this. Of the 110 binocular units submitted to the disparity protocol, 11 cells (10%) were classified as near cells. Typical near cells recorded in area PMLS of the cat can be seen in Figure 6A and 6B. Seven cells (6.4%), including the units seen in Figure 6C and 6D, were classified as far cells as they seemed to prefer stimuli in the uncrossed range.

Insert Figure 6 approx. here

As for the remaining 30 cells, 11 were categorized as insensitive as they failed to significantly vary their discharge rate across spatial disparities. In two cells, their rate of response was higher than the strongest monocular response while in two other units, it was notably lower than the highest monocular response. The other seven cells could be considered to be truly insensitive, in the sense that they did not show any significant binocular interactions. The remaining 19 cells showed complex binocular interactions which precluded their inclusion into a specific category of response profile. Most responded strongly to binocular stimulation, but their unpatterned response

profiles makes it unlikely that the coding they perform can be of use in the treatment of spatial disparity information. Thus, the results indicate that 80/110 (72,7%) of binocular cells in area PMLS of the cat are sensitive to spatial disparity.

Attempts were made to link disparity sensitivity with ocular dominance. Such a relationship has previously been demonstrated to exist in the primary visual cortex (Ferster, 1981; Gardner and Raiten, 1986; LeVay and Voigt, 1988; Lepore et al., 1992) and in area 19 (Pettigrew and Dreher, 1987). Other studies failed to note such a relationship in areas 17 (Ohzawa and Freeman, 1986a), 19 (Guillemot et al., 1993), 21a (Wang and Dreher, 1996) or in the superior colliculus (Bacon et al., 1998) of the cat. The distribution of ocular dominance across the disparity sensitivity categories can be seen in Table 1. Most disparity sensitive cells (60/80) fell within categories 3 or 4 and very few fell into categories 2 or 6. There was also a tendency for insensitive and unclassifiable cells to be more evenly spread along the ocular dominance categories. However, statistical analysis failed to reveal a significant interaction, and ocular dominance therefore does not seem to influence spatial disparity sensitivity in area PMLS of the cat.

Insert Table 1 approx. here

Selectivity to spatial disparity

The tuning-curve width at half-height of the normalized response profile of cells showing an excitatory or inhibitory response peak was evaluated as an indication of their selectivity. The mean tuning-curve width of the 47 cells showing an excitatory peak was 2.53 degrees (σ = 1.17 degrees). The unit shown in Figure 2 is representative of the sample, as its tuning-curve width is 2.49 degrees. More finely tuned cells are shown in Figure 3; these cells, from A to C, have tuning-curve widths of 0.72, 1.52 and 1.61 degrees respectively. Only a few tuned excitatory cells

had a tuning-curve width smaller than 1 degree (4/47), and in some cells (7/47) it was larger than 4 degrees.

The mean tuning-curve width of the 15 units classified as tuned inhibitory was 1.73 degrees (σ = 0.69 degrees). Figure 4A and 4C show typical tuned inhibitory selectivity for area PMLS, as their tuning-curve widths were 1.64 degrees and 1.81 degrees respectively. The unit in Figure 4B, however, was the most finely tuned cell recorded, its tuning-curve width being 0.68 degrees.

The slopes of the normalized response profiles, measured at 50% of the maximum response, of the near and far cells are also indications of selectivity to spatial disparity. The mean slope of the 11 near cells was - 68.2 %/deg (σ = 30.3 %/deg). The near cells shown in Figure 6A and 6B had slopes of - 93.0 %/deg and - 51.3 %/deg respectively. The slopes of most near cells recorded in area PMLS fell into this range. As for far cells, their mean slope was 65.5 %/deg (σ = 35.3 %/deg), and the slopes of the cells in Figure 6C and 6D were 27.0 %/deg and 85.4 %/deg respectively.

For all categories of response profile, selectivity to spatial disparity as defined by the tuning-curve width or slope was compared with receptive field width. It can be seen in Figures 3, 4 and 6 that selectivity appears to be independent of receptive field size, as more selective cells often have a larger receptive field than their less selective counterparts. There nonetheless appeared to be a general tendency for cells with smaller receptive fields to be more selective, although no significant statistical correlation emerged.

DISCUSSION

The main objective of the present study was to determine if single neurons in area PMLS of the cat could code for specific positional depth cues and thus play a role in stereoscopic vision. The results indicate that approximately three-quarters of the cells in area PMLS are sensitive to spatial disparity, which seems to indicate that PMLS can code for stimuli in depth not only through motion cues, including changes in size for looming stimuli, but through positional cues as well.

The single units investigated herein all had receptive fields in the central portion of the binocular-overlap region of the visual field. This translated into relatively small receptive fields, as these tend to considerably increase in size with eccentricity (Spear and Baumann, 1975; Rauschecker et al., 1987; von Grunau et al., 1987). The cells showed a complex receptive field organization and approximately one-third of the receptive fields were surrounded by an inhibitory region, which confirms previous findings (Spear and Baumann, 1975; Camarda and Rizzolatti, 1976). The majority of cells were direction selective, preferring stimuli moving along the horizontal axis and away from the area centralis. These properties are similar to those described in previous reports (Hubel and Wiesel, 1969; Spear and Baumann, 1975; Turlejski, 1975; Camarda and Rizzolatti, 1976; Hamada, 1987; Blakemore and Zumbroich, 1987; Rauschecker et al., 1987; von Grunau et al., 1987).

More than 95% of the cells tested were binocularly driven. As stated earlier, this proportion is higher than what was observed in studies which included cells with more peripheral receptive fields (Spear and Baumann, 1975; Smith and Spear, 1979; Spear et al., 1985; McCall et al., 1988), but similar to that obtained in studies focusing upon central visual field representation (Rauschecker et al., 1987; von Grunau et al., 1987). Such a high level of binocularity in cells subserving the central visual field is to be expected in an area like PMLS, which receives multiple inputs from the two eyes and from cortical areas themselves highly binocular in nature. Moreover,

it has very dense callosal connections, thereby contributing to midline fusion (Berlucchi, 1990) and interocular transfer (Berlucchi and Marzi, 1981), functions which also require binocular convergence.

Disparity coding: comparison with other areas

Of the 110 binocular cells tested in area PMLS, 43% showed a tuned excitatory profile and 14% were of the tuned inhibitory type. Hence, 57% of the disparity sensitive units seemed to be coding for stimuli on the fixation plane. Moreover, a non-negligeable proportion of PMLS single units appeared to be coding for stimuli in front or behind the fixation plane, as 10% of the cells were of the near type and 6% were far cells.

Thus, 73% of PMLS neurons are sensitive to spatial disparity. Such a high proportion of sensitive cells was previously only observed in the primary visual cortex. Indeed, although Ferster (1981) reported that only 37% of cells in area 17/18 were sensitive to spatial disparity, more recent reports agree that the proportion is more in the range of 70-80%. LeVay and Voigt (1987) reported that 74% of the cells appeared sensitive to spatial disparity, but it should be noted that their criterion was not based upon class inclusion, but upon a statistically significant difference between the highest and the least response in the profile. Lepore et al. (1992), using experimental procedures similar to those used in the present study, reported that 71% of cells at the 17/18 border could be included in one of the four disparity classes. However, the 17/18 border units recorded by Lepore et al (1992) were more evenly divided between the four categories, as 13% were tuned inhibitory, 17% were near, 22% were far and only 19% were tuned excitatory cells. Thus, although the proportion of disparity sensitive cells is similar, area PMLS seems more concerned with the fixation plane. This is substantiated by the fact that the excitatory or inhibitory peaks of tuned cells in area PMLS are clustered around null disparity. The functional implications of this will be discussed later.

Disparity sensitivity in other extrastriate areas has not been as thoroughly investigated as it was in area 17/18. Nonetheless, reports of disparity sensitivity in areas 19 (Pettigrew and Dreher, 1987; Guillemot et al., 1993) and 21a (Wang and Dreher, 1996) seem to indicate that disparity sensitivity in these regions is inferior to what was observed herein for area PMLS. Guillemot et al. (1993), using experimental procedures similar to those used in the present study, demonstrated that 34% of the cells in area 19 could be included in one of the four disparity categories. Almost two-thirds of the disparity sensitive cells (14/22) were of the near or far type. Thus, as opposed to PMLS, this area seemed to be more preoccupied with stimuli lying in front or behind the fixation plane. As for disparity sensitivity in area 21a, Wang and Dreher (1996) demonstrated that almost 70% of cells in this area showed significant modulation of their peak response (more than 50%) in response to variations in spatial disparity. Of the 37 cells tested by these investigators, 22 were of the tuned excitatory type and 2 were of the tuned inhibitory type. Only three cells appeared to prefer a broad range of disparities of the crossed or uncrossed type and were classified as near-like (one cell) and far-like (two cells).

The visual region whose disparity coding parameters are closest to those found in area PMLS seems to be the superior colliculus. Indeed, Bacon et al. (1998), investigating collicular cells using procedures similar to those used herein, demonstrated that 65% of cells in the superficial layers of this structure were sensitive to spatial disparity. Moreover, Bacon et al. (1998) demonstrated that although the three other classes of disparity sensitive cells were well represented, tuned excitatory cells were by a wide margin the most abundant. As the superior colliculus and area PMLS are extensively anatomically interlinked, the similarity in disparity sensitivity between the two areas is presumably not a chance occurrence and its implications will be discussed later.

As for the tuning, or selectivity of PMLS single units to spatial disparity, it appears to be considerably coarser than that of cells in areas 17/18 (Ferster, 1981; LeVay and Voigt; 1987;

Lepore et al., 1992) and it also appears somewhat coarser than what was observed in area 19 (Guillemot et al., 1993). However, selectivity appears to be very similar to what can be observed at the collicular level (Bacon et al., 1998). This is consistent with the receptive field sizes and the spatial properties of cells that were observed in areas 17/18 (Maffei and Fiorentini, 1973; Movshon et al., 1978a, 1978b, 1978c) and 19 (Tanaka et al., 1987; Tardif et al., 1997) and those of PMLS (Blakemore and Zumbroich, 1987; Gizzi et al., 1990) and the superior colliculus (Bisti and Sireteanu, 1976; Bacon et al., 1996).

Functional implications

It can be assumed that the precise and vivid perception of three-dimensional objects that stereoscopic vision provides is dependent upon cells with very fine tuning to spatial disparity, such as those found at the level of the primary visual cortex. Thus, the coarser selectivity of PMLS cells precludes against such a role.

The relatively large receptive fields, the strong directional selectivity and their sensitivity for motion along the Z-axis, whether the displacement of the stimuli is real or simulated with size or motion cues (Toyama and Kozaka, 1982; Toyama et al., 1985, 1986a, 1986b) suggest that cells in area PMLS could be involved in the analysis of objects moving away or toward the organism. Moreover, the high number of cells responding to stimuli on the fixation point found in PMLS could be taken as an indication that this area is especially useful in the focusing of the eyes upon an object moving in the third dimension. Such focusing is performed through the mechanisms of vergence and accommodation, which have at times been linked with area PMLS.

It is known since Jampel (1960) that electrical stimulation of extrastriate cortices can affect vergence eye movements and lens accommodation. More recently, area PMLS has been shown to be an important region for these ocular functions. Indeed, lens accommodation has been evoked by microstimulation of area PMLS (Bando et al., 1984, 1989, 1996; Bando, 1985, 1987; Yoshizawa et al., 1991; Sawa et al., 1992) and single neurons discharging prior to lens

accommodation were also found in this area (Bando et al., 1984; Bando et al., 1988). Moreover, it has been shown that microstimulation of PMLS could result in ocular convergence (Toda et al., 1991), that neurons in this region also discharged in relation to ocular convergence (Takagi et al., 1992, 1993) and that the amplitude and peak velocities of convergent eye movements were reduced by a lesion of area PMLS (Hara et al., 1992). Lens accommodation and convergent eye movements are triggered by variations in visual cues generated by stimulus movement in three-dimensional space, such as target size changes and binocular disparity (Westheimer and Mitchell, 1969; Erkelens and Regan, 1986). Thus, neurons selective to spatial disparity in area PMLS could provide the necessary signals to neurons responsible for lens accommodation and convergent eye movements to fixate an object on the appropriate plane.

The pathway through which accommodation and vergence are carried out probably involves not only area PMLS but also the superior colliculus and the pretectum. It is indeed known that area PMLS project directly to these regions (Spear, 1991). Moreover, it was demonstrated that antidromic activation of lens accommodation related PMLS neurons could be evoked by stimulation of the rostral superior colliculus or pretectum (Bando et al., 1984). Moreover, microstimulation of the rostral part of the superior colliculus can also evoke lens accommodation (Sawa and Ohtsuka, 1994). It can thus be proposed that PMLS neurons sensitive to binocular disparity are those that have been shown to be involved in vergence or accommodation, and that these project toward brainstem mechanisms which control these functions via the superior colliculus and the pretectum.

ABBREVIATIONS

PMLS: Postero-medial lateral suprasylvian

%/deg: Percent per degree

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TABLE 1

Ocular dominance and number of disparity sensitive cells in the posteromedial lateral suprasylvian area of the cat

Type of cell	2	3	4	5	6	Total
Tuned excitatory	3	17	19	6	2	47
Tuned inhibitory	1	5	6	3		15
Near			8	3		11
Far		2	3	2		7
Insensitive	3	3	4	1		11
Unclassifiable	1	6	5	4	3	19

FIGURE LEGENDS

Fig. 1: The ocular dominance distribution of single cells recorded in posteromedial lateral suprasylvian area of the cat. *Dark bars*, binocular cells; *light bars*, monocular cells. Categories 1 and 7 include cells driven exclusively through the contralateral or the ipsilateral eye respectively. The intermediate categories include binocular cells with varying ocular dominance.

Fig. 2: Examples of post-stimulus time histograms (PSTH duration: 5s; binwidth: 10 ms), indicating the response at each spatial disparity from which were derived the normalized sensitivity profiles of a disparity sensitive cell of the tuned excitatory type. The response to monocular contralateral (c) and ipsilateral (i) stimulation are shown at the top of the disparity related histograms and are considered as the baseline levels for the binocular responses. This unit showed direction selectivity, preferring stimuli moving along the horizontal axis, and had a receptive field of the complex type. Although its receptive field as mapped with light and dark bars was small (2.4 degrees in width on the axis parallel to the direction of stimulation), stimulation produced a response on a wider positional range, as can be seen in the peri-stimulus time histograms. (receptive field width: 2.9 degrees; receptive field length: 3.5 degrees; sweep amplitude: 20 degrees; velocity: 4 degrees/s; maximum average firing rate: 29.4 spike/s).

Fig. 3: Three normalized response profiles of tuned excitatory cells recorded in posteromedial lateral suprasylvian area of the cat. Almost half of the binocular cells (47/110) were of the tuned excitatory type. **A** This unit was exactly tuned to null disparity and was one of the most finely selective tuned excitatory cell recorded (bandwidth = 0.72 degrees). Its receptive field was not smaller than the mean receptive field width of the sample (4.1 degrees on the axis parallel to the direction of stimulation. This unit had a complex receptive field and did not show direction

selectivity. The peaks of the cells in **B** and **C** are at 0.5 degrees disparity. Their receptive field were similar to that of the cell in **A** (4.9 and 4.0 degrees), although their selectivity was notably coarser. Both these units showed direction selectivity and had receptive field with end-stopping (**B**) and complex (**C**) characteristics. (**A**: receptive field width: 4.1 degrees; receptive field length: 6.2 degrees; sweep amplitude: 20 degrees; velocity: 20 degrees/s; maximum average firing rate: 47.8 spike/s. **B**: receptive field width: 4.9 degrees; receptive field length: 5.4 degrees; sweep amplitude: 20 degrees; velocity: 10 degrees/s; maximum average firing rate: 34.2 spike/s. **C**: receptive field width: 4.0 degrees; receptive field length: 7.3 degrees; sweep amplitude: 20 degrees; velocity: 10 degrees/s; maximum average firing rate: 25.8 spike/s).

Fig. 4: Three normalized response profiles of tuned inhibitory cells recorded in posteromedial lateral suprasylvian area of the cat. These units responded with a substantial decrease in response rate to a small range of spatial disparities around null. **A** The inhibition was maximal at one degree. The receptive field (complex type) width was average (3.6 degrees on the axis parallel to the direction of stimulation) and direction-selectivity was exhibited. **B** This cell's very fine tuning could not be predicted from its receptive field (complex type) width (4.1 degrees). This unit did not show direction selectivity. **C** The inhibition was maximal at 0.5 degrees. Receptive field width was average (4.0 degrees) and its receptive field was end-stopped. This cell preferred stimuli moving along the horizontal axis in either direction (probably an orientation specific cell). (**A**: receptive field width: 3.6 degrees; receptive field length: 4.4 degrees; sweep amplitude: 20 degrees; velocity: 10 degrees/s; maximum average firing rate: 19.3 spike/s. **B**: receptive field width: 4.1 degrees; receptive field length: 4.0 degrees; sweep amplitude: 20 degrees; velocity: 6.67 degrees/s; maximum average firing rate: 11.4 spike/s. **C**: receptive field width: 4.0 degrees; receptive field length: 5.3 degrees; sweep amplitude: 20 degrees; velocity: 6.67 degrees/s; maximum average firing rate: 17.9 spike/s).

Fig. 5: Examples of post-stimulus time histograms (PSTH duration: 5s; binwidth 10 ms), indicating the response at each spatial disparity, for a disparity sensitive cell of the far type. The response to monocular contralateral (c) and ipsilateral (i) stimulation are shown at the top of the disparity related histograms and are considered as the baseline levels for the binocular responses. The rather large receptive field (5.4 degrees on the axis parallel to the direction of stimulation) allowed for the testing of large disparities (up to 4 degrees), which ensured that this cell was not a tuned excitatory cell with its peak in the extreme uncrossed range. This unit did not show direction-selectivity but had a complex receptive field. (receptive field width: 5.4 degrees; receptive field length: 5.1 degrees; sweep amplitude: 20 degrees; velocity: 4 degrees/s; maximum average firing rate: 32.2 spike/s).

Fig. 6: Examples of units which preferred stimuli not appearing directly upon the fixation point. **A, B** Normalized response profiles of two near cells which responded only to crossed disparities. Both cells were direction-selective. The cell in **A** had a large complex receptive field (5.7 degrees in width on the axis parallel to the direction of stimulation) yet was finely tuned to spatial disparity (slope = 93.0%/deg). The cell in **B** had the smallest complex receptive field of the sample (1.5 degrees), yet its selectivity was below average (slope = 51.3%/deg). **C, D** Normalized response profiles of two far cells which responded only to uncrossed. Both cell were direction-selective and had complex receptive field. Note the attenuated slope of the cell in **C** (27.0%/deg) and the sharp slope of the cell in **D** (84.5%/deg) which are representative of the selectivity range of the far cells recorded in area PMLS. (**A**: receptive field width: 5.7 degrees; receptive field length: 4.1 degrees; sweep amplitude: 20 degrees; velocity: 4 degrees/s; maximum average firing rate: 26.0 spike/s. **B**: receptive field width: 1.5 degrees; receptive field length: 3.1 degrees; sweep amplitude: 20 degrees; velocity: 4 degrees/s; maximum average firing rate: 7.8 spike/s. **C**: receptive field width: 6.8 degrees; receptive field length: 6.3 degrees; sweep amplitude: 20

degrees; velocity: 4 degrees/s; maximum average firing rate: 25.2 spike/s. **D**: receptive field width: 3.6 degrees; receptive field length: 4.0 degrees; sweep amplitude: 20 degrees; velocity: 6.67 degrees/s; maximum average firing rate: 13.7 spike/s).

FIGURE 1

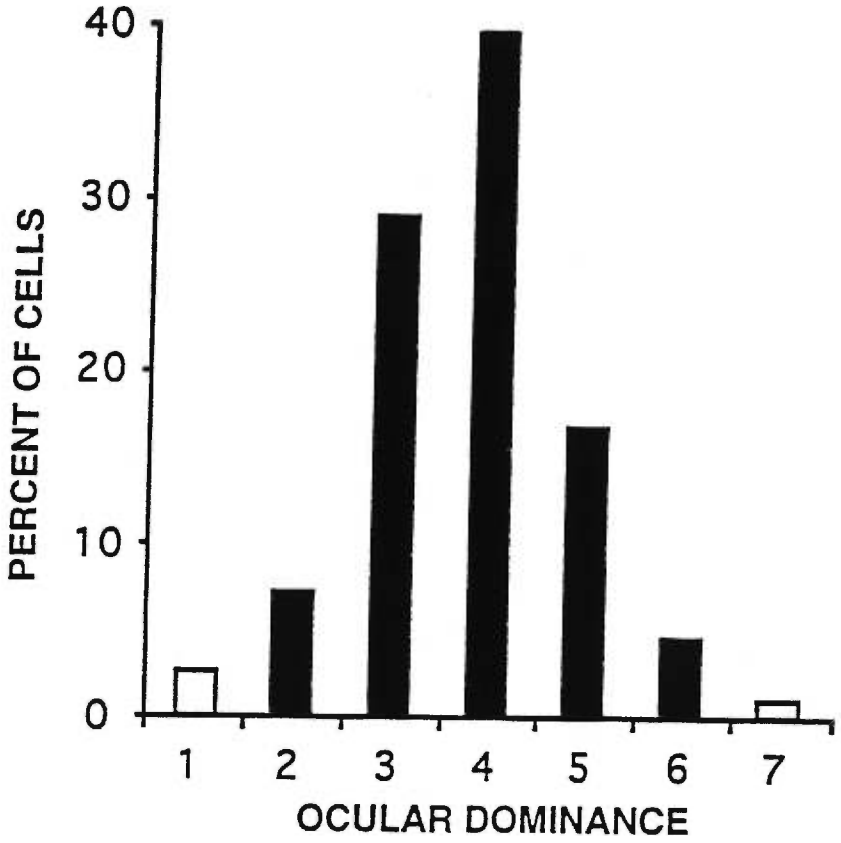


FIGURE 2

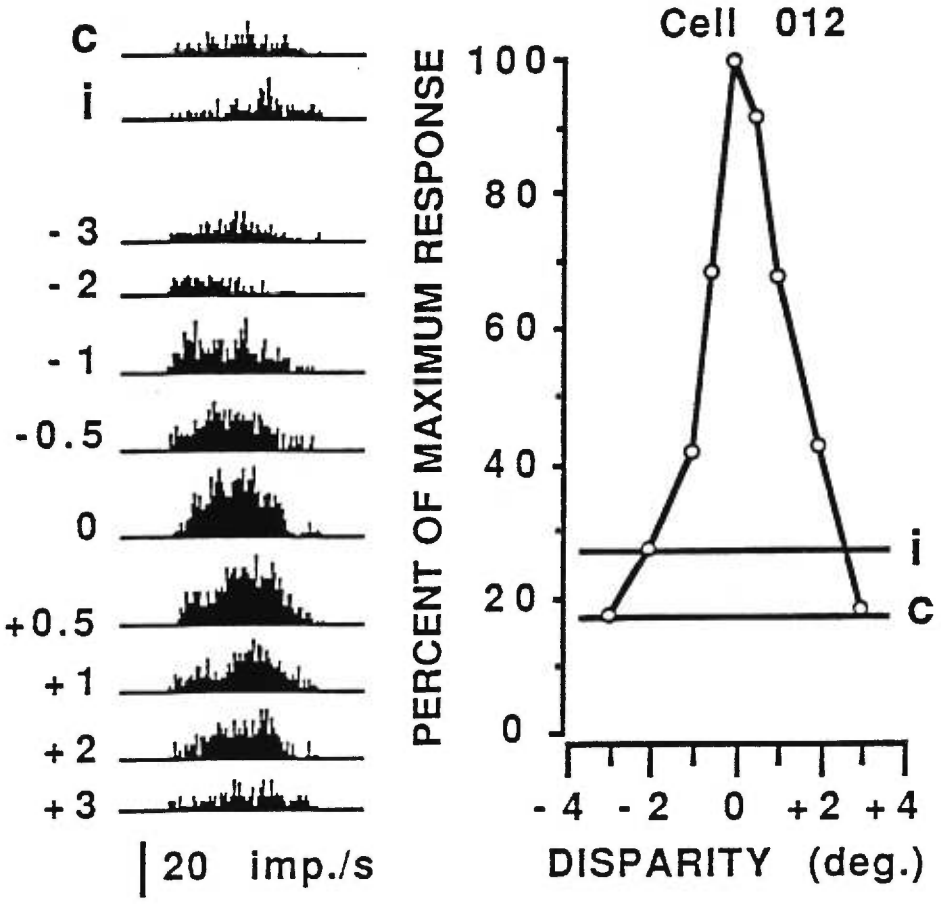

c
i
- 3
- 2
- 1
-0.5
0
+0.5
+1
+2
+3
20 imp./s
Cell 012
PERCENT OF MAXIMUM RESPONSE
100
80
60
40
20
0
i
c
- 4
- 2
0
+2
+4
DISPARITY (deg.)

FIGURE 3

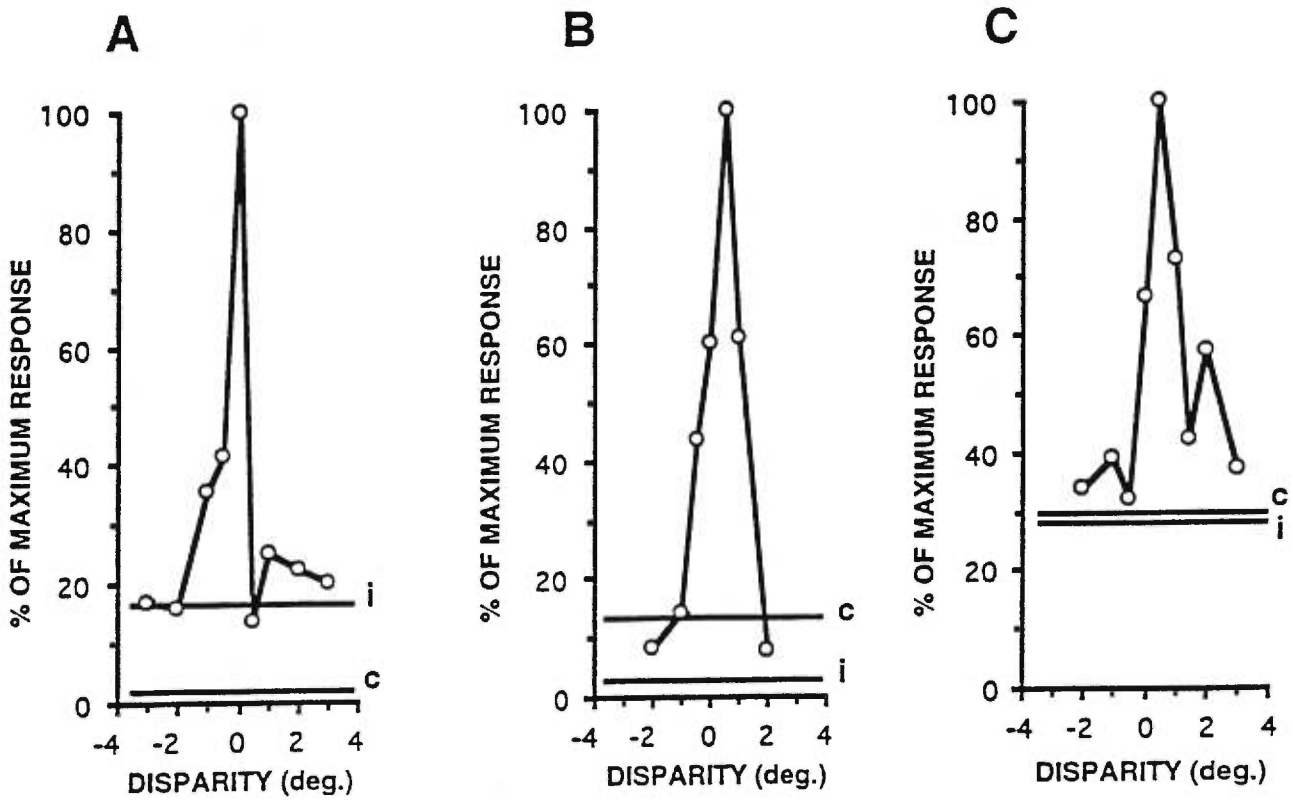

A
B
C
% OF MAXIMUM RESPONSE
100
80
60
40
20
0
-4
-2
0
2
4
DISPARITY (deg.)
i
c

FIGURE 4

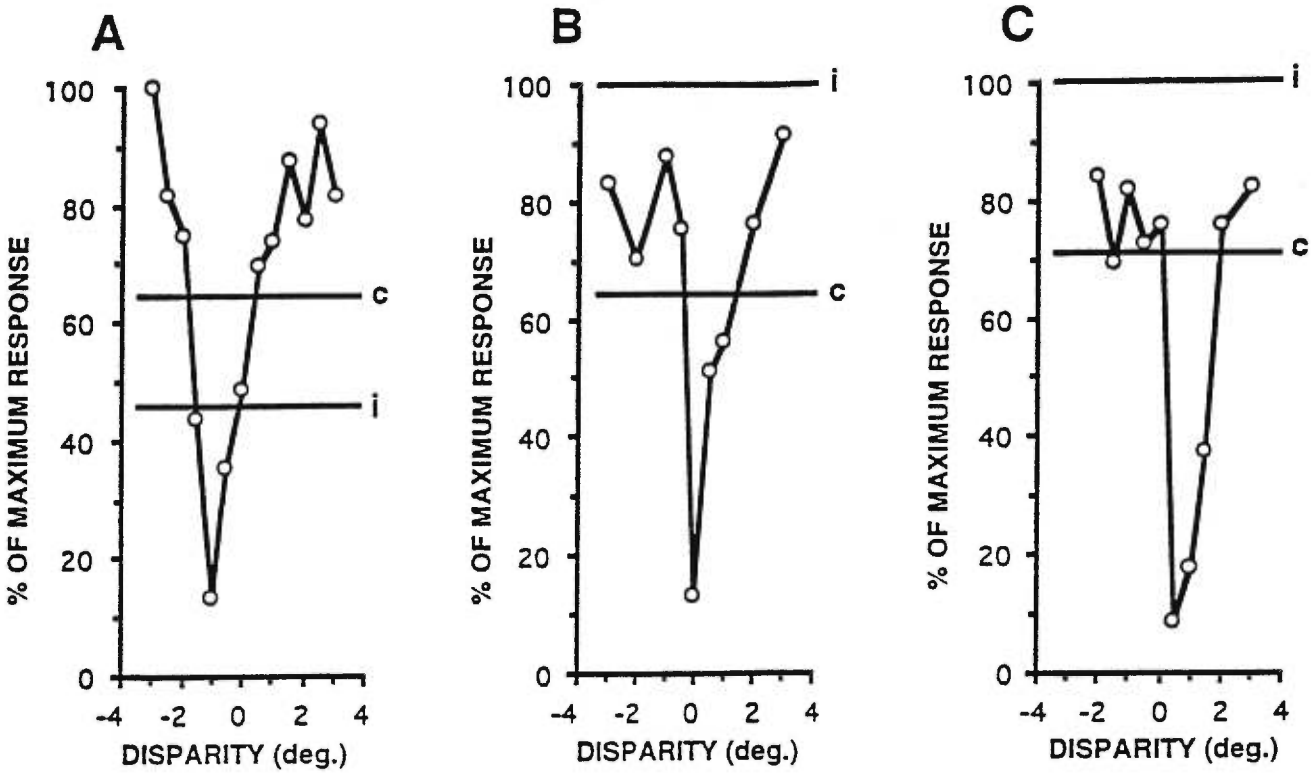

A
B
C
% OF MAXIMUM RESPONSE
100
80
60
40
20
0
-4
-2
0
2
4
DISPARITY (deg.)
c
i

FIGURE 5

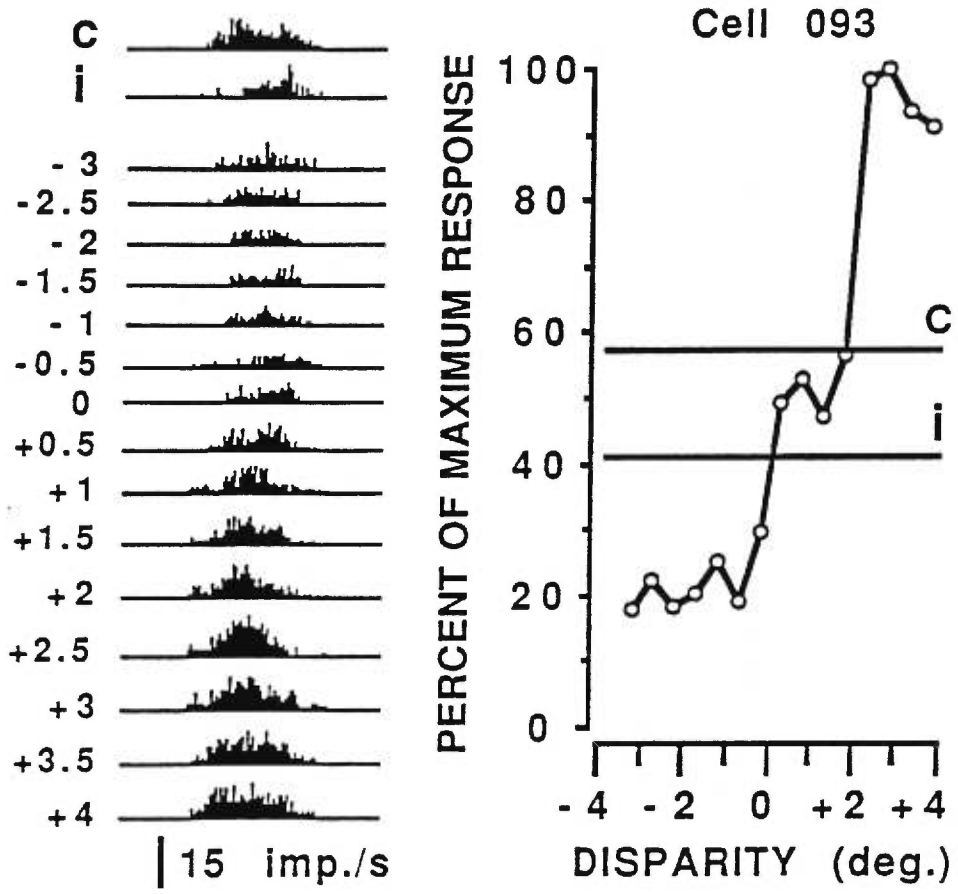
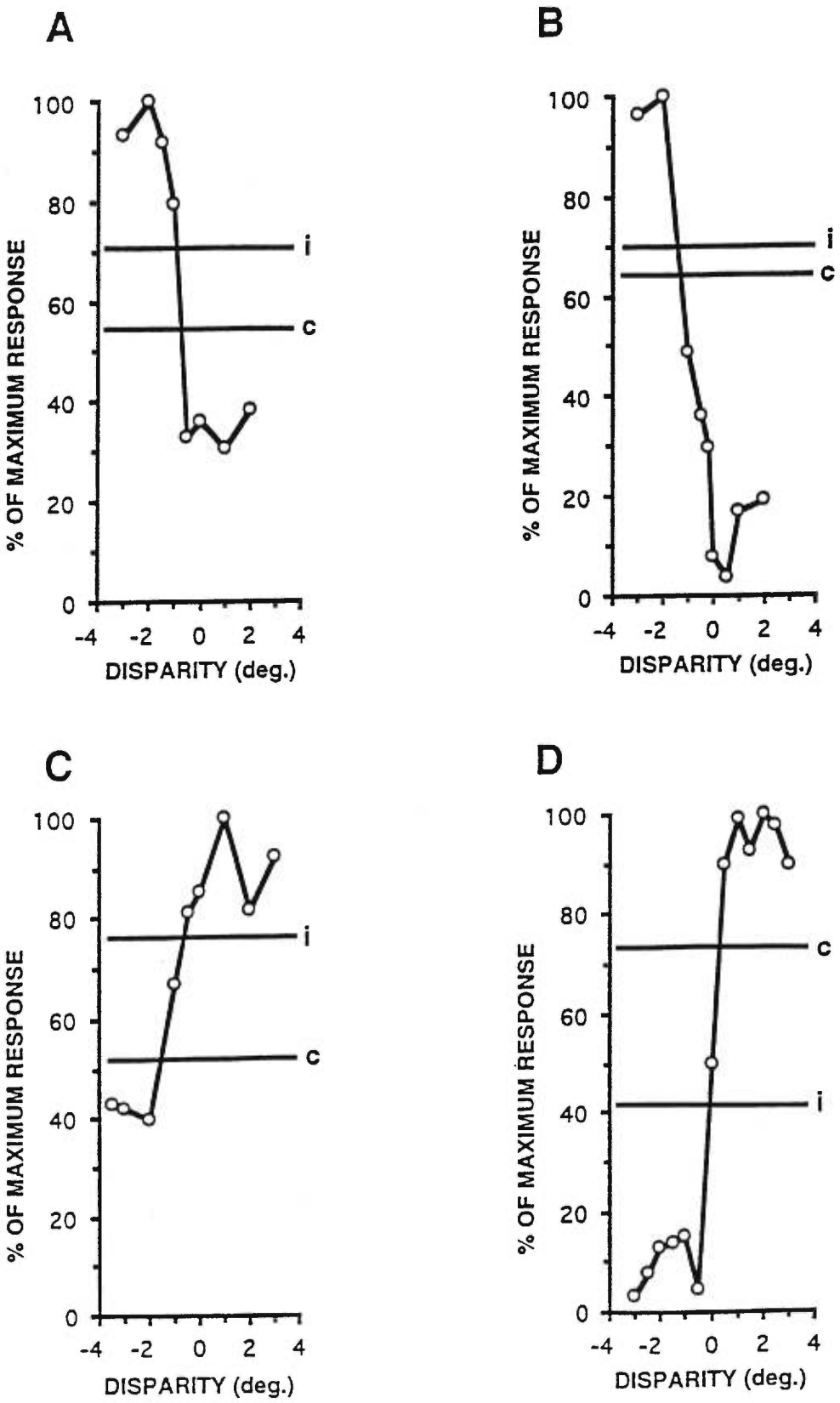

C
i
- 3
-2.5
- 2
-1.5
- 1
-0.5
0
+0.5
+1
+1.5
+2
+2.5
+3
+3.5
+4
15 imp./s
Cell 093
PERCENT OF MAXIMUM RESPONSE
100
80
60
40
20
0
C
i
- 4
- 2
0
+2
+4
DISPARITY (deg.)

FIGURE 6


A
B
C
D
% OF MAXIMUM RESPONSE
DISPARITY (deg.)
100
80
60
40
20
0
-4
-2
0
2
4
i
c

CHAPITRE 4

Article 3:

Spatial disparity coding in the superior colliculus of the cat

Experimental Brain Research, 119, 333-344

SPATIAL DISPARITY CODING IN THE SUPERIOR COLLICULUS OF THE CAT

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Short title: Disparity Coding in the Cat Superior Colliculus.

37 pages, 1 table, 7 figures.

ABSTRACT

Cells in the superficial layers of the superior colliculus of the cat have mainly binocular receptive fields. The aim of the present experiment was to investigate the sensitivity of these cells to horizontal spatial disparity. Unit recordings were carried out in the superficial layers of the superior colliculus of paralyzed and anesthetized cats. Centrally located receptive fields were mapped, separated using prisms and then stimulated simultaneously using two luminous bars optimally adjusted to the size of the excitatory region of the receptive fields. Only binocular cells were tested and 65% of these units were found to be sensitive to spatial disparities. Some cells (20%) were clearly insensitive to spatial disparity and the remaining 15% showed complex, unclassifiable interactions. The sensitive cells could be divided into four classes based on their disparity sensitivity profiles: 38% showed excitatory interactions whereas 9% showed inhibitory interactions. Moreover, 11% and 7% of the cells responded respectively to crossed or uncrossed disparities, and were classified as near and far cells. Whereas the general shapes of the sensitivity profiles were similar to those of cells in areas 17/18, selectivity in the superior colliculus was significantly coarser. The superficial layers of the superior colliculus project topographically to the deep layers of the superior colliculus which are known to contain circuits involved in the control of ocular movements. The results thus suggest that disparity sensitive cells of the superior colliculus could feed information to these oculomotor neurons, allowing for the localization and fixation of objects on the appropriate plane of vision.

Key Words: Disparity sensitivity, binocular interactions, superior colliculus, stereopsis, cat

INTRODUCTION

Depth perception can be achieved in numerous ways. Several monocular cues have been shown to be sufficient to assure this function, such as relative retinal size, the relative apparent movement of retinal images (motion parallax) as the head moves and the loss of details as distance increases. However, the early works of Wheatstone (1838) underlined that a precise and vivid perception of the third dimension could only be achieved in humans through binocular viewing via the fusion of the monocular visual scenes. Indeed, he demonstrated that spatial disparities between the two-dimensional images that objects in the visual field cast upon the retinae are used to estimate their depth and to generate three-dimensional percepts. It was later established that the spatial disparities critical for stereoscopic depth perception were those along the horizontal axis. Julesz (1971) used random-dot stereograms to eliminate monocular cues and form, and observed that the perception of depth emerged even before the perception of form. Behavioral experiments on animals with frontally placed eyes, such as the monkey (Bough 1970; Cowey et al. 1975; Sarmiento 1975; Harwerth and Boltz 1979a, b) and cat (Fox 1981; Lepore et al. 1986; Ptito et al. 1986) have shown that they also have stereoscopic vision.

Hubel and Wiesel (1959, 1962) identified cells responding to the stimulation of both eyes in the primary visual cortex of the cat. The two receptive fields (RFs) are normally very similar in structure and shape, but are often situated at slightly different spatial, and hence retinal, positions (Hubel and Wiesel 1962, 1968; Schiller et al. 1976a, b; Movshon et al. 1978; Mullikin et al. 1984a, b; Skottun and Freeman 1984; Camarda et al. 1985; Maske et al. 1984, 1986; Emerson et al. 1987). Most of these cells, moreover, respond more strongly when the visual stimuli fall on these disparate portions of the retinae (Barlow et al. 1967; Pettigrew et al. 1968; Bishop and Pettigrew 1986). These cells are presumed to constitute the neural substrate of

stereoscopic vision and have been found in the visual cortex of animals with frontally placed eyes such as the cat (Barlow et al. 1967; Nikara et al. 1968; Pettigrew et al. 1968; Ferster 1981; Lepore et al. 1992), monkey (Hubel and Wiesel, 1970; Poggio and Fisher 1977; Poggio et al. 1977; Poggio 1984, 1985; Poggio and Talbot 1981; Hubel and Livingstone 1987), sheep (Clarke et al. 1976) and owl (Pettigrew and Konishi 1976; Pettigrew 1979).

Poggio and Fisher (1977), investigating area V1 of the monkey, described four profiles of cellular response to spatial disparities. Some disparity sensitive cells responded with an increase (tuned excitatory cells) or a decrease (tuned inhibitory cells) in firing rate to a small range of disparities around zero. Others responded differentially to a large range of spatial disparities of the crossed (near cells) or uncrossed (far cells) type. Indeed, the near cells responded best to stimuli appearing to be in front of the fixation plane whereas the far cells responded best to stimuli seeming to be behind this fixation plane. The four types of disparity selective cells were also found in several other visual areas (areas V2, V3, V4, V5) in numbers exceeding those of area V1 (Hubel and Wiesel 1970; Poggio and Fisher 1977; Maunsell and Van Essen 1983; Poggio 1984 1985; Poggio and Poggio 1984; Poggio et al. 1985 1988; Burkhalter and Van Essen 1986; Felleman and Van Essen 1987; Hubel and Livingstone 1987; Livingstone and Hubel 1987).

In the visual system of the cat, disparity sentitive cells having the same general response profiles have also been found in areas 17-18, but their distribution across the other visual areas is somewhat different. Indeed, smaller numbers are found in area 19 (Pettigrew and Dreher 1987; Guillemot et al. 1993a) and 21a (Wang and Dreher 1996) than in areas 17-18 (Fisher and Krueger 1979; Ferster 1981; LeVay and Voigt 1988; Lepore et al. 1992).

At the subcortical level, the superior colliculus of the cat has also been shown to have a large proportion of binocularly driven cells (Sterling and Wickelgren 1969; Berman and Cynader 1972).

Afferents to this structure mainly originate in the retina and, when coupled with the massive projections from cortical areas 17, 18 and 19 and suprasylvian areas to the superficial layers (McIlwain 1973; Huerta and Harting 1984a, b) allow not only for the formation of binocular cells, but also of cells sensitive to spatial disparity. Berman et al. (1975) demonstrated that a significant proportion of cells showed binocular facilitation and summation as well as occlusion. These researchers did not report the presence of cells whose disparity sensitivity profiles resembled near and far cells, possibly because such profiles had not yet been suggested as relevant. More recently, Dias et al. (1991) investigated the rostral pole and the direct binocular region of the superior colliculus of the opossum and also found several tuned excitatory as well as some near cells.

The aim of the present experiment was to determine if all four types of cells sensitive to spatial disparity are present in the superior colliculus of the cat. Their presence, and possible similarity to cortical units, would suggest that this structure could also assure depth perception. The superior colliculus, on the other hand, has been shown to be involved in oculomotor behavior (Schiller 1972), such as visually guided orientation mediated by eye and head movements. The presence of disparity selective cells in the superficial layers of this structure could, via connections to deep layers output neurons (Behan and Appell 1992), mediate eye movements aimed at fixating objects located at different depths in the visual scene.

MATERIALS AND METHODS

Animals

The experiment was carried out on 15 adult cats, weighting between 2 and 4 kg, which came from a Université de Montréal approved supplier. They were all in good health and had no obvious malformations or pathologies. All surgical interventions, manipulations and husbandry were carried out within the guidelines proposed by the Canadian Council on Animal Care (CCAC). Moreover, the guidelines of the American Physiological Society and the Society for Neuroscience regarding the care and use of animals as well as the guidelines of the National Institute of Health (NIH) concerning the preparation and maintenance of higher animals during visual neuroscience experiments were followed. All experimental protocols were approved by the University Animal Care Committee before the beginning of the experiment.

Surgery

On the day prior to the recording session, 2 ml/kg of dexamethasone sodium phosphate (5mg/ml) was injected i.m. to limit inflammation during the surgical intervention. On the day of recording, the cat was injected with atropine (Atro-sol: 0.2 mg/kg) to reduce bronchial secretions and induce mydriasis, after which anesthesia was induced using a face mask with a gaseous solution of nitrous oxide, oxygen (N_2O:O_2, 70:30) and Fluothane (5%). Once anesthetized, the cat was intubated and connected to a respiratory pump. Throughout the surgery, fluothane was kept between 1% and 2% of the total gaseous mixture so as to maintain anesthesia level. The animal was then placed in the stereotaxic apparatus (David Kopf). This apparatus was modified to insure that the eyes were not touched or pressed upon and to avoid obstruction of the visual field.The saphenous vein was cannulated and, throughout the surgery, the animal was administered 5% dextrose in lactated ringer at the rate of 5.6 ml/h to maintain blood pressure and

hydration. The scalp was shaved and the cranial muscles and pressure points were infiltrated with a local anesthetic (xylocaine 2%), a procedure routinely repeated throughout the recording session. A small trepanation (5 mm diameter) was performed over the superior colliculus (A-P: 4-0, L: 1-5) at the coordinates derived from the atlas of Reinoso-Suarez (1961). A small incision was made in the exposed dura mater to allow the vertical penetration of the microelectrode. The entire trepanned area was then covered and sealed with 4% agar in physiological saline.

At the end of the surgery, the fluothane level was progressively reduced (0.5% every 15 min), stabilized at 0.5% and kept at that level for the duration of the recording session (30-33 hours). Stable heart rate, constantly monitored by ECG, and the absence of ear reflexes insured that the anesthesia level was sufficient. From that point on, a solution of 15 ml of gallamine triethiodide (Flaxedil: 200 mg) and d-tubocurarine (Tubarine: 15 mg) dissolved in 30 ml lactated ringer solution with dextrose (5%) was continuously infused through the saphenous vein at the rate of 5.6 ml/h to induce and maintain paralysis of extra-ocular muscles. Respiratory rate and stroke volume were adjusted so as to maintain a constant level of expired CO_2 (4%), which served as an indirect indication of stable blood pressure. Body temperature was also kept constant (37.5°C) with the help of a heating water pad thermostatically controlled with a rectal thermoprobe. EEG, monitored intermittently yet regularly, showed slow-wave activity throughout the recording session. Heart rate was constantly monitored throughout the recording session.

Optical preparation

Pupils were dilated by an i.m. injection of atropine sulfate 1% (Atro-Sol, 0.2 mg/kg) and the nictitating membranes were retracted with topical applications of phenylephrine hydrochloride (Neo-synephrine: 0.1%). To prevent dehydration and to improve image resolution, a zero-power plastic contact lens with a 3 mm artificial pupil was placed on each eye. In order to determine the

relative position of the areae centrales, retinal landmarks such as the optic disks and some major blood vessels were projected on a tangent screen situated 57 cm in front of the animal (Fernald and Chase 1971). The areae centrales were considered to be situated 16° medially and 7.5° below the iso-elevation line of the center of each optic disk (Bishop et al., 1962). Retinoscopy was used to determine the appropriate value of dioptric lenses necessary to focus the eyes on the tangent screen.

Recording and stimulation procedure

Recording was carried out with glass microelectrodes filled with a 3M NaCl solution and having an impedance measured at 1000 Hz of 3 to 6 Mohms. The microelectrode was stereotaxically lowered into the anterior part of the superior colliculus (A-P: 3-4, L: 2-3). The target units were those of the superficial layers having RFs in the center of the visual field, according to published topographical maps (Feldon et al. 1970; Berman and Cynader 1972; Lane et al. 1974). Cellular action potentials were conventionally amplified, displayed on an oscilloscope and transferred to an audio monitor. They were also filtered using amplitude/frequency criteria and transformed into square pulses and fed to a computer for on line and a posteriori analysis.

The stimulation procedure was adapted from Henry et al. (1967). The optic axis of one of the eyes was deviated using prisms so that the RF of each eye would be located on widely separated coordinates on the tangent screen placed at 57 cm from the animal. Two projectors, placed behind the back projection screen permitted the independent stimulation of each eye with light bars equated for luminance and contrast. The luminance of the stimuli was maintained at 48 cd/m^2 while the luminance of the background was 0.6 cd/m^2. The contrast, kept constant throughout the experiment, was defined as $C=(L_s-L_b)/L_b$ where L_s was the luminance of the

stimuli and L_b was the luminance of the background. Two optic benches, controlled independently through a computer, ensured the independent and precise definition of the other stimulus parameters: length and width, orientation and directionality, position in space, stimulus onset, velocity, as well as sweep duration and amplitude.

Upon isolating a binocular cell, the following initial protocol was followed. The RF of each eye was precisely mapped using the luminous spot and narrow slit of a manually controlled projector. During this phase, the best stimulus parameters (size, directionality and velocity) were determined. The optimal parameters were defined as the stimulus configuration which produced the greatest number of spikes, as estimated by ear from the output of the audio monitor. Each cell was tested for directionality and end-stopping. The principal inclusion criteria for the latter class was that the cell preferred a bar of optimal length, such that extending it beyond a determined limit caused a decrease in response.

This qualitative protocol was followed by a quantitative one. Stimulation was carried out using the dual optic bench system: two light bars having the best estimated dimensions were swept at optimal velocity and direction across each RF. Stimulus velocity varied between 1°/s and 20°/s, each sweep covering 20°. Each stimulus condition was presented 10 times and a peri-stimulus time histogram (PSTH) was derived from the responses to these stimulations. Each eye was first stimulated separately to determine the monocular response and the binocular interactions were tested through simultaneous stimulation of both RFs at different spatial disparities.

The two light bars were positioned exactly equidistant from the center of each RF. When the two bars started moving at the same time, they crossed the centers of the RFs simultaneously, and disparity was null. However, if the initiation of the sweep of one bar was delayed with respect to the other, the two bars would at any particular time be situated at non corresponding points

in each RF. The introduction of such a delay thus allowed the creation of crossed and uncrossed disparities. In addition to the null condition, several spatial disparity conditions were tested. These varied from 3° crossed to 3° uncrossed, in 0.5° or 1° steps. If RFs were sufficiently large, disparities up to 5° were tested to insure that cells (especially those of the near and far types) maintained their response characteristics typical of the crossed and uncrossed categories, and were not tuned cells having broad tuning-curve widths. Disparity, therefore, was defined relative to the RFs. These in turn were defined in terms of the coordinate reference points of the eyes. Although null disparity cannot be considered absolute, it is nonetheless a very close approximation limited only by the accuracy of the definition of retinal landmarks.

Data processing

All conditions, each tested a total of 10 times, were interleaved with each other in a pseudo-random fashion. The time interval between each sweep was 10-20 seconds to avoid habituation. For each condition, a PSTH was derived from the cellular responses. The abscissa for these PSTHs was divided into 500 bins, each having a binwidth of 2-40 ms, depending upon the duration of the sweep. For each condition, a second PSTH, of equal duration, was computed prior to each sweep when no stimulation was present to establish a baseline level. Each point on the response curve was obtained by subtracting the averaged number of spikes elicited without stimulation (baseline PSTH) from those elicited during the stimulation (response PSTH).

The two bars moving in the two RFs are intended to simulate a single object moving in superimposed RFs of the awake fixating animal. These bars, even when presented in disparate positions, should give rise to a response histogram reflecting disparity sensitivity. If, on the other hand, the two bars stimulate adjacent but unrelated RFs, as might occur when small RFs are stimulated with bars having large temporal delays (to test large disparities), the resulting response

would reflect at best binocular summation rather than disparity sensitivity. This would give rise to a PSTH having a bimodal shape. To avoid this possible artefact, only disparities smaller than the width of the RFs were tested and any cell showing a PSTH having a bimodal shape was eliminated from the results.

Eye stability control

It is important in this type of study to precisely control for eye position to make certain that they do not move during the recording period. This was controlled in two ways. First, before undertaking the quantitative evaluation, the precise positions of the RFs were determined. These positions were again checked after having terminated the quantitative protocol. Any measurable displacement in the location of either field resulted in the data being discarded. If the response of the cell was still robust, a new quantitative assessment, and consequent control, was carried out. Second, the stability of the eyes was estimated from the positions of major blood vessels and of the optic disks (Fernald and Chase 1971). This evaluation was carried out just before and immediately after having carried out the quantitative protocol for a particular cell. As above, any obvious displacement of the eyes led to the results being discarded. Moreover, the different estimates taken at various intervals during the recording session gave indications as to whether any gross displacement of the eyes had taken place during the time of recording. Since the diameter of the optic disk at this screen distance was fairly large, the major blood vessels radiating from the optic disk were also taken for reference points (Pettigrew et al. 1979). This procedure, therefore, furnishes a useful index of both short and long term stability of eye position. The results obtained indicated that fairly stable eye positions were maintained throughout the 30-33 hours recording session. It must be noted that following the induction of paralysis, recording was delayed for at least four hours to insure eye stabilization.

Histology

Small electrolytic lesions (4 mA, 5 s, tip negative) were performed at the recording sites during penetrations. At the end of the experiment, the cat was deeply anesthetized with 5 % Fluothane, after which it was perfused through the heart with isotonic saline followed by formalin (4%). The brain was removed, placed in formalin (4%), soaked in sucrose and then frozen. The section containing the superior colliculus was sliced (40 μm) along the coronal plane. Every second slice was kept and stained using the Kluver-Barrera method (Kluver and Barrera 1953). In this report, all the cells were located in the superficial layers of the superior colliculus.

RESULTS

A total of 196 units were isolated. Each was tested for binocularity by stimulating each eye individually. Binocular cells were then subjected to the qualitative and quantitative procedures described above. No attempts were made to test the 22 monocular units for the following reasons. First and foremost, there was some possibility that these monocular responses were recorded from retinal fibers. Second, even if they were not truly monocular, localizing the RFs of the unresponding eye was difficult, especially given the rather large RF sizes in some cases. All binocular cells (174) were submitted to the spatial disparity protocol.

Receptive field properties

These data were collected mainly for normative purposes and are therefore only briefly summarized herein. Only neurons whose RF center of the dominant eye was situated in the contralateral hemifield, extending up to a maximum of 10° of eccentricity, and located between +5° and -10° of elevation were tested. Recording was purposefully carried out in this restricted part of the visual field since it is in this region that depth is presumed to be perceived most precisely. The minimum response fields, as tested with light bars and spots, were therefore rather small, as compared to more peripherically located RFs, ranging from approximately 4° to 16° in width on the axis parallel to the preferred direction of stimulation. Movement across the RFs elicited the best response rate, whereas stationary flashed stimuli were less efficient.

The directional selectivity was tested by sweeping an oriented light bar in all directions in approximately 15° steps. Cells were considered directionally selective if a particular stimulus direction clearly evoked a greater response rate than other directions. Of the 174 cells tested, 67 neurons (38.5%) clearly showed directional preferences, whereas 107 cells (61.5%) did not. For most cells, preferred directions of stimulation were along the horizontal axis, which confirms

previous reports (e.g. Sterling and Wickelgren 1969). Indeed, all cells included in this report were tested in a direction deviating not more than 45° from the horizontal plane. As this investigation was concerned with horizontal spatial disparities, the few cells which preferred stimuli moving along the vertical axis were not included in the results.

The RFs of all binocular cells were tested for end-stopping properties. It was found that for 145 of the 174 (83.3%) cells, the minimal response field was located between inhibitory regions from which no responses could be elicited but from which the principal response could clearly be suppressed by extending the stimulus beyond the boundaries of the receptive field.

The ocular dominance index (ODI) of each cell was determined quantitatively by comparing the responses obtained from the independent stimulation of each RF. The classification of Hubel and Wiesel (1959, 1962), which placed all cells on a 1 to 7 continuum, where 1 corresponded to total contralateral dominance and 7 for total ipsilateral dominance, was used. In order to place the binocular cells quantitatively in the intermediate categories 2-6, an index of binocularity was calculated using the formula: ODI = (I/(I+C)) x 100 where I represents the response to stimulation of the ipsilateral eye and C, that to stimulation of the contralateral eye. The ODI thereby obtained allowed for the classification using the following scale: 2: (1-20%); 3: (21-40%); 4: (41-60%); 5:(61-80%); 6: (81-99%).

As illustrated in Figure 1, where the ocular dominance distribution is shown, 7.6% (15 cells) were exclusively driven by contralateral stimulation and 3.6% (7 cells) responded only to ipsilateral stimulation. These monocular cells were not submitted to the spatial disparity protocol. A high proportion of the cells (56.6% or 111/196) were equally driven by stimulation of both eyes (class 4). Of the remaining cells, 26% (51 cells) were more contralaterally driven (classes 2 and 3) and only 6.2% (12 cells) were more ipsilaterally driven (classes 5 and 6). This ODI distribution

is rather typical of collicular cells (Sterling and Wickelgren 1969; Berman and Cynader 1972; Hoffmann and Sherman 1975).

Insert Figure 1

Spatial disparity sensitivity profiles

In order to investigate disparity sensitivity, both RFs were stimulated simultaneously using an array of spatial horizontal disparities. As can be seen in Figure 2, a PSTH was derived for each spatial disparity tested as well as for the two monocular responses. The responses obtained at each spatial disparity are used to draw the normalized disparity sensitivity profile of the cell.

Among the 174 cells tested, different disparity sensitivity profiles emerged. Although collicular cells responded over a larger range of spatial disparities than their cortical counterparts, their sensitivity profiles were similar in shape to those previously described in visual areas of the cat (LeVay and Voigt 1988; Lepore et al. 1992; Guillemot et al. 1993a) and monkey (Poggio and Fisher 1977; Fisher and Krueger 1979; Poggio and Poggio 1984). Therefore, the same criteria and terminology (Poggio and Fisher 1977) were used in the present report.

Insert Figure 2

A neuron whose binocular response at a given disparity exceeded the sum of the monocular responses was classified as a tuned excitatory cell (Figure 2A, Figure 3A). On the other hand, if the binocular response at a given disparity was clearly inferior to the weakest monocular response, the neuron was classified as a tuned inhibitory unit (Figure 2B and Figure 3B). Neurons

were classified as near cells if crossed disparities elicited a greater response than the best monocular response and uncrossed disparities elicited a smaller response than the lesser monocular response. (Figure 2C, Figure 3D). On the other hand, neurons were classified as far cells if their response profiles were the converse of this (Figure 2D, Figure 3E).

The cells termed insensitive failed to show binocular interactions. They gave a similar response to each disparity tested or a response magnitude resembling that obtained to the monocular stimulation (Figure 3C). The cells termed unclassifiable showed some binocular interactions and a disparity sensitivity which could not be fitted into one of the four profiles. One such unclassifiable cell is shown in Figure 3F. The general organization of the profile of this cell indicates a tendency toward the near profile, yet the clear secondary excitatory peak for negative disparities and the lack of constancy of the inhibitory response for positive disparities are inconsistent with the criteria defining this category.

Insert Figure 3

The criterion for tuned excitatory cells of Poggio and Fisher (1977), defined for cortical units, may be stringent when applied to the superior colliculus. Investigating such cells, Berman et al. (1975) used two distinct criteria. The first, facilitation, was identical to that of Poggio and Fisher (1977), and this criterion was also used in the present report. The response shown by the cell in Figure 4A is a typical example of such facilitation. The second, less stringent criterion, called summation, required only that the highest binocular response be clearly superior to the monocular response of the dominant eye. In this report, some tuned excitatory cells failed to show facilitation but nonetheless showed summation. The peak response of the cell in Figure 4B is not

greater than the sum of the monocular responses, yet it is clearly above the monocular response of the dominant eye. Of the 174 binocular cells tested, 52 (29.9%) would be classified as tuned excitatory if the facilitation criteria were used. However, an additional 14 cells (8.0%) could be added to this class if the summation criteria were used.

Insert Figure 4

As can be seen in Table 1, cells showing the other types of disparity profiles were present in lesser proportions than the tuned excitatory units. Indeed, 15 cells (8.6%) were classified as tuned inhibitory, 19 (11%) as near cells and 12 (6.9%) as far cells. A total of 112 cells out of the 174 binocular cells (64.4%) were hence tuned to spatial disparities. Of the remaining cells, 27 (15.5%) showed unclassifiable binocular interactions and 35 (20.1%) were insensitive to spatial disparities.

Insert Table 1

Tuning-curve widths and slopes of disparity profiles

In order to obtain a quantitative measure of the selectivity of the tuned excitatory and tuned inhibitory collicular cells, full-widths at half-height of the tuning function were calculated. The mean tuning-curve width of these collicular cells were 2.97° for the tuned excitatory cells and 1.53° for the tuned inhibitory ones. These results were compared to the tuning-curve width of tuned excitatory and tuned inhibitory units which we have recorded at the 17-18 border of the cat (Lepore et al. 1992), using similar stimulation and recording protocols. The mean tuning-curve

width of these cortical cells were 0.41° for tuned excitatory cells and 0.57° for tuned inhibitory units. This difference in selectivity can be clearly seen in two cells shown in Figure 5. In Figure 5A, the tuning-curve width of the collicular unit is several times larger than that of the cortical cell. The same can also be observed in the tuned inhibitory cells of Figure 5B. Although tuned cells of the superior colliculus show profiles similar to those of their cortical counterparts, these are considerably less sharply tuned and their selectivity to spatial disparity is hence less precise.

Insert Figure 5

Similar comparisons were performed on the near and far collicular cells. The slopes of their tuning functions at 50 % of the maximal response were calculated. The average slope of the near cells was -57.8 and the mean slope of far units was +48.7 These results were compared to the slopes of near and far units recorded in the same laboratory at the 17-18 border of the cat (Lepore et al. 1992). The average slopes of corresponding cortical neurons were -303 for near cells and +254 for far cells. Figure 6A illustrates the difference in tuning of one collicular and one cortical cell. The same difference can be observed for far cells (Figure 6B) as the slope of the cortical unit is considerably steeper than that of the collicular cell. The near and far cells of the superior colliculus show profiles with similar inflection points (around null disparity) and of the same general shape as those of their cortical counterparts. However, the disparities necessary to elicit such profiles are considerably larger, as they were for the tuned cells, and the selectivity to spatial disparity of collicular cells is hence less precise.

Insert Figure 6

For all types of cells, selectivity as described by tuning-curve width or slope was compared to its RF width. Although there was a general tendency for cells which had large RFs to have wider tuning or less abrupt slopes, no statistically significant correlation emerged, probably because tuning widths or slopes were not as greatly distributed as RF widths.

Ocular dominance and disparity sensitivity

The relationship between the type of disparity profile and ODI that was established in previous studies of cortical cells could not be confirmed for collicular cells. In a study in our laboratory investigating cells at the 17-18 border (Lepore et al. 1992), it was found that the tuned excitatory and inhibitory neurons tended to show a balanced ODI, whereas the near and the far cells showed mainly unbalanced dominance. Similar results had also been obtained for areas 17 and 18 by Ferster (1981), as well as LeVay and Voigt (1988). In the present report, however, most collicular cells, regardless of their disparity sensitivity profiles, were confined to ODI category 4 with a certain bias toward contralateral dominance. This bias could be explained by the high proportion of retinal afferents coming to the superior colliculus from the contralateral eye. As most disparity sensitive cells fell in ODI classes 3 and 4, few units were in ODI categories 2, 5 and 6. The paucity of cells in these classes precluded statistical analyses relating ODI and disparity types. Examination of the data, however, did indeed reveal that near cells tended to be more contralaterally driven than the tuned cells, which in turn tended to be more contralaterally driven than the far cells.

The different disparity profiles were also related to RF types. However, no significant relations could be found as the profiles were evenly distributed among the end-stopped and complex categories.

Disparity-dependent direction-selective (DDD) neurons

Roy et al. (1992) were the first to demonstrate the existence of DDD neurons in the medial temporal area (MST) of the monkey. These cells were said to be direction-selective since they changed their disparity sensitivity profile from near to far or vice-versa when the direction of stimulation was changed by 180°. The presence of DDD neurons in the superior colliculus of the cat was investigated by reversing the direction of stimulus drift and repeating the protocol on 4 neurons already identified as near cells and 4 others categorized as far cells. Whereas seven of these cells retained their original profiles following the stimulus drift inversion, the profile of a far cell actually changed to that of a near unit, hinting at the presence of DDD cells in the superior colliculus. The profiles of this far-near neuron can be seen in Figure 7A, which also illustrates the profiles of a far cell which was not altered by the change in stimulus direction (Figure 7B). This preliminary result, based on the examination of only eight cells, certainly deserves to be explored further.

Insert Figure 7

DISCUSSION

The main objective of this experiment was to assess whether disparity sensitive cells are present in the superior colliculus of the cat and to investigate the nature of their selectivity to spatial horizontal disparity. The results indicate that 65% of cells in the superficial layers of the colliculus are sensitive to horizontal disparities.

The RFs of these cells were located in the central part of the visual field, as recording was carried out in the anterior part of the superficial layers. The RFs often straddled the vertical meridian and were, with respect to this structure, of rather small size, in accordance with the description of RFs of cells located in this portion of the superior colliculus (Sterling and Wickelgren 1969; Berman and Cynader 1972). The RF organization of these neurons was strongly biased toward end-stopping. The cells showed a clear preference for moving stimuli as opposed to flashed ones. As movement is known to be a salient cue for detection and orienting behavior, collicular neurons would be expected to be particularly sensitive to motion, as also demonstrated in previous reports (McIlwain and Buser 1967; Sterling and Wickelgren 1969; McIlwain 1970). The neurons were most responsive to stimuli traveling along the horizontal axis, which also confirms previous reports (Sterling and Wickelgren 1969; Hayashi et al. 1973). A significant proportion, slightly less than half, exhibited direction selectivity. This was based on a stringent criterion, which may account for their lower proportion in this experiment than in previous ones, where direction selectivity ranged from slightly more than half to three-quarters (McIlwain and Buser 1967; Sterling and Wickelgren 1969; Berman et al. 1975; Hoffmann and Sherman 1975).

Almost 90% of the cells were binocularly driven. Quantitative evaluation of ODI revealed that more than two-thirds of these cells responded equally well to stimulation of either eye and

that most of the other units showed a preference for stimulation through the contralateral eye. This slightly skewed ocular dominance distribution is typical of cells in the superficial layers of the superior colliculus of the cat (Sterling and Wickelgren 1969; Berman and Cynader 1972; Hayashi et al. 1973; Hoffmann and Sherman 1975).

Disparity sensitivity profiles

Of the 174 binocular cells, 38% showed a tuned excitatory profile and 9% were of the tuned inhibitory type. Another 11% were classified as near cells and 7% as far cells. The four well-documented types of disparity selective cells described previously in cortical areas of the cat (Ferster 1981; LeVay and Voigt 1988; Lepore et al. 1992; Guillemot et al. 1993a) and the monkey (Poggio and Fisher 1977; Poggio and Poggio 1984) are thus present in the superior colliculus of the cat. The presence of tuned inhibitory and tuned excitatory cells was somewhat expected, as Berman et al. (1975) had demonstrated the presence of binocular facilitation, summation and occlusion in this structure. The tuned excitatory cells of the present report are mostly tuned to null disparities, as were the cells showing excitatory binocular interactions of Berman et al. (1975). As stated in the methods section, zero disparity is to be understood in relative terms, in the sense that it is defined with respect to the RFs, which were themselves defined in terms of the optic disk and major blood vessels emanating from it. These landmarks were carefully mapped and frequently checked to avoid the bias of eye drift. This procedure, therefore, does allow for a very close approximation of the positional disparity in absolute terms, limited only by the precision in mapping the RFs and back-projecting the optic disk.

The inhibitory interactions of the cells in the report of Berman et al. (1975) clearly occurred at disparities in the crossed or uncrossed range, whereas the tuned inhibitory cells of our sample were mainly tuned around null disparity. In a rather small proportion of cells described in the

present report, excitatory tuning was obtained in response to a limited range of disparities in the crossed or uncrossed range. These profiles closely resembled the tuned near and tuned far cells described by Poggio and Poggio (1984) in the monkey and also obtained in visual areas of the cat (Ferster, 1981; LeVay and Voigt, 1988; Lepore et al., 1992; Guillemot et al., 1993a; Wang et Dreher, 1996). However, because our procedure does not allow for an absolute definition of zero disparity, which is best obtained in the fixating, behaving animal in cells with small RFs, we cannot with certainty advance that they corresponded to these two subsets of tuned cells.

Several of the cells in our sample demonstrated excitatory binocular interactions to a wide range of crossed disparities and inhibitory binocular interactions for a large range of uncrossed disparities, or vice-versa. They formed the near and far profiles first identified in the monkey by Poggio and Fisher (1977) and which have not been previously identified in the superior colliculus of the cat. However, near cells were reported in the superior colliculus of the opossum (Dias et al., 1991), a species equipped with a less well-developed visual system than the cat. These authors explained the absence of far cells by the fact that the opossum is nocturnal and myopic.

The presence in such a large proportion of disparity selective cells in the superficial layers of the superior colliculus of the cat may appear surprising. LeVay and Voigt (1988) even suggested that collicular neurons should not be sensitive to spatial disparity. However, considering the massive input received by these layers from the primary visual cortex and extrastriate visual areas, it is the absence of disparity sensitive neurons which would have been surprising. Indeed, under identical stimulation procedures, it was found that 71% of cells in area 17-18 of the cat showed disparity tuning (Lepore et al. 1992) and that disparity sensitive cells were even present, albeit in lesser numbers (34%) in area 19 (Guillemot et al. 1993a) which, like the superior colliculus receives its input from W and Y ganglion cells.

The relationship between disparity sensitivity and ocular dominance has been demonstrated several times (Poggio and Fisher 1977; Fisher and Krueger 1979; Gardner and Raiten 1986). The results of the present study confirm those of Poggio and Fisher (1977), Fisher and Krueger (1979) and Ferster (1981) as most of the binocular cells (169/174) belonged to ODI classes 3 and 4. However, since these classes encompassed almost all binocular cells, we could not confirm as in previous studies (LeVay and Voigt, 1988; Guillemot et al. 1993a) that near and far cells are driven more strongly through stimulation of one eye or the other.

Disparity selectivity

The disparity profiles of collicular cells may appear to be very similar to those of disparity selective neurons in cortical areas of the cat. However, closer examination of the scales reveals that collicular cells differ from cortical cells by their rather coarse tuning. Indeed, the tuned excitatory and tuned inhibitory cells of areas 17-18 (Lepore et al. 1992), of the cat had sharp profiles which translated into narrow tuning-curve widths and the near and far cells showed steep slopes, indicating a clear delimitation of the space in front and behind the fixation plane. The tuned excitatory and tuned inhibitory collicular cells tested in this report had much larger tuning-curve widths and the near and far cells showed attenuated slopes. The tuning of these cells was even coarser than that obtained in higher order visual areas such as 19 (Pettigrew and Dreher 1987; Guillemot et al. 1993a) or 21a (Wang and Dreher 1996) of the cat. Such differences may be contrasted with the fact that maximum visual acuity in these areas (Tanaka et al. 1987; Guillemot et al. 1993b; Tardif et al. 1996), as measured with sinusoidal gratings, is comparable to the maximum acuity of collicular cells (Bisti and Sireteanu 1976; Bacon et al. 1996).

Collicular cells can therefore code for stimuli with disparities as large as 3°. Why are their selectivity so coarse? One reason concerns the functional significance of these cells, which will

be discussed below. Another, possibly complementary reason, may lie with the nature of the ganglion projections to this subcortical structure. The superior colliculus receives afferents from all three types of ganglion cells from both eyes. However, most of the collicular cells receiving direct activation from ganglion cells are activated by W-type cells (Hoffmann 1973; Updyke 1977). Approximately 10% of the cells are activated by collateral axons of Y-type ganglion cells (Wässle and Illing 1980). Although it is well established that about 10% of the X-type ganglion cells send collateral axons to the superior colliculus (Wässle and Illing 1980), activation of cells via these X-type cells is believed to be negligible (Stein and Berson, 1995). Those X-type cells are the principal afferents to area 17 and are presumed to mediate sharp discrimination and fine disparity selectivity. On the other hand, Y-type and W-type cells are more concerned with global vision and have lower acuity.

The abundance of tuned cells and the paucity of X-type input to the superior colliculus seems to contradict the hypothesis of Pettigrew and Dreher (1987), who claimed that the X subsystem is responsible for coding on the fixation plane. Moreover, the relatively small proportion of far cells and the large amount of W-type afferents also seem incompatible with their hypothesis that divergent disparities beyond the fixation plane are analyzed through the W system. It must be noted, however, that Pettigrew and Dreher (1987) were investigating the processing of binocular disparity in the retinogeniculocortical pathway and that their suggestions may not apply to the retinocollicular pathway.

The coarse disparity profiles of the cells of the superior colliculus make it unlikely that these cells are involved in the precise evaluation of three-dimensional objects, a role possibly assumed by cortical cells whose disparity tunings are much finer. Rather, it is proposed that these neurons are involved in the formation of a three-dimensional visuo-spatial map which, via topographic

connections to deep layer neurons (Behan and Appell 1992), feed information to structures mediating ocular movement. This information could be used by these structures and their target motor neurons to localize objects with regard to Z-axis coordinates, fixate them in the appropriate plane of vision and maintain fixation.

Indeed, the deep layers of the superior colliculus have been shown to be involved in saccades and input determined eye position (Wurtz and Mohler 1974; Robinson 1975; Schiller and Wurtz 1975; Sparks 1975 1978; Wurtz and Albano 1980). It was also demonstrated that electrical stimulation of neurons located in the rostral third of the deep layers of the superior colliculus of the cat evoked stereotyped saccades for a given locus of stimulation (Guitton et al. 1980). Moreover, the direction and amplitude of those saccades were shown to be independent of original eye position (Munoz 1988; Van Opstal et al. 1990). Guitton (1991) added that when mapped on the surface of the superior colliculus, the vector of each evoked saccade defined the retinotopically coded motor map that is co-extensive with the visual map of the superficial layers. Moreover, the anatomical connections between the superficial and deep layers of the superior colliculus (Behan and Appell 1992; Behan and Kime 1996) point to an interrelation of functions and sensorimotor integration. In the present case, disparity information transmitted down from the visual map to the motor map may facilitate fixation of a point in space and maintenance of fixation upon that point. The fine discrimination and identification of the now foveally located object could then be pursued by the appropriate visual cortical areas, namely, the striate and extrastriate cortex.

Another function which may be mediated by these disparity sensitive neurons concerns vergence eye movements, as proposed for disparity sensitive cortical neurons by Poggio and Fisher (1977). The implication of collicular neurons in such a system was also hinted at (Berman

et al. 1975; Dias et al. 1991).

As microstimulation of the superior colliculus with weak currents can evoke accomodation responses (Sato and Ohtsuka, 1996), it could also be advanced that the disparity sensitive cells of this structure play a role in the control of accomodation. Indeed, these cells could code for spatial disparity and relay this information to accomodative mechanisms, hence allowing for the focusing of the eyes upon stimuli slightly off the fixation point.

The functional utility of the DDD cell, which we found among the eight appropriately tested neurons, if present in sufficiently large numbers, could be reconciled with the role Roy et al. (1992) proposed for them in the monkey cortex. DDD cells come into play when the organism is moving forward yet is fixating his gaze laterally. In this situation, objects situated near the organism appear to be moving in the opposite direction whereas objects further away, beyond the fixation point, appear to follow in the organism's direction. Thus, DDD cells in the superior colliculus might feed disparity information to oculomotor structures to allow localization or fixation of objects in this three-dimensional visual scene seemingly moving in two directions at once.

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TABLE 1

Ocular dominance and number of disparity sensitive cells in the superior colliculus of the cat.

	2	3	4	5	6	Total	%
Tuned excitatory	2	23	34	7		66	37.9
Tuned inhibitory		2	13			15	8.6
Near		3	16			19	11.0
Far			12			12	6.9
Insensitive	2	11	19	3		35	20.1
Unclassifiable		8	17	1	1	27	15.5

FIGURE LEGENDS

Fig. 1: Ocular dominance distribution of 196 collicular cells. *Dark bars,* binocular cells; *light bars,* monocular cells. Categories 1 and 7 include cells driven exclusively through the contralateral eye or the ipsilateral eye respectively. The other categories include binocular cells with intermediate ocular dominance. More than half of the cells are driven equally well by stimulation of either of the eyes (category 4).

Fig. 2: Examples of peri-stimulus time histograms, indicating the response at each spatial disparity, from which were derived the normalized sensitivity profiles of four disparity selective cells. The response to monocular ipsilateral (i) and contralateral (c) stimulation are also shown at the top of each set of histograms. **A** Tuned excitatory cell; **B** Tuned inhibitory cell; **C** Near cell; **D** Far cell.

Fig. 3: Representative examples of normalized profiles of response to spatial disparity found in the superior colliculus of the cat. These different profiles include the tuned excitatory cell (**A**) and tuned inhibitory cell (**B**) which prefer stimuli located on the fixation plane (around null disparity), the former responding with an increase in discharge rate and the latter with a decrease. The insensitive cell (**C**) do not respond differentialy to stimulus disparity. The near cell (**D**) and far cell (**E**) are those units which are excited by a large set of disparities and inhibited by another. The spatial arrangement of the stimuli are such that one can presume that near cells prefer stimuli in front of the fixation plane, whereas far cells prefer stimuli behind the fixation plane. In **F**, an unclassifiable cell which show non-linear interactions but which cannot be categorized as an identifiable response profile is shown. Monocular responses to contralateral (c) and ipsilateral (i) stimulation are indicated on each disparity sensitivity profile.

Fig. 4: Disparity sensitivity profiles of two tuned excitatory cells. In **A**, the peak response exceeds the sum of the monocular responses, as the cell shows facilitation. In **B**, the peak response is superior to the response of the dominant eye only, as the cell responds to the criteria of summation.

Fig. 5:: The bandwidths of two collicular cells (black dots) and two cortical cells recorded at the 17-18 border (white dots) are compared. For tuned excitatory cells (**A**) and tuned inhibitory cells (**B**), it can be seen that although the sensitivity profiles of collicular cells appear similar in shape to the sensitivity profiles of cortical cells, the disparities needed to elicit such tuning functions in collicular cells are much larger.

Fig. 6: The tuning functions of two collicular cells (black dots) and two cortical cells recorded at the 17-18 border (white dots) are compared. The steeper slopes of the cortical cells functions in both the near (**A**) and far (**B**) profiles emphasize that although the general profiles of the cortical and collicular cells appear similar, the cortical cells show a significantly more drastic decrease (near cells) or increase (far cells) of their response rate around null disparity.

Fig. 7: The sensitivity profiles shown in white dots in **A** and **B** represent two far cells tested from the 0° horizontal direction. The sensitivity profiles shown in black dots represent the sensitivity profiles of the same cells when tested in the opposite horizontal direction (180°). It can be seen that the cell in **A** changed its profile from a far cell to a near cell when the direction of the stimulation was changed. Such a change characterizes the cell as a disparity-dependent direction-selective (DDD) unit. The profile of the cell in **B** was not altered by the change of direction.

FIGURE 1

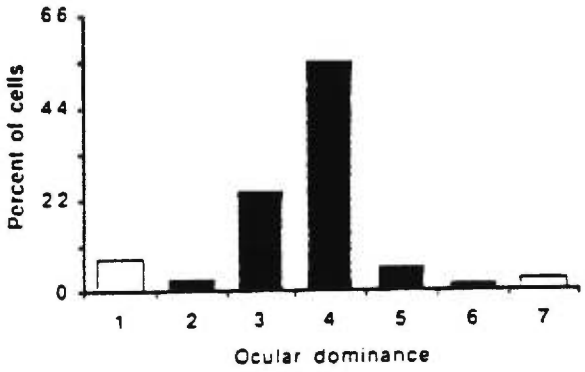


FIGURE 2

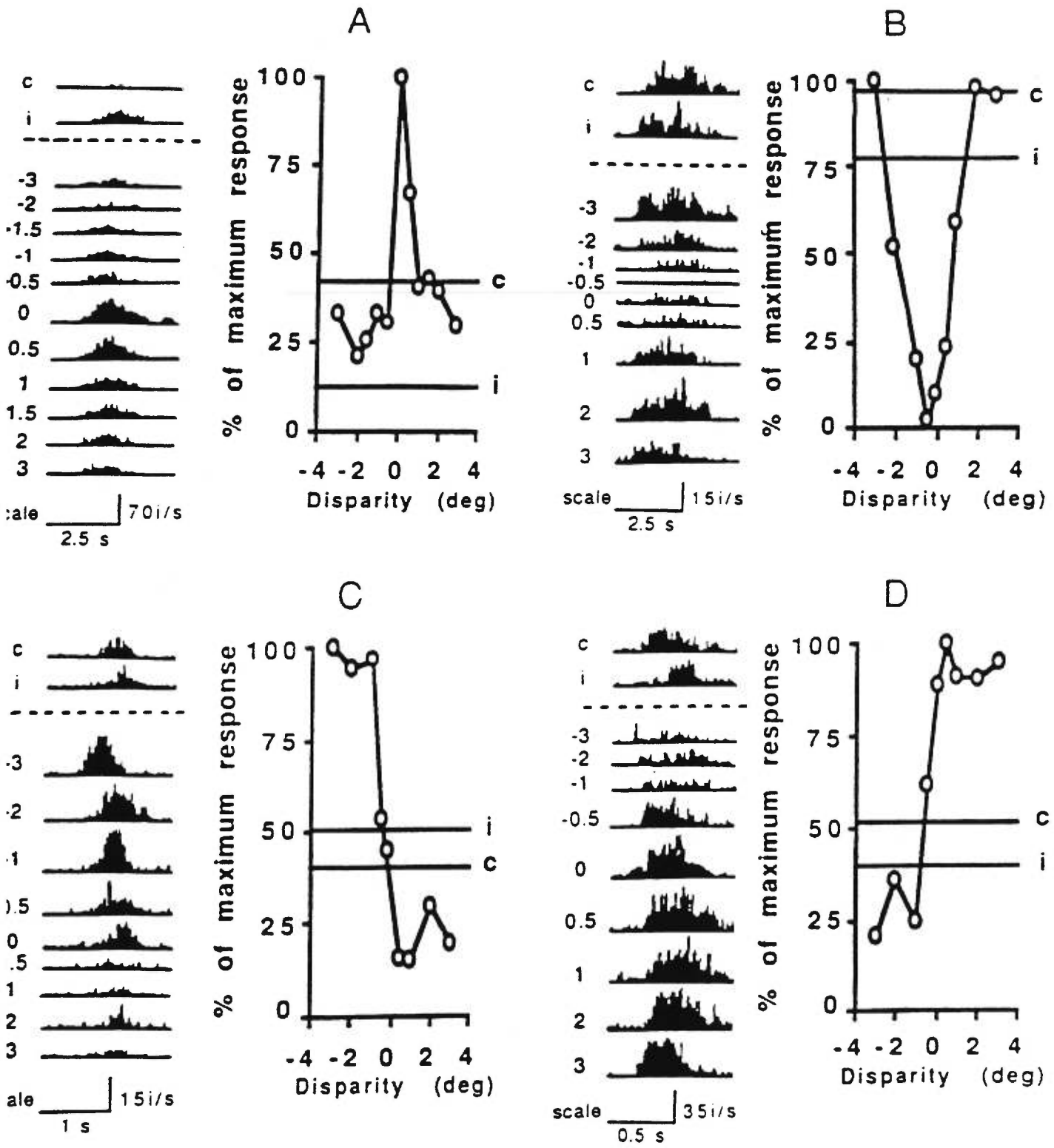

A
B
C
D
c
i
-3
-2
-1.5
-1
-0.5
0
0.5
1
1.5
2
3
70i/s
2.5 s
% of maximum response
100
75
50
25
0
-4 -2 0 2 4
Disparity (deg)
15i/s
1 s
35i/s
0.5 s

FIGURE 3

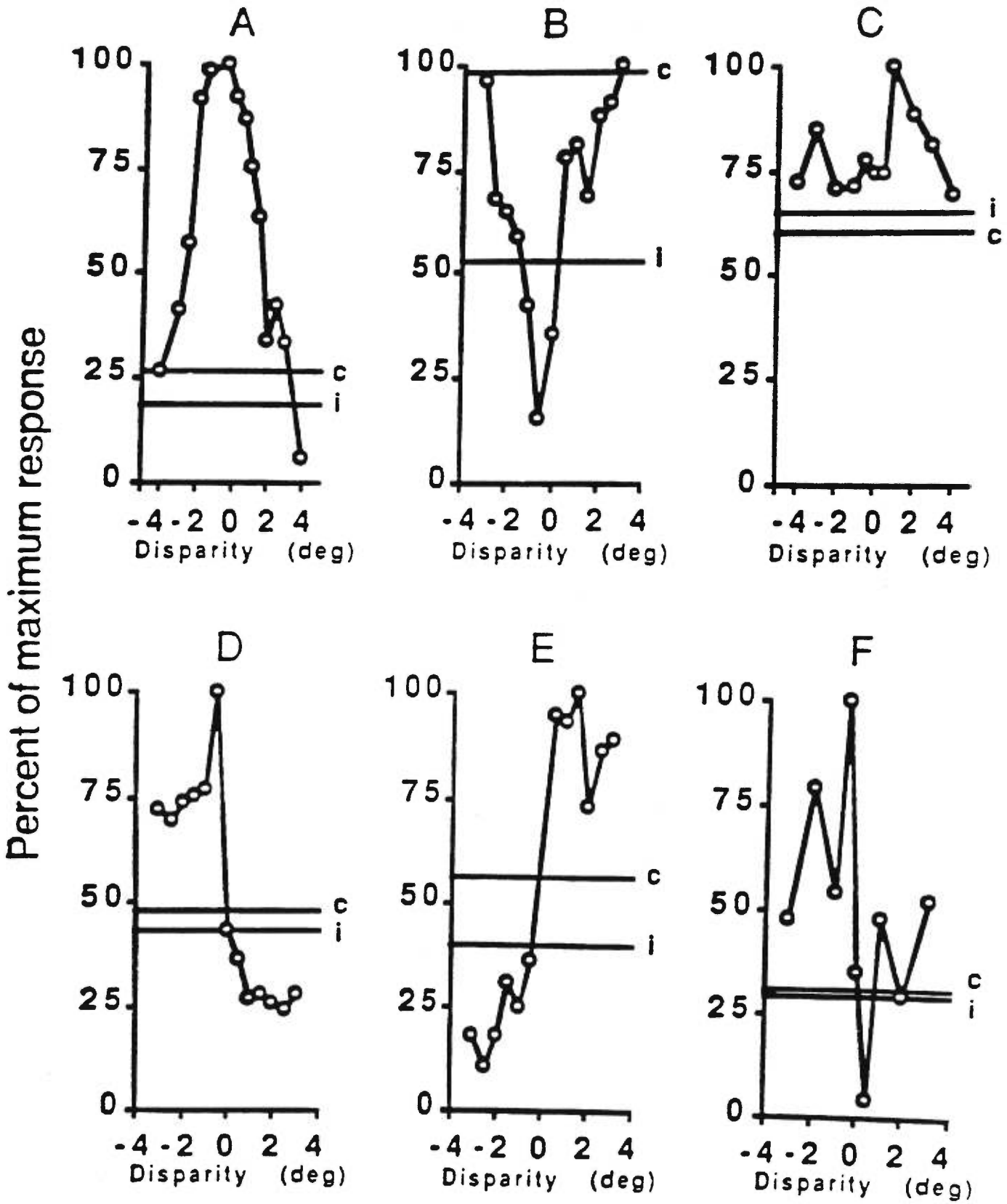

A
B
C
D
E
F
Percent of maximum response
100
75
50
25
0
c
i
-4 -2 0 2 4
Disparity (deg)

FIGURE 4

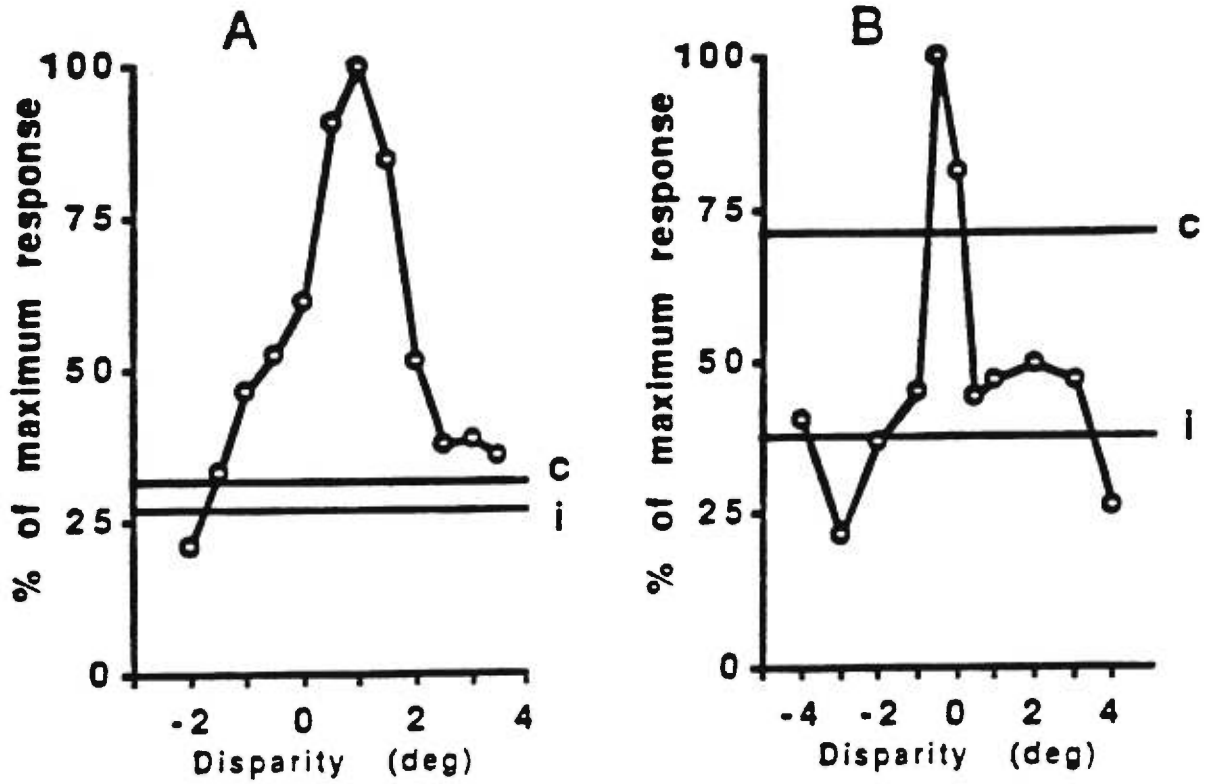

A
100
75
50
25
0
% of maximum response
c
i
-2
0
2
4
Disparity (deg)
B
100
75
50
25
0
% of maximum response
c
i
-4
-2
0
2
4
Disparity (deg)

FIGURE 5

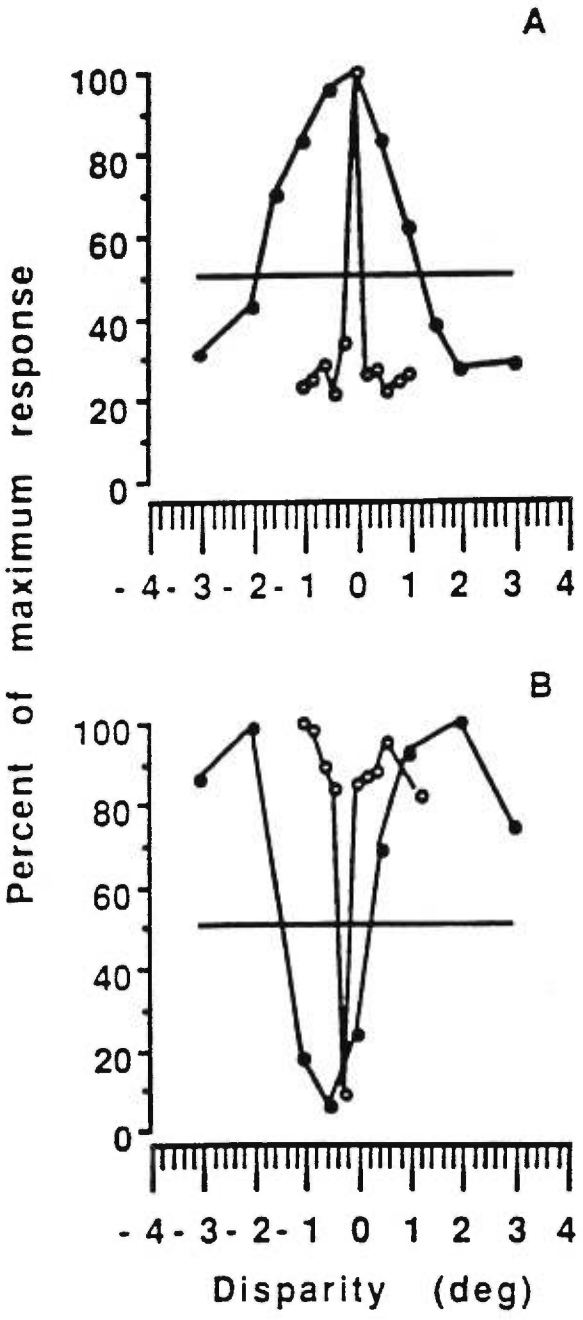

A
B
100
80
60
40
20
0
- 4 - 3 - 2 - 1 0 1 2 3 4
Percent of maximum response
Disparity (deg)

FIGURE 6

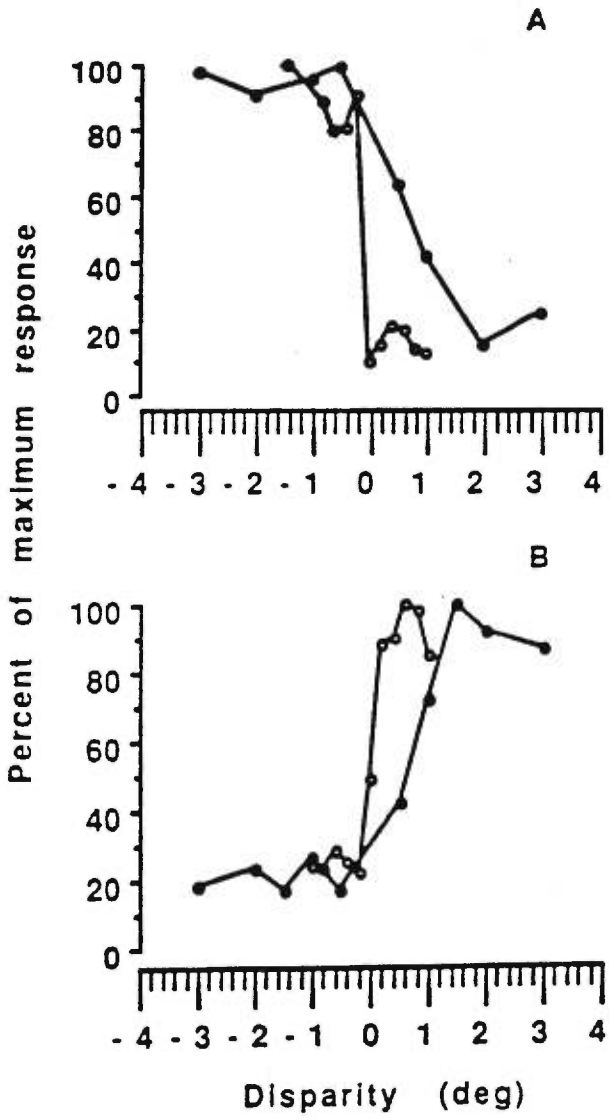
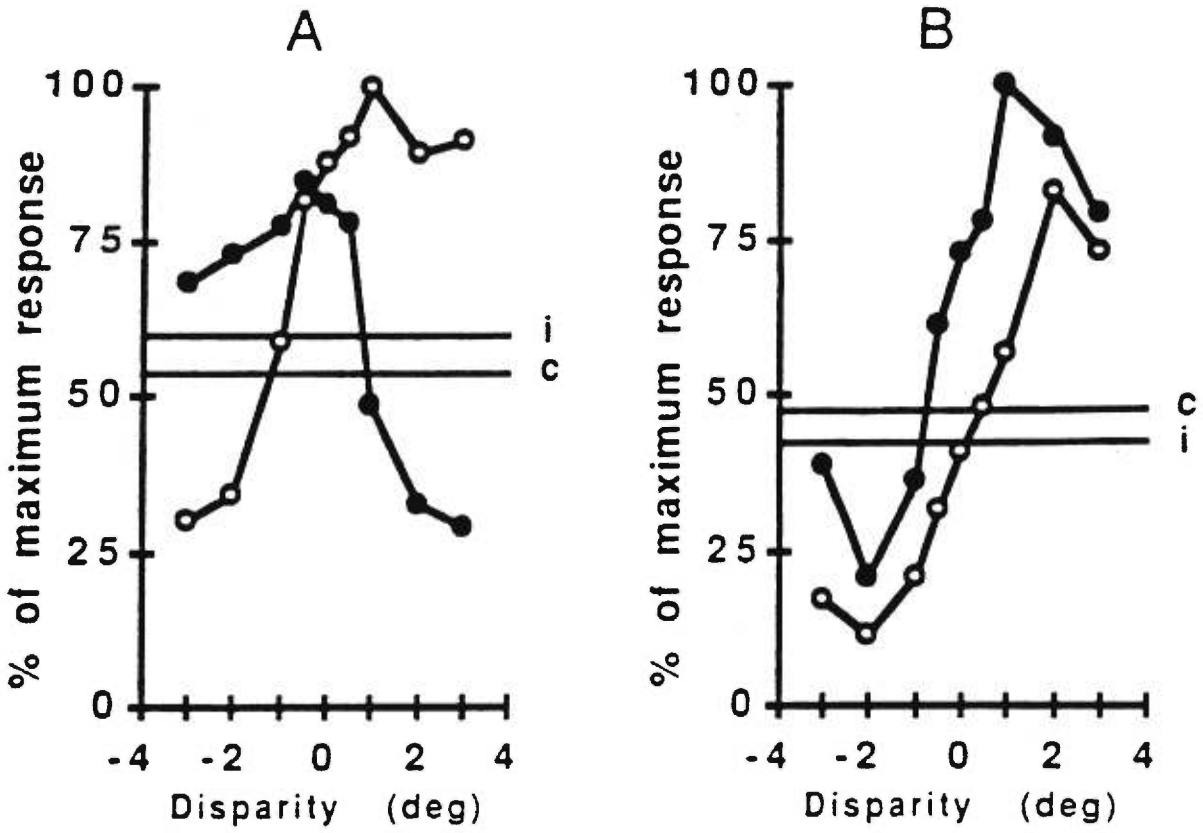

A
B
100
80
60
40
20
0
- 4 - 3 - 2 - 1 0 1 2 3 4
Percent of maximum response
Disparity (deg)

FIGURE 7



CHAPITRE 5

Article 4:

Spatial disparity sensitivity in area PMLS of the Siamese cat

SPATIAL DISPARITY SENSITIVITY IN AREA PMLS OF THE SIAMESE CAT

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Short title: Disparity sensitivity in PMLS of Siamese cats

30 pages, 2 figures

ABSTRACT

Previous studies of the visual system of Siamese cats have shown that binocular cells are scarce in areas 17, 18 and 19, yet significantly more abundant in lateral suprasylvian areas such as PMLS. The present study aims at evaluating the sensitivity to spatial disparity of area PMLS binocular cells in paralyzed and anesthetized Siamese cats. Centrally located receptive fields were mapped, separated using prisms and then stimulated simultaneously using two luminous bars optimally adjusted to the size of the excitatory receptive fields. Delays were introduced in the arrival of the luminous bars in the receptive fields so as to create the desired spatial disparities. Results indicate that approximately half of PMLS units are binocular and that these binocular cells can detect spatial disparity cues. Indeed, although the sample was small, cells of the tuned excitatory, tuned inhibitory, near and far types were identified. These cells might serve as a substrate for coarse stereopsis which has not been tested in Siamese cats but which is present in albino or strabismic humans.

KEY WORDS

Albinism, Binocular interactions, Electrophysiology, Ocular dominance, Stereopsis

INTRODUCTION

Hubel and Wiesel (1959, 1962) have shown that the majority of cells in the primary visual cortex of cats responded to visual stimuli presented to each eye. It was later shown that such binocular cells were also presents in extrastriate cortices (Hubel and Wiesel, 1965, 1969; Spear and Baumann, 1975) and subcortical structures (Sterling and Wickelgren, 1969) of the cat brain. The receptive fields (RFs) of these cells are similar in structure and shape, but are often located at slightly disparate spatial coordinates (Hubel and Wiesel, 1962, 1968; Schiller et al., 1976a, 1976b; Skottun and Freeman, 1984; Maske et al., 1984, 1986).

Barlow et al. (1967) demonstrated that an important proportion of binocular units in the primary visual cortex responded optimally to visual stimuli creating specific retinal disparities. It was proposed that this preference was dependant upon the positional shift between the RFs and that these cells sensitive to spatial disparities formed the substrate of stereoscopic vision. Poggio and Fisher (1977) identified such cells in the primary visual cortex of monkeys and proposed that binocular cells sensitive to spatial disparity could be divided into four specific categories on the basis of their response profile: tuned excitatory, tuned inhibitory, near and far cells.

These four classes of disparity detectors were later identified in several extrastriate areas of the monkey (Poggio and Poggio, 1984; Poggio, 1991) and in area 19 (Pettigrew and Dreher, 1987; Guillemot et al., 1993), area 21a (Wang and Dreher, 1996), the postero-medial lateral suprasylvian (PMLS) area (Bacon et al., submitted) and in the superior colliculus (Bacon et al., 1998) of the cat.

In Siamese cats, it has been demonstrated numerous times that binocular cells were either absent or very scarce in areas 17/18 (Hubel and Wiesel, 1971; Cool and Crawford, 1972; Marzi et al., 1976, 1980; Antonini et al., 1981; Leventhal and Creel, 1985; Toyama et

al., 1991) and 19 (Di Stefano et al., 1984; Toyama et al., 1991). This is believed to depend upon the abnormally massive decussation of ganglion cell (Guillery and Kaas, 1971) which is observed in all albino or hypopigmented mammals, including mice (LaVail et al., 1978), rabbits (Sanderson, 1975), monkeys (Guillery et al., 1984) and humans (Aquaron, 1993).

This lack of binocularity, especially at the primary visual cortex level, is believed to underlie the lack of fine stereopsis observed in Siamese cats (Packwood and Gordon, 1975). Coarse stereopsis, which allows depth discriminations based on the double images produced by large spatial disparities (Bishop and Henry, 1971), has never been tested in Siamese cats. However, studies in humans indicate that albino (Guo et al., 1989; Apkarian and Reits, 1989) or strabismic (Sireteanu, 1982; Kitaoji and Toyama, 1987) individuals which lack fine stereopsis nonetheless possess a degree of coarse stereopsis.

Studies in both cats (Wang and Dreher, 1996; Bacon et al., 1998) and monkeys (Roy et al., 1992; Poggio, 1995) have suggested that coarse stereopsis could be mediated by cells coarsely selective to spatial disparities such as those found in extrastriate cortices and subcortical structures. Thus, coarse stereopsis in albino or hypopigmented mammals, could depend upon binocular cells such as those spared in an important proportion in the lateral suprasylvian region (Marzi et al., 1980; Toyama et al., 1991) and in the superior colliculus (Berman and Cynader, 1972; Antonini et al., 1981) of Siamese cats.

A proportion of cell in area PMLS of the Siamese cat have been shown to respond preferentially to stimuli moving in depth (Toyama et al., 1991). However, the question remains as to whether these units are sensitive to positional depth cues. The present study therefore aims at evaluating the sensitivity to spatial disparity of single units in area PMLS of the Siamese cat and thus determine whether binocular cells in this area could mediate coarse stereopsis in albinism.

MATERIALS AND METHODS

This experiment was carried on a single Siamese cat of the Boston type. This animal was in good health and did not present any malformations or pathologies. As albino or hypopigmented mammals are sometimes strabismic, it is important to specify that this animal was orthoforic. All surgical interventions, manipulations and husbandry were carried out within the guidelines of the Canadian Council on Animal Care (CCAC) and of the National Institute of Health (NIH) concerning the preparation and maintenance of higher animals during visual neuroscience experiments. Moreover, the experimental protocols were approved by the University Animal Care Committee before the beginning of experimentation.

The techniques of animal preparation and care, anesthesia, surgery, optical preparation, recording and histology have been fully described in previous articles (Lepore et al., 1992; Guillemot et al., 1993; Bacon et al.,1998) and will only be briefly summarized herein. The animal was anaesthetized using a face mask with a gaseous solution of nitrous oxide, oxygen (N_2O:O_2, 70:30) and Fluothane (5%). Throughout the surgery, the Fluothane level was kept between 1 and 2%. A small trepanation was performed over area PMLS (A-P: 0-8, L: 10-16) at the coordinates derived from the atlas of Reinoso-Suarez (1961). Unit recordings were performed in the central visual field representation of area PMLS (A-P: 2-7, L: 12-14) according to the coordinates of Reinoso-Suarez (1961) and Palmer et al., 1978), using glass microelectrodes filled with 3M NaCl. Throughout the recording session, the animal was maintained under anesthesia (N_2O:O_2, 70:30, Fluothane, 0.5% of gaseous mixture), the expired CO_2 level was maintained at 4% and ECG was constantly monitored to insure stable heart rate. The absence of reflexes and change in heart rate to stimulation as well as a synchronized slow-wave EEG ensured that the anesthesia level was sufficient. At the end of the surgery and under these conditions, a solution of gallamine triethiodide (Flaxedil: 200

mg) and d-tubocurarine (Tubarine, 15 mg) dissolved in 30 ml lactated ringer solution with dextrose (5%) was infused through the saphenous vein to maintain paralysis of the extra-ocular muscles. EEG and ECG were monitored intermittently yet regularly throughout the recording session to ensure sufficient and stable anesthetic levels.

To prevent eye dehydration and to improve image resolution, a neutral contact lens with a 3 mm artificial pupil was placed on each eye. The optic quality of the eyes was routinely checked during the recording session and the image on the retina was focused on a tangent screen by the use of appropriate dioptric lenses.

The stimulation procedure was adapted from Henry et al. (1967). The optic axis of one of the eyes was deviated using prisms so that the RFs of the two eyes would be located on widely separated coordinates on the tangent screen. This screen was placed 57 cm from the nodal point of the eyes of the animal, such that 1 cm of space corresponded to 1 degree of visual angle. Two projectors, placed behind the screen allowed the independent stimulation of each eye with two light bars equated in luminance and contrast. A dual optic bench system, controlled through a PC computer, ensured the independent and precise definition of the other stimuli parameters: length, width, direction, velocity, position in space, stimulus onset, as well as sweep duration and amplitude.

Upon isolating a binocular cell, the following initial protocol was followed. The RF of each eye was precisely and meticulosely mapped using light and dark bars. During this phase, the best stimulus parameters, defined as the stimulus configuration which produced the greatest cellular response, were determined for both RFs. RF type was determined according to the criteria of Hubel and Wiesel (1959, 1962) and Henry (1977). Each cell was also tested for end-stopping, the principal inclusion criteria for this property was that the cell preferred a bar of optimal length, such that extending the stimulus beyond a determined limit caused a

decrease in response rate. Direction-selectivity was then assessed by sweeping an oriented light bar, from all directions in 15 degrees steps, across the RF. Finally, ocular dominance was established by quantitatively comparing the responses obtained from the independent stimulation of each RF.

The quantitative spatial disparity protocol was then carried out using the dual optic bench system: two light bars having the best estimated dimensions were swept at optimal velocity and direction across each RF. Stimulus velocity varied from 1 deg/s to 20 deg/s, and each sweep covered 20 degrees. Each stimulus condition was presented 10 times and a peri-stimulus time histogram (PSTH) was derived from the responses to these stimulations. Each eye was first stimulated separately to determine the monocular response and the binocular interactions were tested through simultaneous stimulation of both RFs at different spatial disparities.

The two light bars were positioned exactly equidistant from the center of the each RF. When the two bars started moving at the same time, they crossed the centers of the RFs simultaneously, and disparity was null. However, if the initiation of the sweep of one bar was delayed with respect to the other, the two bars would at any particular time be situated at non corresponding points in each RF. The introduction of such a delay hence allowed the creation of crossed and uncrossed disparities. In addition to the null condition, several spatial disparity conditions were tested. All cells were tested using disparities from 3 degrees crossed to 3 degrees uncrossed, in 0.5 or 1 degrees steps. Disparity, therefore, was defined relative to the RFs. These in turn were defined in terms of the coordinate reference points of the eyes. Although spatial disparity cannot be considered in absolute terms, it is nonetheless a very close approximation limited only by the accuracy of the definition of retinal landmarks. It should be added that absolute disparity information is not critical as the present report, like

others of similar nature (LeVay and Voigt, 1988; Freeman and Ohzawa, 1992; Wang and Dreher, 1996) is interested in the general spatial disparity profile and the degree, or range of disparity selectivity.

Cellular action potentials were conventionally amplified, displayed on an oscilloscope, filtered through a time/amplitude discriminator and transferred to an audio monitor. They were also transformed into square pulses and fed to a generic brand PC-486 computer for on line and aposteriori analysis. All conditions, each tested a total of 10 times, were interleaved with each other in a pseudo-random fashion. The time interval between each sweep was 10-20 seconds to avoid habituation. For each condition, a PSTH was built from the cellular responses. These PSTHs were divided into 500 bins, each having a binwidth of 1-40 ms, depending upon the duration of the sweep. For each condition, a second PSTH, of equal duration, was built prior to each sweep when no stimulation is present to establish a baseline level. Each point on the response profiles of a cell was obtained in the following manner. For each condition, the average number of spikes elicited without stimulation was extracted from the baseline level PSTH and the average number of spikes elicited during the stimulation was extracted from the other PSTH. The former average number of spikes was then subtracted from the latter.

Eye stability control was insured by the pre- and post-recording quantitative mapping of the RFs. Any measurable displacement in the location of either field resulted in the data being discarded. The stability of the eyes throughout the recording session was also monitored, through the frequent mapping of the optic disks and major blood vessels. Fairly stable eye positions were maintained throughout the recording session, and failure to maintain stability also resulted in the data being discarded.

Small electrolytic lesions were performed so as to allow the reconstruction of the

electrode tracts and the identification of the recording sites. At the end of the experiment, the brain was removed and the hemisphere in which recordings were performed was sliced (40 μm) along the coronal plane. Every second slice was kept and stained using the cresyl violet method and only cells clearly located in area PMLS were included in the results. The other hemisphere was sliced along the sagittal plane and also stained with cresyl violet. This was done to verify the abnormal lamination of the dorsal lateral geniculate nucleus which is typical of albino or hypopigmented mammals, and therefore provide an additional control of breed purity.

RESULTS

Recordings were first performed in areas 17 and 18 to verify the paucity of binocular cells which in itself represents a control of breed purity. All 30 cells recorded in the central visual field representation of areas 17 and 18 could only be driven through the contralateral eye.

A total of 14 cells were isolated from background activity in area PMLS of the Siamese cat. Exactly half (7/14) of the sample could only be driven through the contralateral eye while the other half (7/14) were binocular. It should be noted that a cell was classified as binocular only if a response could be evoked from the monocular stimulation of each eye. Thus, no attempts were made to identify or test pseudomonocular cells, as mapping the RF of the unresponsive eye is arduous and does not allow the degree of precision required for spatial disparity testing. Thus, only binocular cells were submitted to the spatial disparity protocol described above.

As binocular depth perception is believed to be most precisely perceived in the center of the visual field, only neurons whose RF center of the dominant eye was located less than 10 degrees of eccentricity from the vertical meridian and located between +5 and -10 degrees of elevation were tested. As expected in an area associated with the detection of moving targets like PMLS, stationary or flashing targets were inefficient stimuli while highly contrasted dark or light bars swept across the RFs elicited the best response. Those RFs were rather small as compared to those located in periphery, ranging from 15 to 33 cm_2 in size and from 2.5 to 6.3 degrees in width (mean=3.8), on the axis parallel to the preferred direction of stimulation. The RF sizes observed herein are not significantly different from those mapped in the central visual field representation of area PMLS of both the Siamese (Toyama et al., 1991) and normal (Von Grünau et al., 1987; Rauschecker et al., 1987; Bacon et al., in press)

cats.

All RFs were of the complex type, and for almost half of the binocular cells (3/7), elongating the stimuli beyond the boundaries of the RF caused a clear decrease in firing rate. Previous investigations in normal domestic cats also reported such inhibitory surround regions in 30 - 40% of PMLS cells (Spear and Baumann, 1975; Camarda and Rizzolatti, 1976; Bacon et al., submitted).

More than half of the binocular cells (4/7) clearly preferred stimulation from a particular direction. Two other units were equally responsive to two opposite directions and thus responded to stimuli moving along a particular axis and only one unit was not direction-selective. Previous studies in Siamese (Toyama et al., 1991) and in normal (Hubel and Wiesel, 1969; Spear and Baumann, 1975; Turlejski, 1975; Camarda and Rizzolatti, 1976; Blakemore and Zumbroich, 1987; Rauschecker et al., 1987; Von Grünau et al., 1987; Bacon et al., in press) cats agree that the majority of PMLS neurons are direction-selective.

As for ocular dominance, half of the cells responded only to contralateral stimulation (7/14), while three cells responded equally well to stimulation of each eye and the remaining four cells were binocular yet preferred stimulation through the contralateral eye. This distribution is similar to what was observed by Toyama et al. (1991), although these authors did observe cells that preferred stimulation through the ipsilateral eye.

Binocular Interactions and spatial disparity sensitivity

The small size of the sample has the advantage of allowing a description of all the binocular units recorded. Figure 1shows the PSTHs of the cell presenting the strongest binocular interaction to a specific spatial disparity in the middle range (0.5 degrees). Each histogram represents the average response of the cell to 10 stimulus presentations. Each bin on the histogram was 4 ms in duration and the average amplitude of discharge, in impulses

per seconds, is indicated by the calibration scale under the histograms. It can be seen from the spatial disparity response profile of this unit that monocular responses were both robust and almost equal. Binocular stimulation at the appropriate spatial disparity, however, produced a response rate substantially greater than the sum of the monocular responses, a phenomenon known as binocular facilitation (Berman et al., 1975). Such facilitation was also observed, to a lesser degree, for a spatial disparity of 1 degree.

Insert Figure 1 approx. here

The cell in Figure 2A is of the same general shape as the cell in Figure 1 but differs from the latter in two important ways. First, the peak response, which is obtained in the crossed (-1 degree) rather than the uncrossed range, is not superior to the sum of the monocular responses, but still is superior to the monocular response of the dominant eye. This type of binocular interaction is known as summation (Berman et al., 1975). Second, the profile is broader in shape than the cell in Figure 1, which underlies a poorer selectivity as it will be detailed in a latter section. It is noticeable that the cells in Figure 1 and 2A are of a shape similar to the tuned excitatory cells described first in the monkey (Poggio and Fisher, 1977) and also observed at various levels of visual processing in the domestic cat brain (LeVay and Voigt, 1988; Guillemot et al., 1993; Wang et Dreher, 1996; Bacon et al., 1998) including area PMLS (Bacon et al., submitted).

Insert Figure 2 approx. here

A third type of binocular interaction, namely occlusion (Berman et al., 1975), was

observed in several units. Occlusion describes a binocular response which is inferior to the lesser of the monocular responses. In the cell in Figure 1, occlusion occurred at inappropriate disparities in the crossed and uncrossed range. In the cell in Figure 2B, however, extreme occlusion occurred at null disparity while robust binocular responses were observed in the crossed and uncrossed range. Simultaneous stimulation of the RFs therefore seemed to inhibit the response of the cell, while slightly out of sync stimulation allowed a robust response. The spatial disparity response profile of this unit closely resembles the tuned inhibitory cells observed at various levels of visual processing in the domestic cat brain (LeVay and Voigt, 1988; Guillemot et al., 1993; Bacon et al., 1998; Bacon et al., submitted).

Whereas the units in Figure 1, 2A and 2B showed a peak response (inhibitory or excitatory), the units in Figure 2C and 2D showed a completely different response profile. The cell shown in Figure 2C showed binocular summation in response to disparities in the crossed range and occlusion in response to disparities in the uncrossed range. The cell in Figure 2D shows the exact reverse pattern of response. These profiles are similar to that of near and far cells, which are known to encode disparities in the crossed and uncrossed range respectively and thus are presumed to play a role in the analysis of stimuli located in front of and behind the fixation plane.

As for the other two binocular units, one presented complex, unclassifiable binocular interactions while the other did not vary its response rate across disparities and was considered insensitive. Thus, 5 cells out of 7 (71.5%) were sensitive to spatial disparity, which is similar to what was obtained, under similar stimulation and recording procedure, in area PMLS of the normal cat (80/110 or 72.7%; Bacon et al., submitted)

Selectivity to spatial disparities

The tuning-curve width at half-height of the units showing an excitatory or inhibitory

response peak is an indication of the selectivity of those cells to spatial disparities. The tuning-curve width of the 2 cells showing an excitatory peak were 1.5 and 2.5 degrees while this measure was 3.4 degrees in the single cell with an inhibitory peak.

The slopes of the profiles, measured at 50% of the maximum response, of the cells responding only to crossed or only to uncrossed disparities are also indications of selectivity. The mean slope of the cell preferring crossed disparity was -65.7 while the slope of the cell preferring uncrossed disparities was 30.4.

The small sample size precludes against population statistics and broad overgeneralizations. Nonetheless, it appears reasonable to state that the range of disparities to which these cells are responsive is, like it is in area PMLS of the normal cat (Bacon et al., submitted), similar to the disparities needed for coarse stereoscopic discriminations (Blakemore, 1970; Bishop and Henry, 1971; Roy et al., 1992).

DISCUSSION

The present study demonstrates that binocular cells in area PMLS of the Siamese cats can code for spatial disparity cues. Indeed, although sample size was small, disparity detectors of the four classic subtypes (Poggio and Fisher, 1977; Poggio and Poggio, 1984) have been identified in this area.

Binocularity and disparity sensitivity in area PMLS of the Siamese cat appears to heavily depend upon callosal projections. Indeed, sectioning the corpus callosum of Siamese cats is known to abolish binocularity in the suprasylvian region (Marzi et al., 1980; Zeki and Fries, 1980). Several studies have demonstrated the importance of the corpus callosum in a variety of visual functions that draw upon binocular integration, including interhemispheric transfer (Marzi et al., 1976), fusion of the hemifields (Gross et al., 1977) and coarse midline stereopsis (Mitchell and Blakemore, 1970). It has also been shown in split-chiams preparations that the callosal route can support disparity sensitivity in a non-negligible proportion od area 17/18 (Lepore et al., 1992) and 19 (Guillemot et al., 1993) units.

Several studies in cats using deprivation rearing paradigms, surgically induced strabismus, cortical lesions or genetic mutations (Berlucchi and Rizzolatti, 1967; Berlucchi, 1972; Innocenti and Frost, 1979; Innocenti, 1981; Innocenti et al., 1985; Berlucchi et al., 1986) have shown that these manipulations affect the distribution and function of callosal neurons. Similarly, a more widespread distribution of callosal units has been described in Siamese cats (Shatz, 1977; Berlucchi et al., 1986). Thus, it can be proposed that modifications in corpus callosum maturation partially compensates for the abnormal albino ganglion decussation by a reshaping and redistributing of its connections so as to allow the synthesis of binocularly disparate information and thus preserve, like in albino humans (Guo et al., 1989; Apkarian and Reits, 1989) a degree of stereopsis. Presumably, the larger RFs and

the dense callosal interconnections of PMLS allows for greater compensation via this reorganization than in areas 17, 18 and 19.

Thus, area PMLS appears to be the principal site of binocular convergence in Siamese cats, and therefore an important processing center for binocular functions. These binocular functions have unfortunately not been thoroughly examined. The only study on the subject (Packwood and Gordon, 1975) reports lack of fine stereopsis in Siamese cats, which is consistent with the belief that this function depends upon the finely tuned (LeVay and Voigt, 1988; Lepore et al., 1992) disparity detectors of area 17 and 18. Indeed, subtotal ablation of areas 17 and 18 in normal cats is known to abolish fine stereoscopic discriminations (Ptito et al., 1992) in cats. This is also consistent with the selectivity measurements observed herein, as such coarsely selective units could not generate fine stereoscopic perceptions.

Neither binocular fusion nor coarse stereopsis have been assessed in Siamese cats. However, studies in humans have demonstrated that albino (Guo et al., 1989; Apkarian and Reits, 1989) and strabismic (Sireteanu, 1982; Kitaoji and Toyama, 1987) individuals possessed a degree of both fusion and coarse stereopsis. In that sense, binocular cells in area PMLS could allow a degree of binocular fusion and those coarsely sensitive to spatial disparity could code large disparities and allow a measure of coarse stereopsis. Indeed, it is known that large disparities such as those encoded by the units of the present study can be used to determine whether a stimuli lies in front or behind the fixation plane. Hence, Packwood and Gordon (1975) might have concluded to complete lack of stereopsis in Siamese cats because they presented disparities considerably too small (10' to 20') to be detected and coded by these coarsely selective PMLS units.

Area PMLS has always been linked to the perception of motion. Both in normal and Siamese cats, an important proportion of units in this area can code not only for motion along

the fronto-parallel axis, but also for motion in depth (Toyama and Kozasa, 1982; Toyama et al., 1985, 1986a, 1986b; Toyama et al., 1991). Thus, area PMLS appears to be involved in the detection and analysis of objects moving away or toward the organism. The detection of incoming or outgoing stimuli generate foveation and the focusing of the eyes toward the target. This focusing is performed through the mechanisms of accommodation and vergence.

Electrical stimulation of extrastriate cortices can affect accommodation and vergence eye movements (Jampel, 1960). More recently studies in normal cats have shown that area PMLS is important for these ocular functions. Indeed, pupillary constriction and lens accommodation both have been evoked by microstimulation of area PMLS (Bando et al., 1984, 1989, 1996; Bando, 1985, 1987; Yoshizawa et al., 1991; Sawa et al., 1992) and single neurons discharging prior to pupillary constriction and lens accommodation were also found in this area (Bando et al., 1984; Bando et al., 1988). Moreover, it has been shown that microstimulation of PMLS could result in ocular convergence (Toda et al., 1991), that neurons in this region also discharged in relation to ocular convergence (Takagi et al., 1992, 1993) and that the amplitude and peak velocities of convergent eye movements were reduced by a lesion of area PMLS (Hara et al., 1992).

It has been shown that lens accommodation and vergence eye movements are triggered by variations in visual cues engendered by stimuli moving along the fronto-perpendicular axis, such as target size and especially binocular disparity (Westheimer and Mitchell, 1969; Erkelens and Regan, 1986). Thus, neurons selective to spatial disparity in area PMLS of the Siamese cat could provide the necessary cues to generate lens accommodation and vergence.

Studies in normal cats (Bando et al., 1996; Bacon et al., submitted) have proposed that the elicitation and modulation of lens accommodation and vergence by area PMLS might

be part of a larger pathway including the superior colliculus and the pretectum, which both receive abundant projections from area PMLS. Indeed, it was demonstrated that antidromic activation of lens accommodation related PMLS neurons could be evoked by stimulation of the rostral superior colliculus or pretectum (Bando et al., 1984) and that microstimulation of the rostral part of the superior colliculus could also evoke lens accommodation (Sawa and Ohtsuka, 1994).

Thus, it can be proposed that PMLS neurons coarsely selective to spatial disparity provide depth information to PMLS neurons involved in vergence and that the latter project, via the superior colliculus and the pretectum, toward the structures of the brainstem involved in vergence or accommodation, thus allowing continuous adjustments in the fixation of the outgoing or incoming stimulus.

ACKNOWLEDGMENTS

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ABBREVIATIONS

PMLS	Posteromedial lateral suprasylvian
PSTH	Peri-stimulus time histogram
RF	Receptive field

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FIGURE LEGENDS

Figure 1. A cell showing binocular facilitation in area PMLS of the Siamese cat. Histograms i and c show the cellular response to monocular (ipsi and contralateral) stimulation. The other histograms show the responses to the various binocular spatial disparities presented. The summed responses derived from each histogram are plotted against stimulus disparity to generate the response profile. The excitatory response peak around null disparity (0.5 degrees in the uncrossed range) is similar to that observed in tuned excitatory cells as described by Poggio and Fisher (1977)

Figure 2. Four cells showing different spatial disparity sensitivity profiles in area PMLS of the Siamese cat. The cell in **A** also shows an excitatory peak like the cell in Figure l, but shows binocular summation, not facilitation. This cell also exhibits a broader tuning-curve width at half-height, which is interpreted as coarser selectivity. The cell in **B** shows severe occlusion around null disparity as simultaneous stimulation of the RFs appears to inhibit the response of the cell. The disparity sensitivity profile of this cell is similar to that of tuned inhibitory cells as described by Poggio and Fisher (1977). The unit in **C** shows summation in response to crossed disparities and occlusion in response to uncrossed disparities, while the cell in **D** shows the reverse pattern of response. These profiles are very similar to those of near and far cells respectively, as described by Poggio and Fisher (1977). Thus, the four types of disparity detectors first described in the monkey (Poggio and Fisher, 1977) and later identified in several visual areas of the normal cat (LeVay and Voigt, 1988; Lepore et al., 1992; Guillemot et al., 1993; Wang and Dreher, 1996; Bacon et al., 1998) including area PMLS (Bacon et al., in press) also seem to be present in area PMLS of the Siamese cat.

FIGURE 1

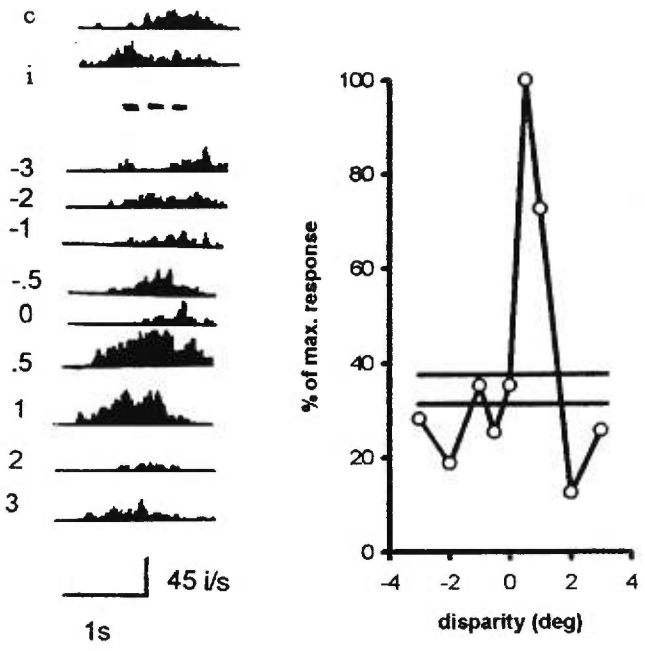
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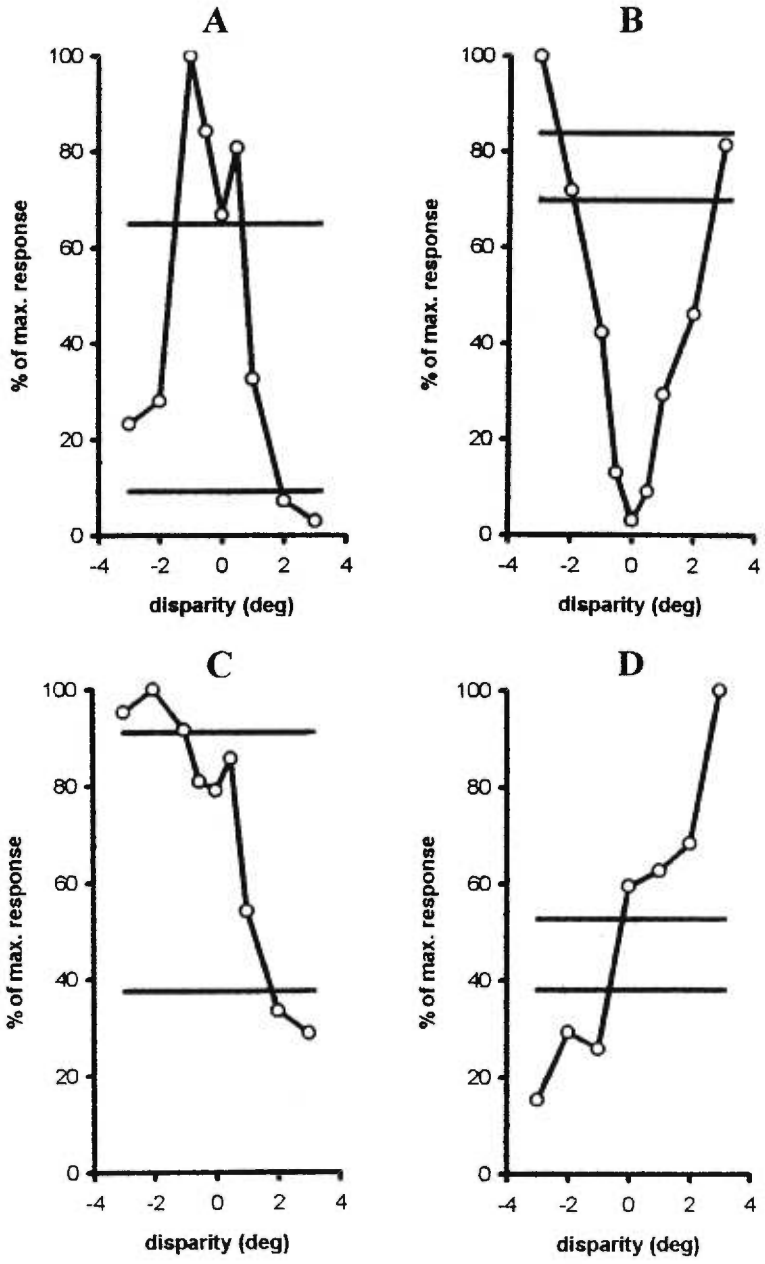
FIGURE 2



CHAPITRE 6

Article 5:

Binocular interactions and spatial disparity sensitivity in the superior colliculus of the Siamese cat

Experimental Brain Research 124, 181-192

BINOCULAR INTERACTIONS AND SPATIAL DISPARITY SENSITIVITY IN THE SUPERIOR COLLICULUS OF THE SIAMESE CAT

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ABSTRACT

In Siamese cats, a genetically determined massive misrouting of retinal ganglion cells toward the contralateral hemisphere, as well as an accompanying strabismus, is believed to underlie the extreme paucity of binocular cells in the primary visual cortex. However, binocular cells have been shown to be present in more important numbers at the collicular level. The present study aims at investigating binocular interactions and sensitivity to spatial disparity in the superior colliculus of the Siamese cat. The activity of single units was recorded in the superficial layers of paralyzed and anesthetized Siamese cats. Although most collicular cells were monocularly driven, a significant proportion could be driven through both eyes (34/216 or 16%). Upon isolation of a binocular cell, the receptive fields were separated, then stimulated simultaneously with two light bars. A temporal delay was introduced between the arrival of the bars in the receptive fields to generate spatial disparities (-3 to +3 degrees, in 0.5 or 1 degree steps). Results showed that some binocular cells presented disparity tuning profiles similar to the tuned excitatory (12/34), tuned inhibitory (2/34), near (2/34) and far (3/34) cells found at various cortical levels in the normal cat. These interactions might allow for coarse binocular fusion as well as play a role in the initiation of vergence and the fixation of the eyes upon the appropriate plane of vision.

KEY WORDS

Binocular vision, electrophysiology, ocular dominance, stereopsis, strabismus.

INTRODUCTION

Organisms with frontally placed eyes can use the small spatial disparities between the retinal images projected by three-dimensional stimuli to precisely evaluate their depth and to generate the tridimensional perception of the visual scene. Disorders in binocular functions, such as albinism and strabismus, are known to interfere with this process (Sclar et al., 1986; Schor, 1991). However, it has been demonstrated that humans with albinism (Guo et al., 1989; Apkarian and Reits, 1989) or strabismus (Sireteanu, 1982; Kitaoji and Toyama, 1987) can retain a measure of stereopsis.

The first prerequisite for stereopsis is a degree of overlap between the visual fields of the two eyes, it has however been demonstrated in birds that binocular overlap is not sufficient in itself for stereoscopic vision (Pettigrew, 1991). Indeed, vivid tridimensional perception also requires a high degree of visual acuity (Pettigrew, 1991) and, most importantly, a special organization of receptive fields (RFs) which allows for the treatment of spatial disparity cues (Barlow et al., 1967; Poggio and Poggio, 1984; Anzai et al., 1997; Ohzawa et al., 1997). These cues can only be encoded by binocular cells, which were first identified in the primary visual cortex of the cat (Hubel and Wiesel, 1959, 1962). Such cells were later found to be present in all visual areas (Hubel and Wiesel, 1965, 1969; Spear and Baumann, 1975; Wimborne and Henry, 1992) as well as in the superior colliculus (Sterling and Wickelgren, 1969; Berman and Cynader, 1972) of the cat.

The two RFs of such binocular cells are normally similar in structure and shape, but are often located at slightly disparate spatial, and therefore retinal, locations (Hubel and Wiesel, 1962, 1968; Schiller et al., 1976a, 1976b; Movshon et al., 1978; Maske et al., 1984, 1986). Most of these cells respond more strongly when a stimulus falls upon these disparate retinal locations (Barlow et al., 1967; Pettigrew et al., 1968; Bishop and Pettigrew, 1986). It has however been proposed that spatial disparities could also be coded through differences in the relative phase of contrast gratings (Ohzawa and Freeman, 1986a, 1986b; Freeman and Ohzawa, 1990; Ohzawa et al., 1990; De

Angelis et al., 1991; Hammond, 1991) and that this coding is more dependent upon the internal organization of the RFs than upon their spatial positions (Anzai et al., 1997; Ohzawa et al., 1997).

Binocular cells coding for spatial disparity cues have been identified in several species such as the sheep (Clarke et al., 1976), owl (Pettigrew and Konishi, 1976; Pettigrew, 1979), opossum (Dias et al., 1991), monkey (Poggio and Poggio, 1984), and cat, where they were first identified (Barlow et al., 1967; Nikara et al., 1968; Pettigrew et al., 1968). In the latter species, it has been demonstrated that cells in areas 17-18 (Ferster, 1981; LeVay and Voigt, 1988; Lepore et al., 1992), 19 (Pettigrew and Dreher, 1987; Guillemot et al., 1993), 21a (Wang and Dreher, 1996) and in the superior colliculus (Bacon et al., 1998) respond differentially to specific spatial disparities.

Most reports agree that binocular cells are conspicuously scarce in the primary visual cortex of the Boston Siamese cat, as most cells can only be driven through the contralateral eye (Hubel et Wiesel, 1971; Cool and Crawford, 1972; Marzi et al., 1976, 1980; Marzi, 1980; Toyama et al., 1991). Area 19 was also shown to be almost devoid of binocular units (Di Stefano et al., 1984; Toyama et al., 1991). This is believed to be the result of the genetically determined misrouting of ganglion cells in the temporal portion of the retinae to the contralateral lateral geniculate nucleus and of the occasional concomitant strabismus (Guillery, 1969; Guillery and Kaas, 1971; Kalil et al., 1971; Weber et al., 1978; Cooper and Pettigrew, 1979; Shatz, 1979). Both the abnormal decussation and the strabismus are caused by the fact that Siamese cats are homozygous for an allele at the albino locus (Creel, 1971; Guillery and Kaas, 1971; Kalil et al., 1971). Albinos or hypopigmented specimens of other species, including mice (LeVail et al., 1978), rabbits (Sanderson, 1975), monkeys (Guillery et al., 1984) and humans (Apkarian, 1991) also show these peculiarities of the visual system.

Notwithstanding these visual anomalies, an important proportion of binocular cells are spared in the lateral suprasylvian area, or Clare-Bishop area (Marzi et al., 1980; Toyama et al., 1991). Some of these units have been shown to prefer stimuli moving in depth (Toyama et al., 1991). The ipsilateral signal to this area is believed to be conveyed via the corpus callosum since transection of

this commissure almost abolished the response to stimulation of the ipsilateral eye (Marzi et al., 1980).

Binocularity is also spared in the superior colliculus of Siamese cats, but the actual proportion of spared binocular units is not clearly determined. Berman and Cynader (1972) demonstrated that in Boston Siamese cats approximately 15% of collicular cells were binocular whereas Antonini et al. (1981) advanced that more than 87% could be driven from both eyes. The fact remains nonetheless that collicular cells of Siamese cats do show some degree of binocularity. From this, coupled with the fact that human subjects with albinism (Guo et al., 1989; Apkarian and Reits, 1989) or strabismus (Sireteanu, 1982; Kitaoji and Toyama, 1987) can retain a measure of stereopsis, it could follow that some of the binocular cells at the collicular level of these animals are sensitive to spatial disparity.

The main objective of the present study, therefore, was to evaluate whether the simultaneous stimulation of the eyes at various spatial disparities produces binocular interactions in collicular cells of the Siamese cat, and especially whether these cells show disparity sensitivity profiles similar to those first identified in the primary visual cortex of the monkey (Poggio and Fisher, 1977). If collicular cells show selectivity to specific spatial disparities, it is expected that this selectivity will be rather coarse, as demonstrated in the superficial layers of the normal cat (Bacon et al., 1998). These cells cannot therefore play a role in fine stereopsis, which is known to be lacking in Siamese cats (Packwood and Gordon, 1975). However, Packwood and Gordon (1975) might have concluded to their lack of stereopsis because the disparities presented in their study were very small (10' to 20'). It was indeed shown that residual stereopsis in albinos or strabismic humans rests mainly upon large disparities (Kitaoji and Toyama, 1987; Apkarian and Reits, 1989; Guo et al., 1989). Cells sensitive to large spatial disparity could code for coarse stereopsis (Bishop and Henry, 1971). For example, it is known that large disparities can be used to determine whether a stimulus lies in front of or behind the fixation plane (Bishop and Henry, 1971; Roy et al., 1992).

MATERIALS AND METHODS

Animals

The experiment was carried out on 3 adult Siamese cats, weighing between 2 to 4 kg who came from a Université de Montréal approved supplier. They were all in good health and had no obvious malformations or pathologies. It should be noted that cats 1 and 2 exhibited a convergent strabismus while cat 3 was slightly divergent which is not uncommon in Siamese cats. The angular separation between the optic disks, which gives an indication of the degree of strabismus, was 15 degrees in cat 1, 24 degrees for cat 2 and 34 degrees for cat 3. All surgical interventions, manipulations and husbandry were carried out within the guidelines proposed by the Canadian Council on Animal Care. Moreover, the guidelines of the American Physiological Society and the Society for Neuroscience regarding the care and use of animals as well as the guidelines of the National Institute of Health concerning the preparation and maintenance of higher animals during visual neuroscience experiments were followed. All experimental protocols were approved by the University Animal Care Committee before the beginning of the experiment.

Surgery

On the day prior to the recording session, 2 ml/kg of dexamethasone sodium phosphate (5 mg/ml) was injected i.m. to limit inflammation during the surgical intervention. On the day of recording, the cat was injected with atropine (Atro-sol: 0.2 mg/kg) to reduce bronchial secretions and induce mydriasis, after which anesthesia was induced using a face mask with a gaseous solution of nitrous oxide, oxygen (N_2O : O_2, 70:30) and Fluothane (5% of total gaseous mixture). Once anesthetized, the cat was intubated and connected to a respiratory pump. Throughout the surgery, fluothane was kept between 1% and 2% of the total gaseous mixture so as to maintain stable levels of anesthesia. The animal was then placed in the stereotaxic apparatus (David Kopf). This apparatus was modified to insure that the eyes were not touched or pressed upon and to avoid obstruction of the visual field. The saphenous vein was cannulated and, throughout the surgery, the animal was administered 5% dextrose in lactated ringer at the rate of 5.6 ml/h to maintain blood

pressure and hydration. The scalp was shaved and the cranial muscles and pressure points were infiltrated with a local anesthetic (Xylocaine 2%), a procedure routinely repeated throughout the recording session. A small trepanation (5 mm diameter) was performed over the superior colliculus (A-P: 4-0, L: 1-5) at the coordinates derived from the atlas of Reinoso-Suarez (1961). A small incision was made in the exposed dura mater to allow the vertical penetration of the microelectrode. The entire trepanned area was then covered and sealed with 4% agar in physiological saline.

At the end of the surgery, the fluothane level was progressively reduced (0.5% every 15 minutes), stabilized at 0.5% and kept at that level for the duration of the recording session (30 - 33 h). Stable heart rate, constantly monitored by ECG, and the absence of reflexes insured that the anesthesia level was sufficient. From that point on, a solution of 15 ml of gallamine triethiodide (Flaxedil: 200 mg) and d-tubocurarine (Tubarine: 15 mg) dissolved in 30 ml lactated ringer solution with dextrose (5%) was continuously infused through the saphenous vein at the rate of 5.6 ml/h to induce and maintain paralysis of extra-ocular muscles. Respiratory rate and stroke volume were adjusted so as to maintain a constant level of expired CO_2 (~4%), which served as an indirect indication of stable blood pressure. Body temperature was also kept constant (37.5 degrees C) with the help of a heating water pad thermostatically controlled with a rectal thermoprobe. EEG, monitored intermittently yet regularly, showed slow-wave activity throughout the recording session. Heart rate was also constantly monitored throughout the recording session.

Optical preparation

Pupils were dilated by an i.m. injection of atropine sulfate 1% (Atro-Sol, 0.2 mg/kg) and the nictitating membranes were retracted with topical applications of phenylephrine hydrochloride (Neo-synephrine: 0.1%). To prevent dehydration and to improve image resolution, a zero-power plastic contact lens with a 3 mm artificial pupil was placed on each eye. In order to determine the relative position of the areae centrales, retinal landmarks such as the optic disks and some major blood vessels were projected on a tangent screen situated 57 cm in front of the animal (Fernald and Chase 1971). The areae centrales were considered to be situated 16 degrees medially and 7.5 degrees below the iso-elevation line of the center of each optic disk (Bishop et al., 1962). The

angular separation between the center of the optic disks were 38 degrees, 34 degrees and 16 degrees for cats number 1, 2 and 3 respectively. Retinoscopy was used to determine the appropriate value of dioptric lenses necessary to focus the eyes on the tangent screen located 57 cm in front of the eyes.

Recording and stimulation procedure

Recording was carried out with glass microelectrodes filled with a 3M NaCl solution and having an impedance measured at 1000 Hz of 3 to 6 Mohms. Recordings were first performed in areas 17/18 of each cat to verify the cortical monocularity typical of Siamese cats. The microelectrode was then stereotaxically lowered into the anterior part of the superior colliculus (A-P: 3 - 4, L: 2 - 3). The target units were those of the superficial layers having RFs in the center of the visual field, according to published topographical maps (Feldon et al. 1970; Berman and Cynader 1972; Lane et al. 1974). Cellular action potentials were conventionally amplified, displayed on an oscilloscope and transferred to an audio monitor. They were also filtered using time/amplitude criteria and transformed into square pulses and fed to a generic brand PC-486 computer for on line and *a posteriori* analysis.

The stimulation procedure was adapted from Henry et al. (1967). The optic axis of one of the eyes was deviated using prisms so that the RFs of the two eyes would be located on widely separated coordinates on the tangent screen. The latter was placed at 57 cm from the animal, such that 1 cm of space corresponded to 1 degree of visual angle. Two projectors, placed behind the back projection screen permitted the independent stimulation of each eye with two light bars equated for luminance and contrast. The luminance of the stimuli was maintained at 48 cd/m^2 while the luminance of the background was 0.6 cd/m^2.

The contrast, kept constant throughout the experiment was defined as C = (Ls - Lb) / Lb, where Ls was the luminance of the stimulus and Lb was the luminance of the background. Two optic benches, controlled independently through a computer, ensured the independent and precise definition of the other stimulus parameters: length and width, orientation and directionality, position in space, stimulus onset, velocity, as well as sweep duration and amplitude.

Upon isolating a binocular cell, the following initial protocol was followed. The RF of each eye was precisely mapped using the luminous spot and narrow slit of the projector. During this phase, the best stimulus parameters (size, directionality and velocity) were determined for both eyes. The optimal parameters were defined as the stimulus configuration which produced the greatest number of spikes, as estimated by ear from the output of the audio monitor. Each cell was tested for directionality and end-stopping. The principal inclusion criteria for the latter class was that the cell preferred a bar of optimal length, such that extending it beyond a determined limit caused a decrease in response.

This qualitative protocol was followed by a quantitative one. Stimulation was carried out using the dual optic bench system: two light bars having the best estimated dimensions were swept at optimal velocity and direction across each RF. Stimulus velocity varied between 1 degree/s and 20 degrees/s, each sweep covering 20 degrees Each stimulus condition was presented 10 times and a peri-stimulus time histogram (PSTH) was derived from the responses to these stimulations. Each eye was first stimulated separately to determine the monocular response and the binocular interactions were tested through simultaneous stimulation of both RFs at different spatial disparities.

The two light bars were positioned exactly equidistant from the center of each RF. When the two bars started moving at the same time, they crossed the centers of the RFs simultaneously, and disparity was null. However, if the initiation of the sweep of one bar was delayed with respect to the other, the two bars would at any particular time be situated at non corresponding points in each RF. The introduction of such a delay thus allowed the creation of crossed and uncrossed disparities. In addition to the null condition, several spatial disparity conditions were tested. These varied from 3 degrees crossed to 3 degrees uncrossed, in 0.5 degrees or 1 degree steps. Disparity, therefore, was defined relative to the RFs. These in turn were defined in terms of the coordinate reference points of the eyes. Although null disparity cannot be considered absolute, it is nonetheless a close approximation limited only by the accuracy of the definition of retinal landmarks. If RFs were sufficiently large, disparities up to 4 degrees were tested to insure that

cells (especially those of the near-like and far-like types) maintained their response rates to crossed and uncrossed disparities and hence to make certain that these were not simply cells tuned to a specific disparity in the crossed or uncrossed range.

Data processing

All conditions, each tested a total of 10 times, were interleaved with each other in a pseudo-random fashion. The time interval between each sweep was 10 - 20 s to avoid habituation. For each condition, a PSTH was derived from the cellular responses. These PSTHs were divided into 500 bins, each having a binwidth of 2 - 40 ms, depending upon the duration of the sweep. For each condition, a second PSTH, of equal duration, was computed prior to each sweep when no stimulation was present to establish a baseline level.

Each point on the curve defining the response profile of a cell was obtained in the following manner. The average number of spikes elicited without stimulation was derived from the baseline PSTH and the average number of spikes elicited during the stimulation was derived from the PSTH. The former average number of spikes was then subtracted from the latter.

As the two bars moving in the two RFs constitute a simulation of a single object moving in superimposed RFs of the awake fixating animal, it is crucial that the RFs be stimulated simultaneously. Failure to obtain simultaneous passage of the stimuli into the RFs, which occurs especially with small RFs and large temporal delays (to test large disparities), would result in the testing of binocular summation rather than disparity sensitivity. To avoid this bias, only disparities smaller than the width of the RFs were tested. Moreover, as non-simultaneous passages of the stimuli form PSTHs of distinct bimodal shape, it was possible to eliminate any such cells from the results.

Eye stability control

It is important in this type of study to precisely control for eye position to make certain that they do not move during the recording period. This was controlled in two ways. First, before undertaking the quantitative evaluation, the precise positions of the RFs were determined. These positions were again checked after having terminated the quantitative protocol. Any measurable

displacement in the location of either field resulted in the data being discarded. If the response of the cell was still robust, a new quantitative assessment, and consequent control, was carried out. Second, the possible drift of the eyes was estimated from the positions of major blood vessels and of the optic disks (Fernald and Chase 1971). This evaluation was carried out just before and immediately after having carried out the quantitative protocol for a particular cell. As above, this measure gave an indication of eye stability during the recording of the activity of one cell. Again, any obvious displacement of the eyes led to the results being discarded. Moreover, the different estimates taken at various intervals during the recording session gave indications as to whether any displacement of the eyes had taken place during the time of recording. Since the diameter of the optic disk at this screen distance was fairly large, the major blood vessels radiating from the optic disk were also taken for reference points (Pettigrew et al. 1979). This procedure, therefore, furnishes a useful index of both short and long term stability of eye position. The results obtained indicated that fairly stable eye positions were maintained throughout the 30 - 33 h recording session. It must be noted that following the induction of paralysis, recording was delayed for at least four hours to insure eye stabilization.

Histology

At the end of the penetrations, small electrolytic lesions were performed to allow the reconstruction of the recording tracks. The cat was then deeply anesthetized with 5 % Fluothane, after which it was perfused through the heart with isotonic saline followed by formalin (4%). The brain was removed, placed in formalin (4%), soaked in sucrose and then frozen. The section containing the superior colliculus in which recordings were performed was sliced (40 μm) along the coronal plane, so as to verify the locus of recording. Every second slice was kept and stained using the Nissl method. All cells included herein were clearly located in the superficial layers of the superior colliculus.

Insert Figure 1 approx. here

Mammals homozygotous for an allele at the albino locus, like the Siamese cat (Guillery and Kaas, 1971; Guillery, 1996), are known to have an abnormally laminated dorsal lateral geniculate nucleus (dLGN). Thus, to verify the dLGN lamination of our animals and provide an additional control of breed purity, the other hemisphere was sliced (40 μm) along the sagittal plane and every second slice was also stained using the Nissl method. As can be seen in Figure 1, the dLGN of the Siamese cat (cat 1; Fig. 1B) is easily discernible from that of a normal cat (Fig. 1A), as were the dLGNs of the other two cats. Indeed, due to the abnormal decussation of the retinal ganglion cells, layer A of the Siamese dLGN expands into layer A1.

RESULTS

It was first deemed important to record in areas 17 and 18, to ascertain that binocular cells were scarce in these areas, as they should be in Siamese cats. Results indicated that all 90 cells isolated in the central visual field representation of areas 17 and 18 of the 3 Siamese cats tested were found to be driven only by stimulation of the contralateral eye.

Overall, 216 cells were successfully isolated from background activity in the superficial layers of the superior colliculus. A total of 34 of these units were found to be binocularly driven (cat 1: 8/50; cat 2: 18/114; cat 3: 8/52) and were submitted to the testing protocol described above. As the present report is concerned with binocular interactions, no attempts were made to test the monocular cells. These monocular cells were almost all driven by the contralateral eye, as it was expected, and most showed a robust response to visual stimulation. It should be noted that a cell was considered binocular only if monocular stimulation of each eye evoked a response. Thus, no attempts were made to identify and test pseudomonocular neurons.

Binocular depth perception is believed to be most precisely perceived in the center of the visual field. Hence, only neurons whose RF center of the dominant eye was located less than 10 degrees of eccentricity from the vertical meridian and located between +5 degrees and -10 degrees of elevation were tested. An important number (17/34) of the binocular units recorded in the present report had RFs abnormally located in the ipsilateral hemifield of the contralateral eye. Those binocular RFs were rather small, as compared to those located in periphery, ranging from 14 degrees^2 to 82 degrees^2 (mean: 26.5 degrees^2, σ = 17.8 degrees^2) and tended to increase in size proportionally to their eccentricity, as expected. The RF sizes observed herein are similar to those measured in the central visual field representation of the superior colliculus of both Siamese (Berman and Cynader, 1972) and normal cats (Berman et al., 1975, Bacon et al., 1998).

The movement of dark or light bars across the RFs elicited the best responses, whereas stationary lights or flashes were considerably less efficient. Almost half of the units tested (44%) decreased their response rate if the stimuli extended beyond the optimal RF, suggesting that this

area was flanked by elongated inhibitory regions. Such end-stopping was similarly observed in the superior colliculus of normal and Siamese cats (Berman and Cynader, 1972).

An important proportion of the binocular cells (24/34) exhibited direction selectivity. Almost half (11/24) of the direction selective cells preferred stimulation along the horizontal plane. It is interesting to note that not one of the binocular cells responded optimally to stimuli drifting along the vertical axis.

Ocular Dominance

The classification of Hubel and Wiesel (1959, 1962) was used to create the ocular dominance histogram that can be seen in Figure 2. Classes 1 and 7 represent monocular cells that could respectively be driven only through stimulation of the contralateral or ipsilateral eye. In order to quantitatively assign cells to the intermediate categories 2 - 6, an ocular dominance index (ODI) for each binocular cell was determined using the formula ODI = (I / (I + C)) * 100 where I represents the response to stimulation of the ipsilateral eye and C that in response to stimulation of the contralateral eye. The ODI thus obtained allowed for classification on the following scale: 2, (1 - 20%); 3, (21 - 40%); 4, (41 - 60%); 5 (61 - 80%); 6, (81 - 99%).

Figure 2 reveals an ocular dominance distribution very similar to that obtained by Berman and Cynader (1972) but different from that of Antonini et al. (1981), who claimed that over 87% of cells in the superior colliculus of the Siamese cat were binocular. Indeed, our results show that an important proportion of cells were monocularly driven through the contralateral eye (180 cells). Nonetheless, 34 units responded to the stimulation of both eyes. Monocular cells that could only be driven through the ipsilateral eye were also observed (2 cells), which is surprising but not unusual, as such cells were also reported, in a similarly small proportion, by Berman and Cynader (1972).

Insert Figure 2 approx. here

Binocular Interactions and spatial disparity sensitivity

Simultaneous stimulation of the eyes evoked cellular responses that often could not have been predicted from the monocular responses. Figure 3 shows the PSTHs for one of the units (cell 030) presenting strong binocular interactions to simultaneous stimulation of the RFs (disparity 0 degree). This cell was direction-selective, preferring stimulation arriving from 225 degrees The cells showing the strongest binocular interactions tended to be direction selective, which was also observed by Berman et al. (1975) in normal cats. Cell 030 preferred stimulation of the contralateral eye (ODI = 3), but the response to monocular stimulation of either eye was not very robust. Binocular facilitation was observed over a wide range of disparities (-2 degrees to 1 degree) but was optimal at null disparity.

The second unit shown in Figure 3 (cell 082) is of the same general shape as cell 030, but differs from the latter in two important ways. First, the peak response is obtained at 1 degree in the uncrossed range. Second, this peak is not greater than the sum of the monocular responses, but still is superior to the monocular response of the dominant eye. This type of binocular interaction is known as summation (Berman et al., 1975).

The first two cells shown in Figure 3 (cells 030 and 082) are of a shape similar to the tuned excitatory cells first described in the monkey (Poggio and Fisher, 1977) and also observed at various levels of visual processing in the normal cat cortex (LeVay and Voigt, 1988; Guillemot et al., 1993; Wang et Dreher, 1996; Bacon et al., 1997). A total of 12 cells showed this characteristic peak. They tended to have small RFs (mean: 22.0 degrees^2, σ = 9.7 degrees^2)to show direction selectivity (9/12), end-stopping (8/12) and a balanced ocular dominance (10/12 have an ODI between 3 and 5). The maximum response peaks of all twelve cells were located 1 degree or less from the vertical meridian.

It should be noted that some cells showed facilitation or summation without having a tuned profile. One such cell is shown in the right part of Figure 3 (cell 190). The response of this cell to monocular stimulation was very weak. Its response to binocular stimulation, however, was

extremely robust, being more than twice the sum of the monocular responses to all disparities tested. Such a binocular cell would probably not code for depth.

A third type of binocular interaction, namely occlusion, was observed. Occlusion describes a binocular response which is inferior to the lesser of the monocular responses (Berman et al., 1975). In two cells, occlusion occurred around null disparity. Figure 4 shows these two units, which closely resemble the tuned inhibitory cells observed at various levels of visual processing in the domestic cat brain (LeVay and Voigt, 1988; Guillemot et al., 1993; Bacon et al., 1998). Both of these cells showed direction selectivity, end-stopping and an ODI of 4.

Insert Figures 3 and 4 approx. here

The cell presented in the left part of Figure 5 (cell 012) showed binocular facilitation in response to disparities in the crossed range and occlusion in response to disparities in the uncrossed range. This pattern of response is reminiscent of near cells, which are presumed to play a role in the analysis of stimuli located in front of the fixation plane. As can also be seen in Figure 5, another unit (cell 036) shows a similar response profile, although it barely reached summation in the crossed range, probably due to the already strong monocular response of the contralateral eye. This pattern of disparity sensitivity, which underlies a preference for crossed disparities, suggest that these cells might code for stimuli that lie in front of the fixation plane.

The reverse pattern was found in three cells, all of which can be seen in Figure 6. These units show a pattern of response reminiscent of far cells (Poggio and Fisher, 1977), although two of the three cells (169 and 021) fail to reach occlusion in the crossed range because of the weak responses to monocular ipsilateral stimulation. These units nonetheless exhibit a pattern of disparity sensitivity which underlies a preference for uncrossed disparity, and therefore for stimuli that appear to lie behind the fixation point.

Insert Figures 5 and 6 approx. here

Selectivity to spatial disparities

The tuning-curve width at half-height of the units showing an excitatory or inhibitory response peak is an indication of the selectivity of the cells to spatial disparities. The mean tuning-curve width of the 12 cells showing an excitatory peak was 3.19 degrees The selectivity of the two units exhibiting inhibitory interactions were 2.47 degrees and 3.59 degrees In comparison, the mean tuning-curve width at half-height of the tuned excitatory and tuned inhibitory cells recorded in the superior colliculus of the normal cat, under similar stimulation procedure, were 2.97 degrees and 1.53 degrees respectively (Bacon et al., 1998).

The slopes of the profiles, measured at 50% of the maximum response, of the cells responding to crossed or to uncrossed disparities are also indications of selectivity. The slope of the cells preferring crossed disparities was - 36.0 and - 53.8 whereas those of the three cells sensitive to the reverse were 34.0, 35.4 and 68.4. In comparison, the mean slopes at half-height of near and far cells recorded in the superior colliculus of normal cats were -57.8 and 48.7 respectively (Bacon et al., 1998).

DISCUSSION

The present study confirms that a degree of binocularity is spared in the superior colliculus of the Siamese cat and demonstrates that some of these binocular units are sensitive to spatial disparity.

Binocularity

The ocular dominance distribution found in the present study closely resembles that of Berman and Cynader (1972) and is strikingly different from that of Antonini et al. (1981), whose proportion of binocular cells is more similar to that found in the normal cat than the Siamese. Antonini et al. (1981) proposed that the significant difference between their binocularity level and that of Berman and Cynader (1972) rested upon two factors.

First, they state that the absence of pharmacological anesthesia in their study might have allowed for a better expression of the weak ipsilateral input. Since the latter input is probably not a direct retinotectal input but reaches the superior colliculus through an indirect cortico-cortical collicular pathway, its activation might be somewhat sensitive to the level of anesthesia. They cite as suggestive proof for this proposition the fact that the proportion of binocular receptive fields in areas 17 and 18 of the Siamese recorded under no anesthesia (Antonini et al., 1981) was higher than that found in the same areas of similarly recorded Siamese cats but using light barbiturate anesthesia (Marzi et al., 1976). For this argument to hold in the present case, it would have to follow that the cortical area from which originates the collicular input, in most probability the binocularly driven cells in suprasylvian cortex (Marzi et al., 1980), should manifest little or no activation from the contralateral cortex when its cells are recorded under anesthesia. Yet numerous studies which have recorded in the posteromedial lateral suprasylvian visual cortex (PMLS) of anesthetized cats using various types of anesthesia have shown that its cells are mostly binocularly driven (Hubel and Wiesel, 1969; Rizzolatti and Camarda, 1975; Spear and Baumann 1975; Di Stefano et al., 1985; Morrone et al., 1986; Blakemore and Zumbroich, 1987; Rauschecker et al., 1987; Zumbroich and Blakemore, 1987; Sherk, 1988; Spear, 1988), including in split-chiasm cats where all binocularly driven cells get one of their inputs from the contralateral hemisphere

(Antonini et al., 1983). While one cannot exclude that cortical neurons in Siamese cats are particularly sensitive to anesthesia, it is highly unlikely that this could completely explain the major discrepancy between the results of Antonini et al. (1981) and those obtained in the present experiment. Also related to the present argument, Gordon and Gummow (1975) studied ocular dominance in the superior colliculus of normal cats with and without anesthesia and reported no significant differences.

Second, Antonini et al. (1981) stated that the absence of visible strabismus in their animals might underlie the high binocularity level they observed. However, the visual anomalies found in hypopigmented and albino mammals, such as horizontal nystagmus, abnormal eye-movement control and strabismus (Collewijn et al., 1978, 1985; Mangini et al., 1985; Apkarian, 1991) are believed to be consequences of chiasmatic and cortical abnormalities (Guillery, 1996) and not their cause. It is nonetheless admitable that strabismus might potentiate the negative effects of the abnormal decussation upon binocularity at all levels. Binocularity at the cortical level was also reported to be greater in the study by Antonini et al. (1981) than in the present report. The proportion of binocular cells reported by Antonini et al. (1981) was 18% and exceeded 30% in some cats. It should be noted that these proportions are difficult to reconcile not only with the present report but also with that of others on cortical binocularity of siamese cats (Hubel and Wiesel, 1971; Cool and Crawford, 1972; Di Stefano et al., 1984; Toyama et al., 1991).

All the cats studied by Antonini et al. (1981) were orthoptic. In the present experiment no difference in the three animals was observed despite varied eye alignments (8/50, 18/114 and 8/52 binocular cells in cats 1, 2 and 3 respectively. The dLGN laminations were typical of siamese cats; they were however not shown by Antonini et al. (1981).

Anatomical considerations

Before discussing the results on disparity sensitivity, it may be appropriate to comment on what across the midline route is taken by the visual signal from the ipsilateral eye to the superior colliculus. One obvious possibility lies with the collicular commissure which could directly relay retinal information. However, a brain-stem section including this commissure does not appear to

influence collicular binocularity (Antonini et al., 1981). As no binocular cells could be found in the primary visual cortex, and all monocular cells were contralaterally driven, descending pathways from areas 17-18 have to be dismissed. Area 19 is similarly devoid of binocular cells (Di Stefano et al., 1984; Toyama et al., 1991). However, the Clare-Bishop (suprasylvian) area has been shown to contain numerous binocular cells (Marzi et al., 1980; Toyama et al., 1991).

Suprasylvian units receive binocular information via two converging routes. The contralateral signal is carried through ipsilateral areas 17-18 and 19 and directly from the interlaminar geniculate nucleus (Kaas and Guillery, 1973; Cooper and Pettigrew, 1979). On the other hand, ipsilateral information is transferred from the contralateral suprasylvian area through the corpus callosum (Shatz, 1977; Marzi et al., 1980). Indeed, the suprasylvian area has very dense callosal interconnections, and this area is believed to vastly contribute to interocular transfer (Berlucchi and Marzi, 1982). Moreover, it has been shown that sectioning the corpus callosum practically eliminates all ipsilateral eye influence on suprasylvian units in Siamese cats (Marzi et al., 1980). The ipsilateral input to the superior colliculus of Siamese cats is probably mostly dependent on projections from the ipsilateral PMLS area. However, non-callosal routes such as the tectal commissure (Edwards, 1977), the crossed cortico-tectal pathway (Powell, 1976; Baleydier, 1977) or the supraoptic commissure (Graybiel, 1978) may also contribute in a limited fashion to collicular binocularity.

Binocular interactions and disparity sensitivity: functional implications

A non-negligible proportion of collicular units has herein been shown to be binocular (16%) and more than half of these cells were sensitive to variations in the spatial disparity of the stimuli presented. The selectivity to spatial disparity of these units, as defined by the half-widths and slopes of their tuning-curve functions was coarse, more so than similarly tuned units in the cortex of the normal cat. It is clear that these units could not play a role in fine stereopsis. This is consistent with the behavioral demonstration that fine stereopsis (10' to 20') is lacking in Siamese cats (Packwood and Gordon, 1975). Coarse stereopsis has never been tested in Siamese cats, but studies in humans (Guo et al., 1989; Apkarian and Reits, 1989) suggest that a degree of coarse

stereopsis might be spared in albinism or hypopigmentation. It is possible that these neurons constitute the neurophysiological substrate of these residual binocular functions.

Cells sensitive to broad spatial disparities, especially the tuned excitatory or tuned inhibitory cells such as those found herein, could support coarse stereopsis and thus make it possible to determine whether a stimulus lies in front of or behind the fixation plane (Bishop and Henry, 1971; Roy et al., 1992). This function might in turn be critically involved in the control of oculomotor behavior. Indeed, information concerning the relative depth of an object assured by these coarse disparity sensitive cells, might be relayed via topographic connections (Behan and Appell, 1992; Behan and Kime, 1996), to the deeper layers of the superior colliculus. The deep layers, which have been shown to be involved in saccades and input determined eye positions (Wurtz and Mohler, 1974; Robinson, 1975; Schiller and Wurtz, 1975; Sparks, 1975 1978; Wurtz and Albano, 1980) could then use this information to generate conjugate or vergence eye movements, which cats have the ability to perform (Hughes, 1972; Stryker and Blakemore, 1972) and thereby fixate the eyes upon the appropriate plane of the tridimensional visual scene.

Vergence and stereopsis are indeed linked in more than one way. It is known that vergence can give information as to target depth through triangulation and that manipulation of vergence affect depth judgments (Judge, 1991). Vergence and stereopsis therefore are engaged in a reciprocal relationship, in the sense that vergence is necessary for the precise integration of disparity cues, which are in turn necessary to drive precise vergence movements. Anatomical evidence suggest that the source of visual input to the vergence system is indeed the superior colliculus (Harting et al., 1980). Moreover, it has been demonstrated that horizontal binocular disparity is a sufficient stimulus to trigger vergence eye movements (Rashbass and Westheimer, 1961a, b; Westheimer and Mitchell, 1969; Erkelens and Regan, 1986). It could therefore be advanced that coarse disparity detectors are sufficient to initiate vergence, as proposed by Marr and Poggio (1979), that vergence eye movements to large disparities can be initiated by low frequency visual information as furnished by collicular cells and that higher spatial frequency information leading to fine stereopsis is only relevant to smaller vergence movements or at the later stages of larger movements.

Therefore, cells sensitive to coarse spatial disparity at the collicular level could allow not only for coarse stereopsis of the kind obtained in albino (Guo et al., 1989; Apkarian and Reits, 1989) and strabismic subjects (Sireteanu, 1982, Kitaoji and Toyama, 1987), but could also influence conjugate eye movements and vergence eye movements. Some support for this argument is furnished by the demonstration that the principal source of input to the superior colliculus, area PMLS, is involved in vergence in cats (Bando et al., 1996)

It could further be proposed that cells showing binocular interactions in the superior colliculus, such as those found in the Siamese cats, play a role in accommodation mechanisms, which cats are known to possess (Elul and Marchiafava, 1964). It is indeed known that stimulation of the superior colliculus can evoke accommodative responses (Sawa and Ohtsuka, 1994). The cells coding for spatial disparity could relay the information via topographically organized circuits (Sato and Ohtsuka, 1996) to the structures mediating accommodation, hence allowing for the focus to be made.

Finally, collicular cells selective to coarse spatial disparity could be involved in the analysis of motion in depth, as occurs when the organism is moving through its environment. It has been suggested that this movement is coded by units with large binocular RFs (Roy and Wurtz, 1990; Roy et al., 1992) such as those found in the present study. Such cells with large RFs that can code spatial disparity cues could convey information concerning the gross changes in depth of stimuli as the organism is moving, and thus play a role in the global analysis of the optic flow.

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FIGURE LEGENDS

Figure 1. Sagittal sections of the left dorsal lateral geniculate nucleus (dLGN) of a normal cat (A), shown here as control, and of the right dLGN of one of the Siamese cats (cat 1) used in the present study (B). It can be seen that the three laminae (A, A1 and C) of the normal dLGN are smooth and regular, whereas the lamination of the Siamese dLGN seems distorted. In the latter, layer A1, which receives input from the ipsilateral eye, is clearly being infringed upon by layer A which receives an abnormally high number of fibers from the contralateral eye because of the massive misrouting of ganglion cells that characterizes Siamese cats. The dLGN of the other Siamese cats used in the present study (cats 2 and 3) were similarly laminated. Scale bar = 1 mm; a: anterior, d: dorsal.

Figure 2. Ocular dominance distribution of cells in the superficial layers of the superior colliculus of the Siamese cat. The majority of cells can only be driven through the contralateral eye.

Figure 3. Peri-stimulus time histograms (PSTH) and disparity sensitivity profile of a single neuron (Cell 030) showing binocular facilitation in the superior colliculus of the Siamese cat. PSTHs i (ipsilateral) and c (contralateral) show the cellular response to monocular stimulation. The other PSTHs show the responses to the various binocular spatial disparities presented. The summed responses derived from each histogram are plotted against stimulus disparity to generate the normalized response profile. The response peak at null disparity is reminiscent of tuned excitatory cells. Cell 082: disparity sensitivity profile of a cell showing the same general shape, but which shows binocular summation. Cell 190: this unit shows binocular facilitation across all disparities tested without being selective to a specific one. These three cells did exhibit end-stopping but only cell 030 was direction selective (225 degrees)

Figure 4. Two cells showing occlusion around null disparity. Both cells were direction selective (cell 148: 0 degree; cell 114: 180 degrees) and did not exhibit end-stopping. It can be seen from the PSTHs of Cell 148 that simultaneous stimulation of the receptive fields appears to inhibit the response of the cell. Both Cell 148 and Cell 114 can be compared to tuned inhibitory units.

Figure 5. The unit for which peri-stimulus time histograms are shown (Cell 012) was end-stopped, direction selective (315 degrees) and showed facilitation in response to crossed disparities and occlusion in response to disparities in the uncrossed range. Only one other unit, Cell 036, presented a similar pattern of response, which can be compared to that of near cells. This unit was not direction selective and did not show end-stopping.

Figure 6. Peri-stimulus time histograms (Cell 169) and disparity sensitivity profile of three neurons (Cell 169, Cell 064 and Cell 021) which responded vigorously to uncrossed disparities and were inhibited by disparities in the crossed range. This profile is characteristic of far cells, which are presumed to code stimuli located behind the fixation plane.

Figure 1

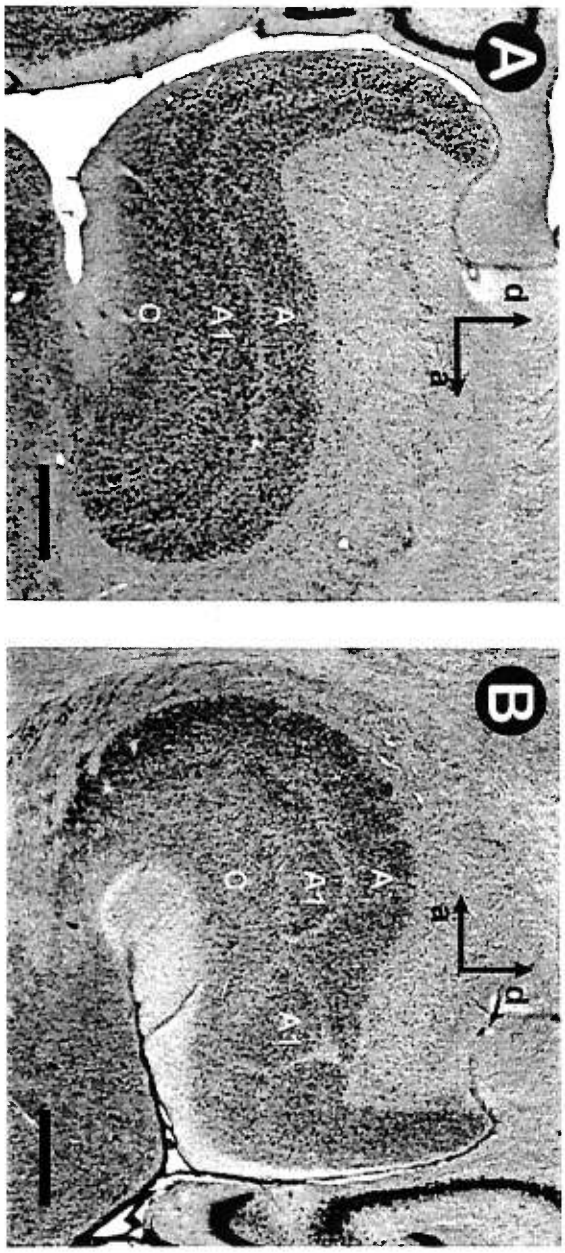


Figure 2

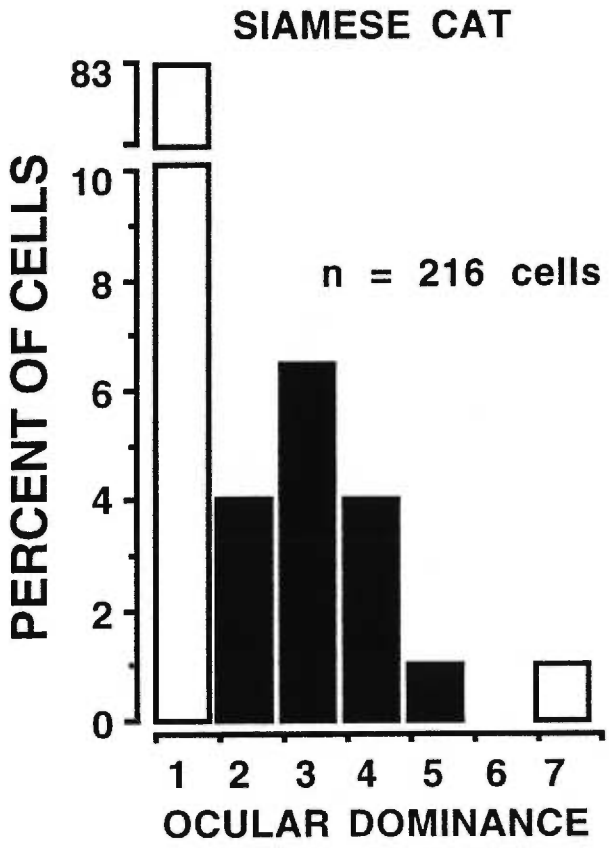

SIAMESE CAT
83
10
8
6
4
2
0
PERCENT OF CELLS
n = 216 cells
1 2 3 4 5 6 7
OCULAR DOMINANCE

Figure 3

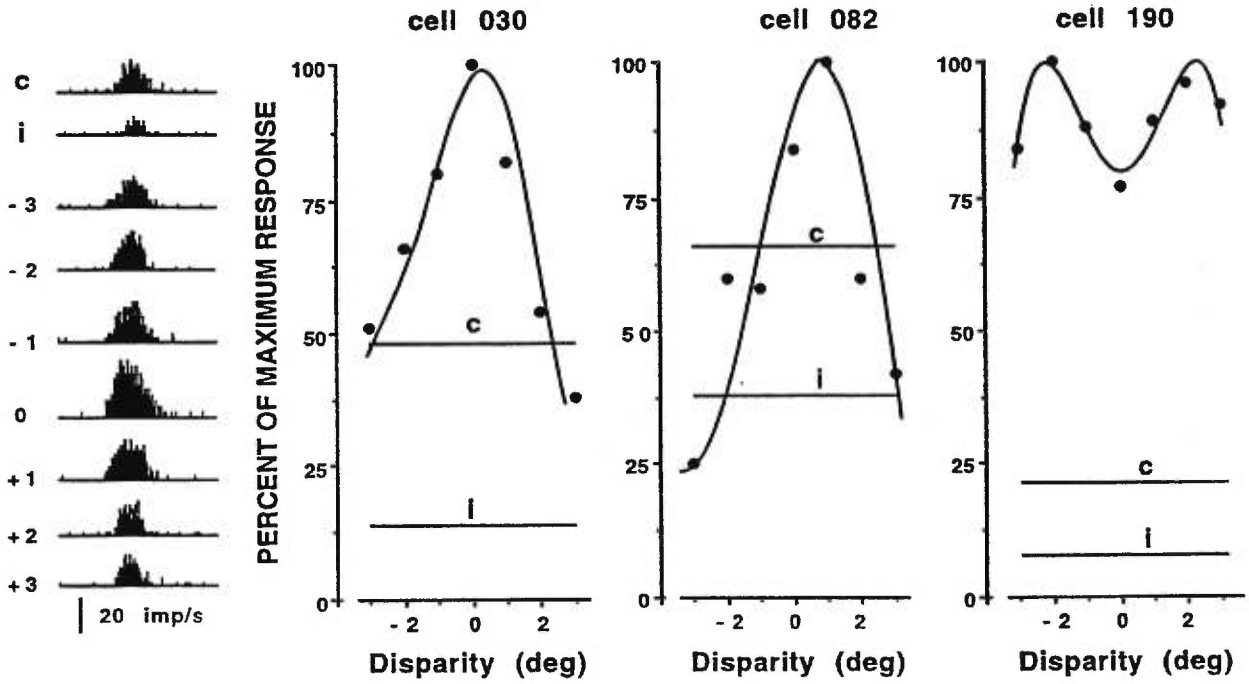
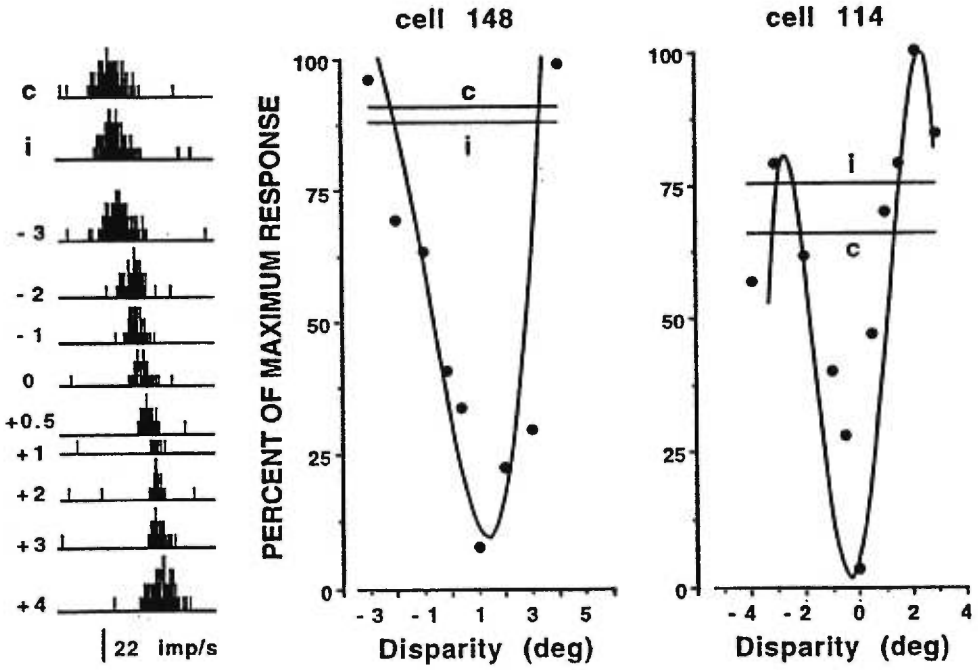

c
i
- 3
- 2
- 1
0
+ 1
+ 2
+ 3
20 imp/s
PERCENT OF MAXIMUM RESPONSE
cell 030
cell 082
cell 190
100
75
50
25
0
c
i
- 2
0
2
Disparity (deg)

Figure 4


c
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- 3
- 2
- 1
0
+0.5
+1
+2
+3
+4
22 imp/s
cell 148
PERCENT OF MAXIMUM RESPONSE
100
75
50
25
0
c
i
- 3
- 1
1
3
5
Disparity (deg)
cell 114
100
75
50
25
0
i
c
- 4
- 2
0
2
4
Disparity (deg)

Figure 5

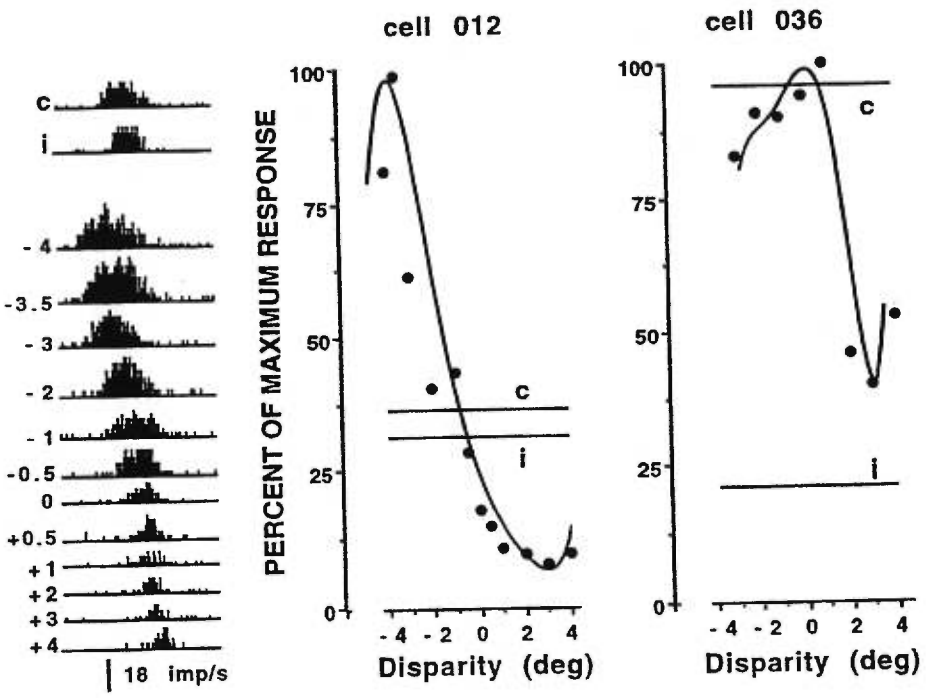
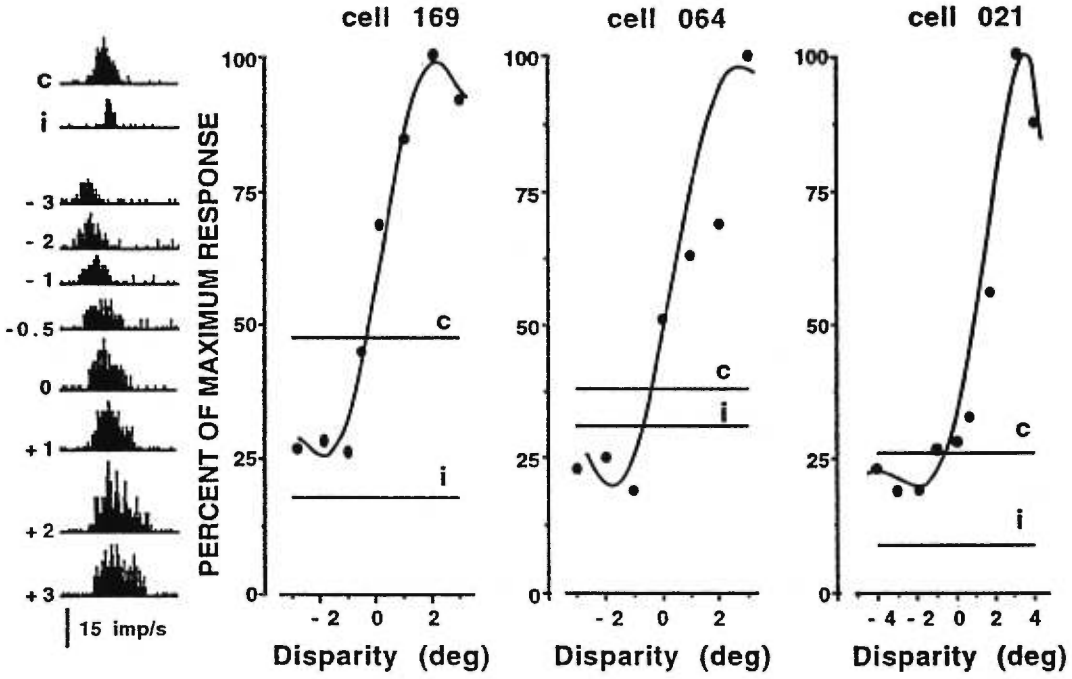

cell 012
cell 036
c
i
- 4
-3.5
- 3
- 2
- 1
-0.5
0
+0.5
+1
+2
+3
+4
18 imp/s
PERCENT OF MAXIMUM RESPONSE
100
75
50
25
0
- 4 - 2 0 2 4
Disparity (deg)

Figure 6


cell 169
cell 064
cell 021
c
i
- 3
- 2
- 1
- 0.5
0
+ 1
+ 2
+ 3
15 imp/s
PERCENT OF MAXIMUM RESPONSE
100
75
50
25
0
- 2
0
2
- 4
4
Disparity (deg)

CHAPITRE 7

Discussion générale

Les études qui constituent le corps du présent ouvrage requièrent une discussion générale en trois volets. D'abord, ces études démontrent que la disparité spatiale n'est pas encodée de manière identique dans les régions visuelles étudiées. Ceci sous-tend que ces dernières offrent des contributions fonctionnelles différentes et complémentaires à la vision binoculaire et à la stéréopsie; ces différents rôles seront détaillés, contrastés et intégrés. Ensuite, ces études ont pour prémisse que l'encodage des disparités rétiniennes dépend d'un décalage entre la position des CR mais elles reconnaissent toutefois que cet encodage peut aussi dépendre d'un décalage dans l'organisation interne des CR; cette apparente contradiction sera commentée. Finalement, ces études ne considèrent que la disparité spatiale horizontale, alors que cette dernière n'est pas le seul indice binoculaire de profondeur; la disparité spatiale verticale et les autres types de disparité seront donc décrits et intégrés, de manière à brosser un tableau plus complet des mécanismes stéréoscopiques.

Les rôles des différentes aires visuelles et du collicule supérieur

Cette question a été abordée, à différents degrés et sous différents angles, dans les chapitres précédents. Il semble toutefois important de regrouper et synthétiser ces propositions fonctionnelles afin de fournir un point de vue plus global des contributions relatives des différentes régions visuelles dans la vision binoculaire et la perception stéréoscopique.

Les contributions des aires 17/18 et 19

Le cortex visuel primaire semble jouer un rôle prépondérant dans l'encodage des indices de disparité spatiale et dans la perception stéréoscopique du chat normal. En effet, plus de 70% des cellules binoculaires des aires 17/18 sont sensibles à la disparité spatiale et celles-ci sont équitablement

réparties entre les quatre classes de détecteurs de disparité. De plus, leur sélectivité à la disparité spatiale est extrêmement fine, beaucoup plus que dans toute autre aire visuelle. Cette sélectivité fine reflète l'apport des inputs de type X vers le cortex visuel primaire et va de pair avec les petits CR (Hubel et Wiesel. 1959, 1962; Orban, 1984, 1991) et la haute résolution spatiale (Movshon et al., 1978c) des cellules de ces aires. Ainsi, les cellules sensibles à la disparité spatiale dans le cortex visuel primaire semblent former un substrat idéal pour la perception de la stéréopsie fine.

Des études comportementales (Kaye et al., 1981; Ptito et al., 1991, 1992) semblent substantiver cette affirmation. Ces études se basent sur le principe suivant pour démontrer l'importance du cortex visuel primaire dans la perception stéréoscopique.

> "Given that fine disparity seems to be processed in areas 17/18 and that cells in the 'next-up' area appear to treat mainly coarse disparity information, would the ablation of the primary visual cortex abolish fine disparity-based depth discrimination. A positive answer to this question would not only validate the general structure-function hypothesis which underlies the theme of this paper but it would also indicate that despite the existence of parallel retino-thalamic pathways projecting directly to extrastriate areas, successful resolution of fine disparity-based stereoproblems must necessarily involve areas 17/18." (Ptito et al., 1991)

Certaines de ces études (Ptito et al., 1991, 1992) utilisent des stimuli formés de points aléatoires qui ont l'avantage d'assurer l'absence des indices de profondeurs monoculaires et/ou dépendants de la perception de la forme. Ces stimuli nécessitent toutefois une analyse stéréoscopique globale et en ce sens, la relation entre les cellules sensibles à la disparité spatiale "locale" et la perception de la profondeur par un processus stéréoscopique "global" n'est pas directe. Néanmoins, comme la perception globale dépend invariablement de l'intégration des indices locaux, il est possible d'imaginer un organisme possédant des cellules sensibles à la disparité spatiale qui ne percevrait pas la stéréopsie globale, mais il est difficile d'envisager l'inverse. Ainsi, l'ablation des aires 17/18 chez

le chat abolit toute discrimination stéréoscopique basée sur de petits indices de disparité spatiale, ce qui confirme l'importance des cellules très sélectives à la disparité spatiale du cortex visuel primaire dans la stéréopsie fine.

Ces études comportementales démontrent aussi que les voies géniculées parallèles vers les aires extrastriées, bien qu'elles soient adéquates pour servir certaines fonctions visuelles de haut niveau comme la discrimination de patterns (Doty, 1961; Cornwell et al., 1976; Sprague et al., 1977, 1985), ne peuvent à elles seules soutenir la stéréopsie fine. Pettigrew et Dreher (1987) avancent néanmoins que les cellules de l'aire 19 sont particulièrement sensibles aux disparités homonymes et que l'ablation de cette aire produirait des déficits dans la perception de la profondeur d'objets éloignés. Guillemot et al. (1993a) démontrent toutefois que les cellules sensibles aux disparités homonymes ne sont pas sur-représentées dans l'aire 19 et que tous les types de cellules sensibles à la disparité spatiale y sont plutôt rares. De plus l'analyse de la sélectivité des cellules de l'aire 19 confirme que ces cellules ne pourraient pas jouer un rôle dans l'analyse des petits indices de disparité spatiale et dans la stéréopsie fine. Ainsi, le rôle de l'aire 19 dans l'encodage de la disparité spatiale et la perception stéréoscopique semble limité.

Ceci peut sembler surprenant à la lumière des projections massives des aires 17/18 vers l'aire 19. En effet, les propriétés cellulaires sont souvent maintenues le long du "functional stream" visuel. L'encodage de la disparité spatiale dans l'aire 19 s'explique en partie par les inputs parallèles massifs en provenance des couches C du CGLd, du NIM et, à un moindre degré, du complexe LP-pulvinar (Stone, 1983; Dreher, 1986). L'input de type majoritairement W vers ces structures semble générer des propriétés cellulaires non-favorables à l'élaboration de la sensibilité à la disparité spatiale. L'aire 19 contient néanmoins une importante proportion de cellules binoculaires, lesquelles ont de petits CR

et des propriétés spatiales assez fines. En ce sens, cette aire pourrait servir de substrats à d'autres aspects de la vision binoculaire, tels que la fusion binoculaire et l'intégration des différents indices de profondeurs.

Chez le chat Siamois, comme le confirme les chapitres 5 et 6, les cellules binoculaires sont extrêmement rares dans les aires 17/18 (Hubel et Wiesel, 1971; Cool et Crawford, 1972; Cooper et Blasdell, 1980; Marzi et al., 1976, 1980: Antonini et al., 1981; Leventhal et Creel, 1985: Toyama et al., 1991) ainsi que dans l'aire 19 (Di Stefano et al., 1984; Toyama et al., 1991). Ceci se reflète directement par l'absence de stéréopsie fine observée chez ces chats (Packwood et Gordon, 1975). L'absence de cellule binoculaires dans les aires 17/18 du chat Siamois et l'absence concomitante de stéréopsie fine corrobore ainsi l'importance de ces aires dans ces fonctions stéréoscopiques, de la même manière que les études de lésion du cortex visuel primaire du chat normal (Kaye et al., 1981; Ptito et al., 1991, 1992).

Les contributions de l'aire PMLS et du collicule supérieur

Comme le démontrent les chapitres 3 et 4 de cette thèse, la détection et l'analyse des indices de disparité spatiale semblent s'effectuer de manière similaire dans l'aire PMLS et dans les couches superficielles du collicule supérieur du chat normal. En effet, ces deux régions visuelles contiennent une forte proportion de cellules sensibles à la disparité spatiale (73% dans l'aire PMLS et 64% dans le collicule supérieur), et la majorité de ces cellules sensibles sont de type excitatrices. Les cellules sensibles à la disparité spatiale de ces deux régions visuelles sont aussi caractérisées par une sélectivité moins fine qui reflète leurs piètres propriétés spatiales et qui laisse supposer des contributions dans les aspects plus grossiers de la stéréopsie, tel que la localisation de stimuli. En ce sens, le collicule

supérieur des mammifères supérieurs semble impliqué dans des fonctions stéréoscopiques similaire aux tectum optique des espèces phylogénétiquement moins évoluées. La tectum optique de la grenouille, par exemple, contient en effet des cellules binoculaires montrant un décalage inter-CR (Gaillard, 1985) et ces cellules semblent former le substrat neurologiques de la localisation stéréoscopique des stimuli qui permet à la grenouille une grande précision dans la capture de ses proies (Fite et Scalia, 1976, Collett, 1977).

L'aire PMLS et le collicule supérieur sont fortement interconnectés et font tous deux partie de la voie visuelle du "Où?" (Schneider, 1967, 1969). De plus, les cellules binoculaires de l'aire PMLS et des couches superficielles du collicule supérieur possèdent de grands CR, de la sélectivité à la direction, une haute résolution temporelle et ne répondent qu'à des stimuli mobiles (McIlwain et Buser, 1967; Sterling and Wickelgren, 1969; Hubel et Wiesel, 1969; McIlwain, 1970; Spear et Baumann, 1975; Pinter et Harris, 1981; Blakemore and Zumbroich, 1987) ce qui laisse présumer que ces régions visuelles jouent un rôle dans la détection et l'analyse du mouvement. L'implication de ces régions visuelles dans la détection de stimuli en mouvement sur l'axe fronto-parallèle à d'ailleurs été démontrée à plusieurs reprises (Sterling et Wickelgren, 1969; Hayashi et al., 1973; Spear et Baumann, 1975; Berman et al., 1975; Hoffmann et Sherman, 1975; Turlejski, 1975; Camarda et Rizzolatti, 1976; Bisti et Sireteanu, 1976; Hamada, 1987; Rauschecker et al., 1987; von Grünau et al., 1987).

Les études de Toyama et ses collaborateurs (Toyama et Kozasa, 1982; Toyama et al., 1985, 1986a, 1986b) démontrent que certaines cellules de l'aire PMLS répondent sélectivement au mouvement de stimuli sur l'axe Z. Le mouvement d'un stimulus sur l'axe fronto-parallèle peut être interprété par l'évaluation de l'amplitude du déplacement rétinien ou du mouvement oculaire qu'il engendre. Par contre, l'analyse du mouvement dans la troisième dimension tel que celui encodé par

certaines cellules de l'aire PMLS requiert la détection et l'analyse d'une séquence infinie de disparités spatiales, lesquelles génèrent des mouvements d'accommodation ou de vergence (Westheimer et Mitchell, 1969; Erkelens et Regan, 1986) qui permettent la fovéation continue du stimuli dans l'espace tridimensionnel. Le grand nombre de cellules excitatrices, qui préfèrent les stimuli situés au point de fixation, dans l'aire PMLS soutient l'hypothèse de l'implication de cette aire dans la fovéation. Ainsi, l'implication de l'aire PMLS dans l'accommodation (Bando et al., 1988) et la vergence (Bando et al., 1996) dépend d'un input des cellules sensibles à la disparité spatiale de cette aire et probablement d'un output via les couches superficielles vers les couches profondes du collicule supérieur (Bando et al., 1996).

Le collicule supérieur est en effet le principal centre de contrôle des mouvements oculaires (Stein et Meredith, 1993). Il a en effet été fréquemment démontré que les couches profondes de cette structure jouent un rôle dans le contrôle des saccades, de la position oculaire déterminée par un input visuel (Wurtz et Mohler, 1974; Robinson, 1975; Schiller et Wurtz, 1975; Sparks, 1975, 1978; Wurtz et Albano, 1980; Guitton et al., 1980; Van Opstal et al., 1990; Guitton, 1991) et de l'accommodation (Sawa et Ohtsuka, 1994; Sato et Ohtsuka, 1996).

Les couches superficielles, qui contiennent les cellules sensibles à la disparité spatiale, envoient des efférences organisées de manière topographique vers les couches profondes (Behan et Appell, 1992; Behan et Kime, 1996). Ainsi, il peut être avancé que les cellules sensibles à la disparité spatiale des couches superficielles du collicule supérieur et les cellules sensibles à la disparité spatiale de l'aire PMLS qui se projettent vers ces couches forment une carte spatiale tridimensionnelle qui permet aux couches profondes de localiser les stimuli visuels dans la troisième dimension. Ces informations sur la scène visuelle tridimensionnelle permettent aussi aux couches profondes de guider la fovéation des

stimuli en indiquant leurs coordonnées non seulement en X et en Y mais aussi en Z aux structures oculomotrices du tronc cérébral. Une fois la fovéation accomplie, une analyse stéréoscopique plus fine est alors effectuée par les structures appropriées, c'est à dire le cortex visuel primaire. En ce sens, l'analyse stéréoscopique d'un stimulus s'effectue en deux temps: la localisation dans l'espace tridimensionnel, la fovéation et le maintien de la fixation, sous contrôle des mécanismes suprasylviens et colliculaires, puis l'analyse précise de son relief et la reconstruction de sa "solidité" stéréoscopique par les mécanismes de stéréopsie fine du cortex visuel primaire.

Chez le chat Siamois, les cellules binoculaires de l'aire PMLS et du collicule supérieur jouent probablement les mêmes rôles que chez le chat normal en terme de contrôle de la fovéation, de la vergence et de l'accommodation. Il est aussi probable que ces cellules remplissent aussi un rôle palliatif dans la perception stéréoscopique de la profondeur et de la troisième dimension, permettant ainsi au chat Siamois de percevoir un certain degré de stéréopsie grossière similaire à ce qui est observé chez l'humain albinos (Guo et al., 1989; Apkarian et Reits, 1989).

Les contributions des autres aires visuelles

La sensibilité à la disparité spatiale a été étudiée systématiquement dans une seule autre aire visuelle du chat: l'aire 21a (Wang et Dreher, 1996). Ces auteurs rapportent une forte proportion de cellules sensibles (69%), une forte majorité de cellules de type excitatrices et une sélectivité qui, bien qu'elle ne soit pas explicitement calculée, semble grossière. Ainsi, bien que l'aire 21a soit significativement différente de l'aire PMLS en terme de sélectivité à la direction et de propriétés spatio-temporelles (Dreher et al., 1996), elle semble similaire à l'aire PMLS en ce qui à trait à la sensibilité à la disparité spatiale. Wang et Dreher (1996) avancent que l'aire 21a semble jouer un rôle

important dans la discrimination binoculaire et que cette aire doit être impliquée dans l'analyse des aspects de "haut niveau" de la vision stéréoscopique. En effet, ces auteurs proposent que l'aire 21a serait essentielle à la conscience (awareness) de la perception stéréoscopique de la profondeur.

Les études de Toyama chez le chat normal (Toyama et Kozasa, 1982; Toyama et al., 1985, 1986a, 1986b) et Siamois (Toyama et al., 1991) démontrent qu'une proportion des cellules de l'aire Clare-Bishop répondent sélectivement au mouvement de stimuli se déplaçant sur l'axe fronto-perpendiculaire. Les coordonnées stéréotaxiques où les pénétrations ont été effectuées incluent la totalité de l'aire PMLS, mais incluent aussi une grande partie de l'aire AMLS (Palmer et al., 1978). Ceci suggère que certaines cellules de l'aire AMLS répondent sélectivement au mouvement sur l'axe des Z et laisse croire qu'elles pourraient être sensibles à la disparité spatiale. Toutefois, l'indifférence relative à la stimulation visuelle d'une importante proportion des cellules de l'aire AMLS et leurs propriétés spatiales grossières (Minville et al., 1997) suggèrent que peu de cellules de l'aire AMLS seraient des détecteurs de disparité spatiale efficaces.

Dans la même veine, von Grünau et al. (1987) rapportent qu'une proportion importante (50%) des cellules de l'aire PLLS montrent de la sommation ou de l'inhibition binoculaire; cette proportion est toutefois considérablement inférieure à ce qui est observé par les mêmes auteurs dans l'aire PMLS (82%). De plus, les cellules de l'aire PLLS ont des CR beaucoup plus grands moins bien définis que ceux des cellules de l'aire PMLS. Von Grünau et al. (1987) avouent ne pas être en mesure de suggérer des fonctions précises pour les cellules binoculaires de l'aire PLLS et en ce sens, il serait surprenant que l'aire PLLS joue un rôle prépondérant dans l'analyse de la disparité spatiale et la stéréopsie. Le même raisonnement s'applique probablement aux autres aires suprasylviennes (ALLS, DLS, VLS) qui ont été considérablement moins étudiées. Quant aux cellules des aires 20a, 20b et

21b, la taille gigantesque et la mauvaise définition de leurs CR (Markuska, 1978; Payne et Siwek, 1990; Tardif, 1998) suggèrent qu'il est peu probable que ces aires puissent détecter et analyser des indices de disparité spatiale.

La disparité de position (décalage inter-CR) versus la disparité de phase (décalage intra-CR)

Le mécanisme qui permet aux cellules binoculaires de détecter et d'analyser les indices de disparité spatiale reste mal défini. Deux possibilités sont entretenues: le décalage entre la position des CR (inter-CR) et le décalage dans l'organisation interne des CR (intra-CR). Ces deux modèles seront décrits tour-à-tour, puis leur importance relative sera évaluée dans une perspective intégrative.

Le décalage inter-CR

Les deux CR d'une cellule binoculaire sont similaires en terme de taille, de forme et de structure, mais les deux CR de plusieurs de ces cellules occupent des coordonnées spatiales légèrement différentes (Hubel et Wiesel, 1962, 1968; Schiller et al., 1976a, 1976b; Mullikin et al., 1984a, 1984b; Maske et al., 1984, 1986; Camarda et al., 1985; Emerson et al., 1987). Ainsi, depuis Barlow et al. (1967), il est présumé que la sensibilité et la sélectivité à la disparité spatiale des cellules binoculaires dépendent de ce décalage entre la position spatiale des CR.

Le concept de la disparité de position ne sous-tend pas l'établissement d'un lien direct entre la taille du CR et le décalage inter-CR, et par conséquent entre la taille du CR et la sélectivité à la disparité spatiale de la cellule. En effet, bien que la taille et le décalage semblent aller de pair chez plusieurs cellules, il est tout à fait possible que les CR d'une cellule binoculaire soient petits tout en

montrant un important décalage inter-CR ou encore soient très grands tout en étant parfaitement superposés dans l'espace. La disparité de position est donc compatible avec la corrélation positive observée entre la taille des CR et la sélectivité à la disparité spatiale tout en étant réconciliable avec les études neurophysiologiques qui montrent des cellules avec de grands CR et une sélectivité fine à la disparité spatiale, ou l'inverse (Pettigrew et al., 1968; Ferster, 1981; Pettigrew et Dreher, 1987; LeVay et Voigt, 1988).

Le décalage intra-CR

L'importance du décalage intra-CR dans l'encodage de la disparité spatiale à été démontrée et soutenue par Ralph D. Freeman et ses collaborateurs (Ohzawa et Freeman, 1986a, 1986b; Freeman et Ohzawa, 1990; Ohzawa et al., 1990, 1997; De Angelis et al., 1991, 1993a, 1993b, 1995; Anzai et al., 1997).

Ohzawa et Freeman (1986a) ont stimulé les cellules simples du cortex visuel primaire du chat à l'aide de présentations dichoptiques de réseaux identiques (direction, fréquence temporelle, contraste) de fréquences spatiales modulées sinusoïdalement. Ils démontrent ainsi que ces cellules simples montrent des interactions binoculaires dépendantes de la phase relative des réseaux. Plus précisément, la plupart de ces cellules répondent optimalement à une phase spécifique et sont inhibées par la phase opposée (180 degré de plus) à la phase optimale. Ces interactions dépendantes de la disparité de phase disparaissent lorsque les réseaux balaient les CR dans des directions orthogonales. Ces auteurs avancent que les interactions binoculaires de la plupart des cellules simples sont issues d'une sommation linéaire des zones excitatrices et inhibitrices des CR, telles que révélées par la réponse cellulaire aux présentations monoculaires des réseaux de fréquences spatiales.

Ces mêmes auteurs (Ohzawa et Freeman, 1986b) démontrent aussi que 40% des cellules complexes montrent des interactions binoculaires dépendantes de la phase et prétendent que ces interactions sont également générées par un mécanisme de sommation linéaire. La seule autre étude portant sur le sujet chez le chat (Hammond, 1991) confirme que la plupart des cellules simples montrent des interactions binoculaires dépendantes de la phase relative de réseaux de fréquences spatiales modulés sinusoïdalement, mais démontrent par contre que la grande majorité des cellules complexes ne sont pas sensibles aux variations de phase. Des études récentes démontrent que la phase est encodée de manière similaire dans le cortex strié du singe (Smith et al., 1997).

Les interactions binoculaires dépendantes de la phase telles qu'expliquées par un processus de sommation linéaire sous-tendent l'existence d'un décalage entre les zones excitatrices et inhibitrices des deux CR d'une cellule binoculaire. Hubel et Wiesel (1962) ainsi que Maske et al. (1984) prétendent que toutes les cellules corticales ont une organisation spatiale interne identique, mais leur techniques campimétriques ne sont possiblement pas assez précises pour révéler le décalage intra-CR. En utilisant la méthode de la corrélation inversée (Eggermont et al., 1983; Jones et Palmer, 1987a, 1987b) qui permet une évaluation très précise de la position spatiale des zones excitatrices et inhibitrices qui constituent les CR, Freeman et ses collaborateurs (Freeman et Ohzawa, 1990, Ohzawa et al., 1990; De Angelis et al., 1991, 1995) démontrent l'existence du décalage intra-CR et ainsi corroborent leur propre théorie. Cette méthode est basée sur l'inversion du sens de la recherche d'une relation de causalité entre le stimulus et la réponse.

> "A spike is observed and then we look backward in time to determine the stimulus that led to the generation of the spike. There is an optimal value for this time delay for each neuron, determined primarily by the visual latency of the pathway involved. From the work of Jones and Palmer (1987a, 1987b) and from our own data, we know that a 50 msec delay is very effective for recordings from cells in the striate cortex. We thus identify the causal stimulus by using a fixed correlation delay, i.e. 50 msec." (Freeman and Ohzawa, 1990)

Ce modèle implique une relation plus directe entre la taille du CR et la sélectivité à la disparité spatiale de la cellule. En effet, les cellules ayant de petits CR ne peuvent avoir un grand décalage intra-CR et sont par conséquent sensibles aux petites disparités spatiales. De la même manière, les cellules ayant des CR plus grands sont sensibles à des disparités spatiales plus grandes puisque les grands CR sont, en ce qui a trait à leur structure interne, des versions agrandies des petits CR (Howard et Rogers, 1995). En ce sens, ce modèle sous-tend que la taille du CR permet de prédire l'ordre de grandeur du décalage intra-CR et subséquemment la sélectivité à la disparité spatiale d'une cellule donnée; ce qui n'est pas toujours vrai.

Encodage de la disparité spatiale: position versus phase

De nombreuses études neurophysiologiques soutiennent les deux modèles décrits précédemment. Ainsi, la communauté scientifique accepte la coexistence des deux mécanismes d'encodage de la disparité spatiale (Wagner et Frost, 1993; Fleet et al., 1996; Zhu et Qian, 1996; Ohzawa et al., 1997; Anzai et al., 1997). Gian F. Poggio, un des chercheurs les plus influents du domaine, formule ainsi son acceptation de la validité des deux mécanismes proposés.

> "Horizontal disparity sensitivity is obtained because left and right RFs of the cortical neuron are not spatially matched, either because of a positional incongruity of two fields of identical structure, or because of a lateral spatial misalignment of synergistic subfields within the left and right fields which are as a whole coextensive over corresponding retinal regions." (Poggio, 1995a).

Dans la même veine, il faut aussi accepter un degré d'interaction entre le décalage inter-CR et le décalage intra-CR. En effet, une cellule binoculaire montrant un décalage inter-CR peut également montrer un décalage intra-CR. Il est donc possible, voir probable, que ces deux types de décalages s'annulent ou s'additionnent et ainsi contribuent ensemble à déterminer la sélectivité à la

disparité spatiale de la cellule. D'ailleurs, pour une cellule binoculaire donnée, toute incertitude vis-à-vis la position des CR monoculaires produit automatiquement une incertitude correspondante dans la calibration du décalage intra-CR par cette cellule. En ce sens, le décalage intra-CR n'est pas indépendant du décalage inter-CR (Howard et Rogers, 1995). Poggio (1995b), conscient de l'indissociabilité des deux mécanismes, préfère ainsi intégrer les concepts de disparité de position (décalage inter-CR) et de phase (décalage intra-CR) pour parler simplement de disparité de CR.

> "Regardless of its structural basis, the phenomenon of receptive field disparity is thought to play a basic role in stereopsis because under conditions of binocular fixation, different groups of cortical neurons will be selectively activated by objects at different relative depths." (Poggio, 1995b)

Freeman et ses collaborateurs (Ohzawa et al., 1997; Anzai et al., 1997) persistent toutefois à tenter de démontrer la prédominance du décalage intra-CR et de la disparité de phase. Ohzawa et al. (1997) étudient la sensibilité à la disparité de phase de cellules corticales sans jamais aborder la question de la disparité de position. Tout en admettant ignorer les fonctions relatives de la disparité de position et de la disparité de phase, ils adoptent une position dichotomique en faveur de la disparité de phase et terminent leur article sur ce commentaire laconique et paradoxal:

> "Although the relative role of phase and incongruency encoding remains to be determined, we believe the system outlined here (phase disparity) may be primary in the neural processing of retinal disparity." (Ohzawa et al., 1997)

L'étude de Anzai et al. (1997) semble à première vue plus apte à apporter de l'eau au moulin, puisqu'elle est la seule qui examine le décalage inter-CR et le décalage intra-CR dans un même échantillon de cellules corticales. Ces auteurs démontrent que les distributions des deux types de décalages montrent toutes deux une courbe quasi-normale centrée autour de zéro. Ils montrent aussi que l'écart-type des décalages intra-CR (0.59 degrés) est plus grand que l'écart-type des décalages

inter-CR (0.52 degrés, ou 0.37 degrés après l'ajustement qu'ils proposent pour obtenir la disparité de position "vraie" a partir de la disparité de position relative qu'ils mesurent en utilisant une cellule de référence). En se basant sur ces écart-types, ils avancent ceci:

> "We find that RF position disparities are generally limited to small values that are not sufficient to encode large binocular disparities. In contrast RF phase disparities cover a wide range of binocular disparities... These results indicate that binocular disparity is mainly encoded through RF phase disparity. However, RF position disparity may play a significant role for cells with high spatial frequency selectivity, which are constrained to small RF phase disparities." (Anzai et al., 1997)

Ces conclusions semblent hâtives et peu défendables. En effet, un examen détaillé des méthodes et des résultats de cette étude révèlent un certain nombre de points litigieux. Premièrement, le décalage inter-CR n'a été évalué que pour 29 cellules, comparativement à 97 cellules pour le décalage intra-CR. Deuxièmement, l'évaluation précise du décalage inter-CR chez le chat anesthésié et paralysé comporte un certain niveau d'incertitude puisque cette préparation rend impossible la fixation et subséquemment la superposition des CR. Troisièmement, la méthode de la cellule de référence utilisée par Anzai et al. (1997) ne fournit que des valeurs relatives. Ainsi, bien qu'elle permette l'élaboration d'une distribution globale des décalages inter-CR, elle ne permet pas de corrélation entre le décalage inter-CR et la sensibilité à la disparité spatiale d'une cellule donnée. Ces auteurs reconnaissent implicitement cette lacune en ne montrant aucun profil de sensibilité à la disparité spatiale. Quatrièmement, toutes les cellules de cette étude sont de type simple et ont été enregistrées dans le cortex visuel primaire. Ce double biais d'échantillonnage favorise la disparité de phase puisque les cellules simples y sont beaucoup plus sensibles que les cellules complexes (Ohzawa et Freeman, 1986a, 1986b) et que des cellules sensibles à la disparité de phase n'ont pas été identifiées ailleurs que dans le cortex visuel primaire. Cinquièmement, la distribution des décalages inter-CR montre que certaines cellules ont un décalage de deux degrés, ce qui est aussi large que la taille moyenne des CR de cette région (Hubel et Wiesel, 1959, 1962; Movshon, 1978c, LeVay et Voigt,

1988; Lepore et al., 1992) et en aucun cas représente un décalage "limited to small values that are not sufficient to encode large binocular disparities" (Anzai et al., 1997). Sixièmement, la distribution des décalages inter-CR correspond mieux aux disparités optimales des cellules de l'aire 17 que la distribution des décalages intra-CR. En effet, les cellules de l'aire 17 montrent des disparités optimales, qui sont en grande partie (Ferster, 1981; LeVay et Voigt, 1988) ou en presque totalité (Lepore et al., 1992) inférieures à un degré. Septièmement et finalement, Anzai et al., (1997) avouent eux-même l'indissociabilité des deux mécanismes: "Position and phase disparity are largely independent of each other; they may add up or partially cancel each other" (Anzai et al., 1997), mais n'en tiennent aucunement compte dans l'interprétation de leurs résultats.

La disparité de position et la disparité de phase sont indissociables et toute tentative de ségréguer leurs effets pour démontrer la suprématie de l'un aux dépends de l'autre semble vain. Ces faux problèmes à saveur dichotomiques sont malheureusement fort populaires dans les milieux scientifiques; il suffit de penser aux débats millénaires de l'hérédité versus l'environnement et du déterminisme versus le libre arbitre. Ainsi, il semble raisonnable d'accepter que les décalages inter- et intra-CR interagissent pour former la disparité de CR (Poggio, 1995) et déterminent ainsi ensemble la sélectivité à la disparité spatiale des cellules binoculaires, à tout le moins au niveau du cortex visuel primaire. En effet, la situation n'est peut être pas identique dans les aires extrastriées ou au niveau du collicule supérieur. La prépondérance de cellules complexes (Hubel et Wiesel, 1965, 1969; Sterling et Wickelgren, 1969; Berman et Cynader, 1972; Spear et Baumann, 1975; Spear, 1985) et les vastes décalages inter-CR (Berman et al., 1975; Pettigrew et Dreher, 1987; Wang et Dreher, 1996) des cellules binoculaires des aires extrastriées et du collicule supérieur laissent croire que la disparité de position serait prépondérante dans ces régions visuelles, comme le laissent supposer les études de cette thèse. Cette perspective, qui semble soutenue par le fait qu'aucune étude ne montre

des interactions binoculaires dépendantes de la phase à l'extérieur du cortex visuel primaire, rejoint le modèle classique de De Valois et De Valois (1988).

Un regard plus large sur les mécanismes stéréoscopiques

La disparité spatiale horizontale joue un rôle majeur dans la perception de la profondeur et de la troisième dimension (Wheatstone, 1838; Julesz, 1960, 1971) mais il ne faut toutefois pas croire que c'est le seul indice binoculaire utile à la perception stéréoscopique. En effet, la disparité spatiale verticale, la disparité d'orientation, la disparité de périodicité spatiale et la disparité de courbure ont aussi leur importance, bien que leurs fonctions soient plus effacées. De plus, il faut considérer l'importance du mouvement dans la perception de la profondeur. Tous ces indices semblent nécessaires pour une parfaite compréhension de la scène visuelle tridimensionnelle.

La disparité spatiale verticale

Des disparités spatiales verticales non-désirables sont constamment créées par le mauvais alignement (vertical ou torsionnel) des yeux. Des études psychophysiques démontrent que la perception de la profondeur basée sur des disparités spatiales horizontales se détériore lorsque de telles disparités spatiales verticales, même infimes, sont introduites (Ogle, 1955; Fender et Julesz, 1967; Nielsen et Poggio, 1984). Poggio (1995a, 1995b) corrobore ces résultats au niveau neurophysiologique en démontrant qu'une disparité verticale de 0.1 degré réduit considérablement ou même abolit la réponse à la disparité spatiale horizontale des cellules des aires V3 et V3A du singe. Ces disparité verticales peuvent sembler nuisibles, mais elles remplissent en fait une fonction très importante. En effet, elles servent de stimuli pour la vergence verticale (Duwaer et van den Brink,

1981, 1982) et la cyclovergence (De Bruyn et al., 1992), deux mécanismes qui assurent un alignement oculaire parfait et ainsi une perception optimale des indices de disparité spatiale horizontale.

Des disparité spatiales verticales sont aussi engendrées par la stéréogéométrie de l'information lumineuse qui est réfléchie sur les surfaces de la scène visuelle pour par la suite s'imprimer sur les deux rétines. En effet, le facteur de magnification linéaire de chaque image rétinienne peut être différent pour un stimulus donné, selon sa position sur l'axe vertical et sa distance, particulièrement lorsque cette dernière est courte. Ce type de disparité spatiale verticale semble jouer un rôle dans la perception de l'inclinaison des surfaces frontales, tel que démontré par l'effet induit (Green, 1889; Lippincott, 1889; Ogle, 1938; Mayhew et Longuet-Higgins, 1982; Gillam et Lawergren, 1983; Rogers et Koenderink, 1986). Cet effet, tel que démontré en plaçant une lentille aniséikonique devant un oeil (Ogle, 1938; Gillam, 1968) implique que la magnification verticale d'une des images rétiniennes créé la perception de l'inclinaison autour de l'axe vertical d'une surface verticalement disposée sur le plan fronto-parallèle. Ainsi, lorsque l'image rétinienne droite d'une telle surface est magnifiée verticalement, cette surface semble plus près de l'observateur à droite qu'à gauche. Comme cette impression de profondeur est créée en l'absence de tout indice de disparité spatiale horizontale, il faut accepter que dans certaines conditions, la disparité spatiale verticale joue un rôle important dans la perception stéréoscopique.

Plus récemment, il a aussi été proposé que la disparité spatiale verticale joue un rôle dans la perception non seulement de l'inclinaison, mais aussi de la profondeur absolue, de la taille et de la forme des surfaces frontales (Rogers et Bradshaw, 1993, 1995). Ces auteurs utilisent des stimuli énormes (75 degrés en moyenne) et avancent que l'absence de ces effets rapportés précédemment (Sobel et Collett, 1991; Cummings et al., 1991) est due à la taille trop petite (11 degrés en moyenne)

de leurs stimuli. L'importance de la taille des stimuli est corroborée par les études psychophysiques de Westheimer (1978, 1984) qui démontrent que la sensibilité à la disparité verticale est approximativement dix fois moindre que la sensibilité à la disparité spatiale horizontale.

Au niveau neurophysiologique, plusieurs cellules montrent un décalage inter-CR vertical indépendamment de leur décalage inter-CR horizontal (Hubel et Wiesel, 1962, 1965, 1969; Barlow et al., 1967; Berman et al., 1975; De Angelis et al., 1991; Anzai et al., 1997) et plusieurs cellules montrent aussi une certaine sensibilité à la disparité spatiale verticale (Barlow et al., 1967; Pettigrew et al., 1968; De Angelis et al., 1991). Le substrat neurologique de l'encodage de la disparité spatiale verticale semble donc similaire, voir identique, à celui de l'encodage de la disparité spatiale horizontale. De Angelis et al. (1991) notent que les cellules de l'aire 17 préférant les stimuli orientés horizontalement et dont l'input principal est la disparité spatiale verticale semblent avoir très peu ou pas du tout de décalage intra-CR. Ceci laisse supposer que la disparité spatiale verticale est principalement encodée par le décalage inter-CR et dépend donc fortement du mécanisme de la disparité de position.

Les autres indices de disparité binoculaire

Pour plusieurs cellules binoculaires du chat, l'orientation d'un stimulus produisant la réponse cellulaire la plus robuste diffère d'un CR à l'autre (Blakemore et al., 1972). Cette différence est habituellement petite, mais peut atteindre 15 degrés (Blakemore et al., 1972; Nelson et al., 1977). Ces auteurs démontrent aussi de la facilitation binoculaire lorsque les stimuli présentés aux deux CR sont optimaux en terme d'orientation et une baisse progressive de la réponse cellulaire à mesure que les orientations des stimuli s'éloignent de ces valeurs. Ces différences interoculaires et ces interactions

binoculaires, qui ont aussi été observées en l'absence d'indice de forme chez le singe éveillé (Hänny et al., 1980; Hänny et van der Heydt, 1982), suggèrent que différentes cellules sont sensibles à différentes disparités d'orientation. Des études psychophysiques (Braddick, 1979; Gillam et Rogers, 1991) suggèrent que ces disparités d'orientation peuvent être utilisées par l'organisme pour évaluer la profondeur et l'inclinaison de surfaces frontales.

Dans la même veine, Hammond et Pomfrett (1991) démontrent que pour la majorité des cellules binoculaire du cortex visuel primaire du chat, la fréquence spatiale optimale pour la stimulation de chaque CR est légèrement différente. Le même phénomène a aussi été démontré dans l'aire 19 (Bergeron et al., 1998). Ces cellules préfèrent habituellement des fréquences spatiales plus hautes dans l'oeil dominant. Des études extrêmement récentes démontrent que des stimulations dichoptiques avec des réseaux de fréquences spatiales légèrement différents produisent des interactions binoculaires pouvant être reliés à des mécanismes de fusion et de rivalité binoculaire, mais aussi à la perception de surfaces frontales inclinées (Saint-Amour et al., 1998).

Enfin, Rogers et Cagenello (1989) démontrent qu'une légère différence dans la courbure de lignes présentées dichoptiquement produit une sensation marquée de courbure tridimensionnelle, comparable a celle d'une surface bombée de manière concave ou convexe. De Angelis et al. (1994) montrent d'ailleurs des cellules binoculaires répondant sélectivement à différents degrés de courbure et soutiennent que cette sélectivité est fortement corrélée avec la sensibilité relative des CR d'une cellule à la longueur des stimuli.

La détection du mouvement dans l'espace tridimensionnel

Bien que certaines cellules corticales et colliculaires répondent à la présentation monoculaire de stimuli semblant s'approcher ou s'éloigner de l'organisme (Updyke, 1974; Zeki, 1974; Regan et Cynader, 1979; Rind et Simmons, 1992; Colby et al., 1993), des mécanismes binoculaires semblent remplir des fonctions clés dans la détection et l'analyse du mouvement le long de l'axe des Z.

Pettigrew (1973) et Zeki (1974) montrent des cellules répondant à des direction opposées dans chaque oeil; un mouvement de ce genre est généré par les côtés (edges) d'un objet s'éloignant de l'organisme ou s'approchant directement vers ce dernier. Chez l'humain, David Regan et ses collaborateurs montrent que les potentiels visuels évoqués par un stimuli dichoptique simulant un mouvement fronto-perpendiculaire sont différents de ceux simulant un mouvement fronto-parallèle (Regan et Spekreijse, 1970) et que les potentiels évoqués par des stimuli simulant l'approche d'un objet sont différents des potentiels évoqués par des stimuli simulant son éloignement (Regan et Beverley, 1973).

Cynader et Regan (1978, 1982) présentent stéréoscopiquement des stimuli simulant le déplacement d'une barre dans différentes directions sur le plan horizontal et enregistrent la réponse des cellules binoculaires du chat aux différentes directions simulées. Ils divisent ainsi les cellules en trois catégories de détecteurs. Les premières répondent de manière robuste à des présentations simulant un impact avec la tête du chat; ces cellules répondent donc optimalement à des directions de mouvement opposées dans les deux CR. Les secondes répondent optimalement à des présentations simulant des objets se déplaçant dans une trajectoire tridimensionnelle, mais sans être dans une trajectoire de collision avec l'animal; ces cellules répondent donc optimalement à des directions

identiques, mais des vitesses différentes dans les deux yeux. Les troisièmes répondent optimalement aux stimuli se déplaçant sur l'axe fronto-parallèle, soit se déplaçant dans la même direction et à des vitesses identiques dans les deux CR.

Des cellules répondant au mouvement tridimensionnel sont aussi présentes dans les aires suprasylviennes médianes du chat (Toyama et Kozasa, 1982; Toyama et al., 1985, 1986a, 1986b) et dans les aires 17 et 18 du singe (Poggio et Talbot, 1981). Spileers et al. (1990) qui répliquent les études de Cynader et Regan (1978, 1982) laissent supposer, comme cela a déjà été suggéré en parlant des cellules sensibles à la disparité spatiale, que ces cellules forment une carte tridimensionnelle permettant l'analyse du flux optique.

La synergie et la complémentarité entre les multiples indices binoculaires de profondeur

Les expériences psychophysiques de Wheatstone (1938) et de Julesz (1960, 1971) démontrent que des indices de disparité spatiale horizontale peuvent à eux seuls créer une impression marquée de profondeur, même en l'absence d'indices structuraux. De plus, la détection de la disparité spatiale horizontale est de loin le plus précis des mécanismes stéréoscopiques; une variation rétinienne d'un micron est suffisante pour détecter une différence de profondeur entre deux stimuli (Yellot, 1981).

La disparité spatiale horizontale génère une perception encore plus précise de la profondeur et une impression encore plus marquante de la tridimensionnalité lorsqu'elle coexiste avec des indices monoculaires. Plusieurs études relèvent notamment une interaction particulièrement importante entre la disparité spatiale horizontale et la parallaxe de mouvement (Graham et Rogers, 1982; Adelson et Movshon, 1982; Richards, 1985; Nawrot et Blake, 1989; Qian, 1994; Bradshaw et Rogers, 1996).

Au niveau neurophysiologique, les études décrites dans le présent ouvrage et ailleurs (Maunsell et Van Essen, 1983; Roy et Wurtz, 1990, Roy et al., 1992; Grasse et al., 1994; Bradley et al., 1995; Ohzawa et al., 1996) démontrent d'ailleurs que plusieurs cellules sont sélectives à la fois au mouvement et à la disparité spatiale et que ces deux éléments interagissent au niveau cellulaire.

L'intégration de la disparité spatiale et du mouvement au niveau physiologique est logique, puisque la plupart des mouvements comportent un gradient de fronto-perpendicularité et génèrent ainsi automatiquement des disparités spatiales. Ceci est particulièrement vrai lorsque l'organisme se déplace dans l'espace. Que ce soit l'organisme ou l'objet qui se déplace sur l'axe des Z, la fovéation et le maintien de celle-ci demande des ajustements continuels de vergence et d'accommodation, qui sont initiés et contrôlés par les indices de disparité spatiale (Rashbass et Westheimer, 1961a, 1961b; Westheimer et Mitchell, 1969). Donc, la détection et l'analyse du mouvement tridimensionnel dépend au moins partiellement des indices de disparité spatiale, directement et/ou indirectement par le biais de l'angle de vergence ou du degré d'accommodation que ces indices commandent (Ritter, 1977; von Hofsten, 1979; Foley, 1980; Morrisson et Whiteside, 1984; Bishop, 1989; Collett et al., 1991; Cummings et al., 1991; Trotter, 1995). L'importance des cellules sensibles à la disparité spatiale de l'aire PMLS et du collicule supérieur dans ces mécanismes a déjà été commentée dans les chapitres 3 et 4 de cette thèse. Ces interactions entre le mouvement, la disparité et les mécanismes oculomoteurs suggèrent aussi que la disparité spatiale est liée à l'analyse du flux optique et ainsi dans l'analyse de la progression d'un organisme dans son environnement (Roy et al., 1992). Les cellules sensibles à la disparité spatiale et sélectives à la direction du mouvement de Roy et al. (1992) et des présentes études démontrent d'ailleurs qu'un des attributs principaux du mouvement, la direction, est intégré avec la disparité spatiale au niveau de la cellule et que l'un influence la réponse de la cellule à l'autre.

La disparité spatiale horizontale est donc un indice stéréoscopique extrêmement puissant et efficace; ses fonctions dans la perception de la profondeur sont nombreuses et diversifiées. En ce sens, les autres indices de disparité binoculaire peuvent sembler superflus. Il faut toutefois reconnaître que ces indices, en plus de contrôler les mouvements compensatoires de vergence verticale et de cyclovergence, jouent un rôle important dans la perception stéréoscopique des surfaces frontales. Ces surfaces, particulièrement lorsqu'elles sont uniformes, produisent peu d'indices de disparité horizontale et la détermination de leur profondeur ou de leur inclinaison, que l'organisme effectue sans efforts et sans erreurs, doit dépendre largement des autres indices de disparité (Braddick, 1979; Gillam et Rogers, 1991; Rogers et Bradshaw, 1993, 1995; Saint-Amour et al., 1998). Cette situation où les perceptions stéréoscopiques ne peuvent dépendre exclusivement de la disparité spatiale horizontale semble toutefois n'être que l'exception qui confirme la règle.

CONCLUSION GÉNÉRALE

Les études de la présente thèse démontrent que la disparité spatiale est encodée par des cellules binoculaires tout au long du système visuel du chat. Ces études démontrent aussi que les différentes régions visuelles étudiées n'encodent pas la disparité spatiale de manière identique. Sur la base de ces différences d'encodage (pourcentage de cellules sensibles, types de détecteurs de disparité, sélectivité à la disparité spatiale), les études de cette thèse proposent que les différentes régions visuelles jouent des rôles distincts dans la perception stéréoscopique de la profondeur et de la troisième dimension.

En résumé, nos résultats suggèrent que l'analyse stéréoscopique d'un stimulus, chez le chat normal, s'effectue en deux temps: la localisation dans l'espace tridimensionnel, la fovéation et le maintien de la fixation, sous contrôle des mécanismes suprasylviens et colliculaires, puis l'analyse précise du relief de l'objet et la reconstruction de sa "solidité" stéréoscopique par les mécanismes de stéréopsie fine du cortex visuel primaire.

Si le rôle du cortex visuel primaire dans la stéréopsie fine est bien démontré, particulièrement par lésion de cette région visuelle, les mécanismes spécifiques par lesquels les cellules sensibles à la disparité spatiale de l'aire PMLS et du collicule supérieur contrôlent la vergence et le maintien de la fixation restent mal définis. Des expériences chez l'animal éveillé ont démontré la présence de cartes sensorielles du plan fronto-parallèle dans les couches superficielles du collicule supérieur. Ces cartes sont d'ailleurs coextensives avec les cartes motrices des couches profondes qui contrôlent les mouvements oculaires. La suite logique de ces expériences et de celles décrites dans cette thèse est donc de tenter de cartographier des cartes tridimensionnelles de l'espace visuel dans le collicule supérieur ou même dans l'aire PMLS d'animaux éveillés, et ce en utilisant des stimuli se déplaçant sur l'axe des Z. Une telle cartographie confirmerait l'importance des mécanismes d'encodage de la

disparité spatiale suprasylviens et colliculaires dans la détection et la fovéation d'objets dans l'espace tridimensionnel.

Les expériences de cette thèse montrent aussi des cellules sensibles à la disparité spatiale dans l'aire PMLS et dans le collicule supérieur du chat Siamois. Ceci laisse supposer que ces chats jouissent de capacités stéréoscopiques grossières, ce qui se doit d'être testé et démontré comportementalement. La suite logique de ces études serait alors de pratiquer des lésions de l'aire PMLS et/ou du des couches superficielles du collicule supérieur chez ces chats et ainsi démontrer que ces capacités stéréoscopiques grossières sont bien générées par les cellules colliculaires et suprasylviennes sensibles à la disparité spatiale. La combinaison de ces études chez le chat Siamois avec celles proposées précédemment chez le chat normal éveillé permettrait de définir avec plus de certitude les fonctions colliculaires et suprasylviennes dans la stéréopsie.

Finalement, il serait particulièrement intéressant de conduire des études portant sur l'intégration sensori-motrice de tous les indices de profondeurs, tant visuels qu'auditifs, au niveau colliculaire. En combinant des protocoles comportementaux et électrophysiologiques, il serait possible d'évaluer où et comment ces différents indices de profondeur sont intégrés et il serait peut-être même envisageable d'évaluer, à l'aide de lésions sélectives ou d'inactivations temporaires, où et comment l'organisme planifie et exécute les réponses comportementales appropriés.

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