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Mécanismes de la perception du mouvement : Implications des boucles cortico-thalamiques

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Table of Contents

Résumé

Parmi la multitude de fonctions que le système visuel effectue, la perception du mouvement est l'une des plus importantes. Il a été clairement démontré qu'il existe des sites cérébraux spécifiques pour la détection, l'analyse et l'intégration du mouvement. De façon classique, les mécanismes neurophysiologiques qui sous-tendent ces processus sont attribués aux aires corticales. Le thalamus quant à lui, est généralement considéré comme un « relais passif », c'est à dire qui transmet l'information sensorielle vers le cortex sans modifier le signal entrant.

Le but de ce projet sera de préciser les mécanismes nerveux impliqués dans la perception et l'intégration du mouvement et plus précisément, la contribution des régions cérébrales sous-corticales et corticales intimement liés par des connexions réciproques. Ces régions sont: le complexe LP-pulvinar, situé dans le thalamus, l'aire extra-striée postero-médiane suprasylvienne (PMLS) et le cortex ectosylvien visuel antérieur (AEV); deux régions corticales ayant un rôle spécialisé dans l'analyse du mouvement.

Les expériences ont été réalisées sur des chats adultes normaux anesthésiés. Une microélectrode d'enregistrement a été descendue dans ces trois sites afin d'enregistrer l'activité des neurones. Les réponses neuronales à des réseaux sinusoïdaux, des patrons texturés (« bruit visuel ») et des « plaids » ont été caractérisé pour étudier les mécanismes

qui sous-tendent l'intégration du mouvement au niveau cellulaire. Afin de caractériser d'avantage ce lien, l'influence des aires corticales sur les propriétés thalamiques a été déterminée par inactivation locale réversible (i.e. micro-injection de l'acide γ-aminobutyrique; GABA) ou par inactivation permanente plus vaste (i.e. ablation chirurgicale).

Les résultats de cette étude se résument comme suit : 1) les propriétés des réponses neuronales du PMLS au bruit visuel sont similaires à celles du LP-pulvinar. Ce résultat suggère que les processus d'analyse impliquant une boucle cortico-thalamique PMLS-LP sont comparables au niveau cortical et sous-cortical. 2) les neurones du PMLS et du LP peuvent coder le mouvement relatif entre un objet et son arrière-plan. De plus, l'inactivation réversible du LP perturbe ces réponses au niveau du PMLS. Ces résultats sont essentiels dans l'établissement d'un lien fonctionnel entre ces deux régions quant à l'analyse de certains aspects du mouvement. 3) certains neurones du complexe LP-pulvinar sont capables d'intégrer l'information directionnelle telle que définie par des « plaids ». Ceci constitue la première démonstration de propriétés de haut-niveau en dehors du cortex. De plus, cette découverte suggère que le LP-pulvinar participe de façon parallèle et en coopération avec le cortex dans l'analyse de scènes visuelles complexes via l'exploitation des boucles cortico-thalamiques.

Les résultats de cette étude sont importants non seulement pour appuyer des notions théoriques novatrices sur le rôle du thalamus, mais aussi dans le but de réévaluer et de préciser les mécanismes nerveux qui sous-tendent la perception du mouvement et l'intégration sensorielle en général.

Summary

Among the multitude of functions the visual system carries out, the perception of motion is one of the most important. It has been clearly demonstrated that the visual system contains numerous specialised areas implicated in the detection, analysis, and integration of motion. Classically, the neurophysiological mechanisms underlying these processes have been uniquely attributed to regions of the cerebral cortex. The thalamus for its part, has generally been regarded as a passive relay transferring information to the cortex without any modification of the sensory signal.

The purpose of this study is to investigate the neurophysiological mechanisms implicated in the perception and integration of motion and more specifically, delineate the contribution of cortical and subcortical structures that are intimately related via reciprocal connections. These areas are: the LP-pulvinar complex; located in the thalamus, and the extrastriate posteromedial lateral suprasylvian (PMLS) and anterior ectosylvian visual (AEV) cortical areas; two regions whose role in motion analysis are well established.

Experiments were carried out on normal adult anaesthetised cats. A recording microelectrode was descended in one of the aforementioned areas to record neuronal activity. Neuronal responses to drifting sine-wave gratings, moving texture patterns ("visual noise"), and "plaid patterns" were recorded in order to investigate the mechanisms underlying the

integration of motion information at the neuronal level. As a continuation of the study, the influence of cortical motion areas on recorded thalamic responses will be determined by local reversible deactivation (i.e. micro-injection of γ-aminobutyric acid; GABA) or by irreversible deactivation (i.e. surgical ablation).

The results of the study are as follows: 1) Response properties of PMLS neurons to moving texture patterns are similar to those found in the LP-pulvinar complex. These results suggest that motion processing along both components of the PMLS-LP cortico-thalamic loop is carried out within a similar envelope of analysis. 2) Neurons in both PMLS and LP are able to code the relative motion of an object with respect to its background. Furthermore, reversible deactivation of LP disrupts these responses in PMLS. These results are important in establishing that both these areas are functionally linked in the analysis of specific aspects of motion. 3) The fact that pattern-selective responses to moving plaids can be found in the LP-pulvinar complex suggests that this area is capable of carrying out higher-order motion computations. The importance of this later results is two-fold. First, these findings represent the first demonstration that higher-order properties exists outside extrastriate cortical areas. Second, they further suggest that certain thalamic nuclei, via the establishment of cortico-thalamic loops, participate in parallel and in co-operation with the cortex in the analysis of complex visual scenes.

The results of this study are important not only to reinforce current and novel theoretical notions regarding the role of the thalamus, but also in the re-evaluation of the neurophysiological mechanisms involved in motion perception and sensory integration as a whole.

List of Figures

List of Abbreviations

AEV	anterior ectosylvian visual cortex
deg	degrees
°/sec	degrees per second
GABA	γ-aminobutyric acid
LGN	lateral geniculate nucleus
LP	lateral posterior nucleus
LPl	lateral part (striate recipient zone) of the lateral posterior nucleus
LPm	medial part (tectal recipient zone) of the lateral posterior nucleus
LS	lateral suprasylvian cortex
msec	milliseconds
MT	middle temporal area
MST	medial superior temporal area
PMLS	posteromedial lateral suprasylvian cortex
PSTH	peri-stimulus time histogram
RF	receptive field
sec	seconds
SEM	standard error of the mean
SC	superior colliculus
SD	standard deviation error
SF	spatial frequency
Sp/sec	spikes per second
TF	temporal frequency
V1	primary visual area
V5	visual area 5 (equivalent to area MT)

To my father for his honour and my mother for her courage,

To all of you who believed in me at a time when I was learning to believe in myself,

…and finally, to the Sven, Danny, and Dylan in all of us.

…the cause and purpose of God's invention and gift to us of sight was that so we should see the revolutions of intelligence in the heavens above and use their untroubled course to guide the troubled revolutions of our own understanding…

-Plato

1. Introduction

1.1 General Introduction

Vision is the sense we rely on the most to perceive the world around us. Of all the functions of which the visual system subserves, the perception of motion is arguably the most well-understood sensory sub-system (Cavanagh and Mather, 1989; Movshon, 1990; Albright and Stoner, 1995). Motion perception allows many species throughout the evolutionary scale to interact effectively with their environment and this basic computational task has likely evolved early on. This latter statement is supported by the fact that not all organisms possess the ability to perceive all attributes of a visual scene such as colour and depth. However, the great majority are able to detect motion to varying degrees. It is not surprising therefore that sophisticated mechanisms for analysing and integrating motion exist within the visual brain (van Essen and

Gallant, 1994). To date, the lasting problem in sensory neurophysiology has been to identify and understand these mechanisms, and how they mediate our perception of the visual world (Movshon et al., 1985; Nakayama, 1985; Maunsell and Newsome, 1987; Movshon, 1990; Stoner and Albright, 1994).

1.2 Motion Perception: Historical Perspectives

One of the most compelling accounts pointing to the existence of a specific area of the brain implicated in motion analysis was the "motion blind" patient reported by Zihl and colleagues (Zihl et al., 1983). In a well-documented case study, a patient named L.M. had suffered severe bilateral cerebral vascular damage (superior sagittal sinus thrombosis) affecting the lateral temporo-occipital cortex and underlying white matter while the striate cortex was apparently unaffected. Brain imaging analysis revealed that the locus of the cerebral damage encompassed the posterior part of the middle temporal gyrus. Clinical assessment of her visual field showed that there was no restriction nor associated scotoma, and her visual functions such as acuity, binocularity, and perception of colour and form appeared to be normal. However, she was unable to perceive the motion of objects in all three dimensions in several tasks. For example, when presented with light targets moving at speeds greater than 10-

14°/sec, she was uncertain whether targets were stationary or in motion. Specifically, she would report seeing the appearance of the target at successive positions with no continuity in movement. Furthermore, this disturbance was specific to the visual modality as she was nonetheless able to perceive motion elicited by auditory and tactile cues.

> *"...She had difficulty, for example, in pouring tea or coffee into a cup because the fluid appeared to be frozen, like a glacier. In addition, she could not stop pouring at the right time since she was unable to perceive the movement in the cup when the fluid rose."*
>
> *from Zihl et al., 1983*

In an earlier study in the *macaque* monkey, Zeki (1974) reported that a cortical area buried within the posterior bank of the superior temporal sulcus was apparently specialised for visual motion analysis. Neurons in this extrastriate area (termed visual area 5, or "V5") were highly selective for stimulus direction and speed, and relatively insensitive to colour and form (Zeki, 1974). Parallel studies in the owl (New World) monkey have referred to this region as the middle-temporal area (or "MT") and represents an alternative term to V5 (Maunsell and van Essen, 1983a,b).

Given the localisation of cortical damage and specificity of the visual disturbance regarding the patient reported by Zihl and colleagues (1983) (later termed "akinetopsia"; Zeki, 1991), it seemed likely that the cortical area affected was comparable to the visual motion area identified in the monkey (Newsome et al., 1985[1]; Tootell et al., 1995; Tootell and Taylor, 1995).

Together, the results of these findings were instrumental in advancing two very important concepts: the first was the establishment of functional specialisation within the visual cortex, and the second was the fact that motion perception appeared to have a designated cortical locus situated well beyond the primary visual cortex (Zihl et al., 1983; Zeki, 1991; Rizzo et al., 1995, Tootell et al., 1995; Tootell and Taylor, 1995).

1.3 The Integration of Motion: Computational Considerations

Much of the conceptual framework underlying motion perception was inspired from the pioneering work in electrophysiology of Barlow in rabbit retina (e.g. Barlow and Levick, 1965) and Hubel and Wiesel in cat visual cortex (see Hubel, 1988). These studies were among the first to demonstrate that visual neurons could be highly selective to elementary properties such as the direction and speed of a moving object. However, the visual world around us is much more complex. Thus, much of the recent work in motion perception has focused on how the visual system combines and integrates local information signals belonging to a common

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[1] Behavioural studies by this group in primates have confirmed that bilateral chemical lesioning of area MT produces deficits in the monkey's ability to discriminate and perceive complex motion.

physical object in order to provide a unified and stable percept (Movshon et al., 1985; Stoner and Albright, 1994). In theoretical studies (e.g. Marr, 1982), the obstacle concerning motion detection has been termed the "Aperture Problem". The problem stems from the directional ambiguity that results when observing a limited portion of a moving image (as is the case when observing through a small finite aperture). Figure 1 illustrates the problem with the motion of a two-dimensional diamond-shape object (A). As the diamond moves to the right, the direction of the local motion measurement signalled through a circular aperture is diagonally downward and to the right. This first observation illustrates that the direction of motion signalled by the motion detector does not correspond to the overall direction of motion of the object. Further complicating matters, if the identical diamond now moves downwards, the *same* local direction of motion detected previously (diagonally downward and to the right) is signalled by the detector. Thus, local measurements of motion are inherently limited and insufficient in defining the motion of the entire object. Resolving the ambiguity would necessitate an integration of local motion signals from at least two sources (B). The formal solution would be extracted by the intersection of constraints (i.e. vectorial sum) imposed by the moving edges in order to signal the true direction of motion of the object (Adelson and Movshon, 1982; Movshon et al., 1985; Movshon, 1990, Stoner and Albright, 1994).

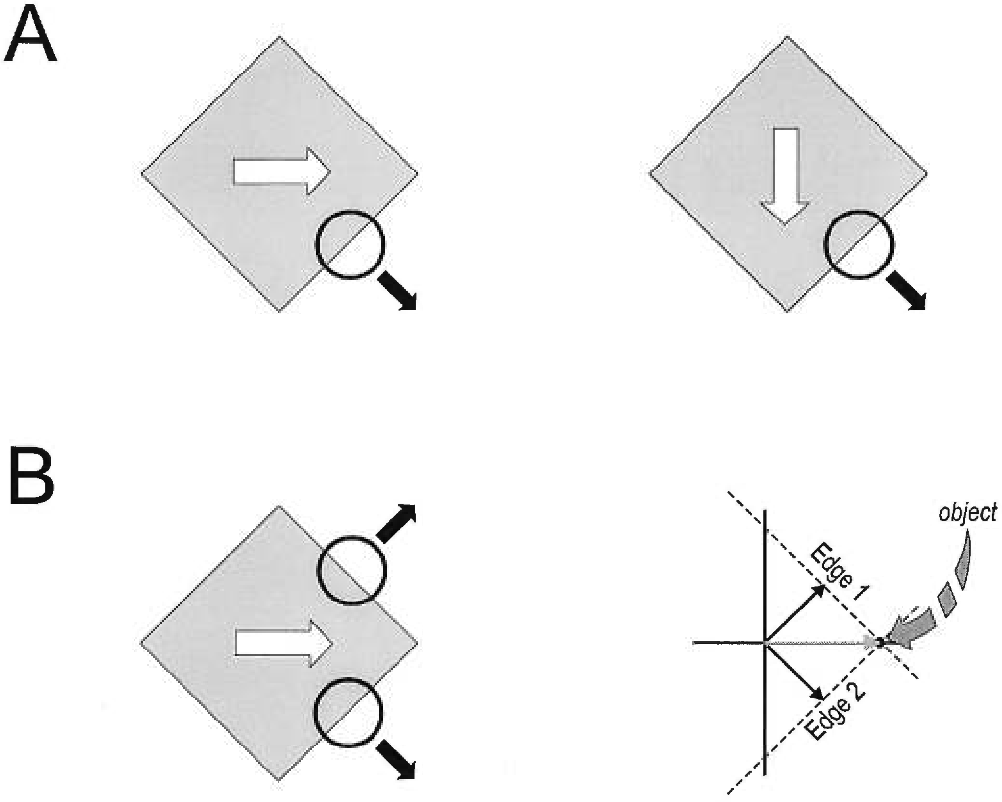

Figure 1. The Aperture Problem. (A) Different directions of motion of a two-dimensional object (rightward and downward, open arrows) yield identical local measurements (filled arrows) when viewed through a small aperture. The ambiguity results from the fact that local measurements do not reflect the overall motion of objects. (B) The formal solution is based on the intersection of the constraints imposed by the moving edges ("families" of possible motions). The neurophysiological implementation of this solution implies a two-stage integrative process where lower-order cells (signaling local component movements) would project to higher-order cells (integrating local motion cues) signaling the veridical direction of motion of the object. *Adapted from Movshon et al. (1985) and Movshon (1990).*

The neurophysiological implementation of this solution would require the existence of direction-selective cells that integrate the measurements of local detectors and signal the veridical direction of motion of an object. It would follow that these neurons would provide motion signals that are dependent on the motion of an object as a whole rather than on the oriented contours comprising that object. In addition, these higher-order neurons would represent a level of abstraction and integration not seen at lower levels of the motion analysis pathway (Movshon, 1990).

The middle temporal area (MT) has been the subject of intense study as the possible site of motion integration in the primate visual system. Numerous studies (Adelson and Movshon, 1982; Albright, 1984; Movshon et al., 1985; Rodman and Albright, 1989; Stoner and Albright, 1992; Albright and Stoner, 1995) have addressed this issue by using a visual stimulus ("plaid pattern") that recreates the ambiguities of the aperture problem and allows the investigation of how the visual system integrates multiple motion signals into a coherent moving percept. A plaid pattern is composed of two identical superimposed drifting gratings differing in orientation (see figure 2). A human observer perceives the motion of the entire plaid pattern moving coherently. The direction and velocity of the pattern are uniquely consistent with the constraints imposed by the motion of the individual components (part A). At the neuronal level

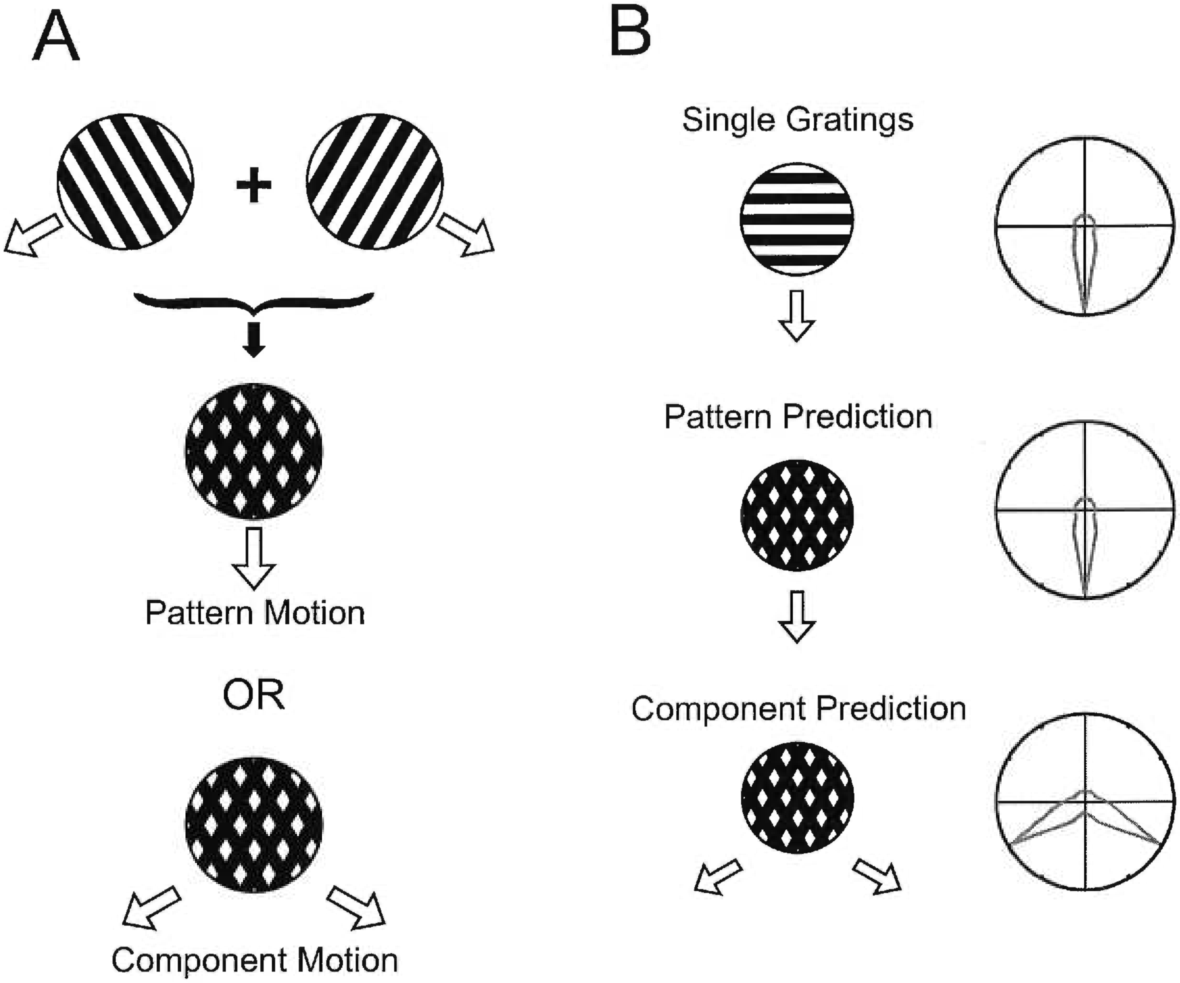

Figure 2. (A) Generation of a plaid pattern. Under normal viewing conditions, two identical drifting gratings differing in orientation are perceived to move coherently as a rigid pattern. (B) Hypothetical neurophysiological response profiles. A cell integrating the component motions of the plaid pattern will exhibit a response profile similar to that of a single grating moving in the integrated direction of motion (pattern prediction). A cell unable to signal the veridical direction of motion of the plaid pattern will respond with a bi-lobed response profile corresponding to the component motions of the plaid pattern (component prediction).

(part B), a cell that is selective for the global motion of the plaid pattern shows a similar response profile to that of a single grating moving in the integrated direction (pattern motion selectivity). A cell unable to signal the veridical direction of the pattern would show a symmetrically bi-lobed profile corresponding to the motions of the oriented components comprising the pattern (component motion selectivity).

It has been shown that area MT contains two distinct populations of direction-selective cells (e.g. Albright, 1984; Movshon et al., 1985). The first, "component-type" cells (like those in area V1) respond only to the motion of the oriented components and provide local motion information regarding the plaid pattern. The second type, "pattern-type" cells, combine and integrate local information signals (presumably from component-type cells) and signal the veridical motion of the plaid pattern as a whole. The finding of MT neurons capable of signalling the veridical direction of a moving plaid pattern has established the importance of this area in global motion processing (see Maunsell and Newsome, 1987; Movshon, 1990; Stoner and Albright, 1994 for reviews), and has led to the proposition that motion perception is in effect, a two-stage process (Adelson and Movshon, 1982; Sereno, 1993; Stoner and Albright, 1994; Nowlan and Sejnowski, 1995). Figure 3 illustrates the selection model of motion processing in primate visual cortex. The first stage would involve the extraction of local object features as one-dimensional components (carried

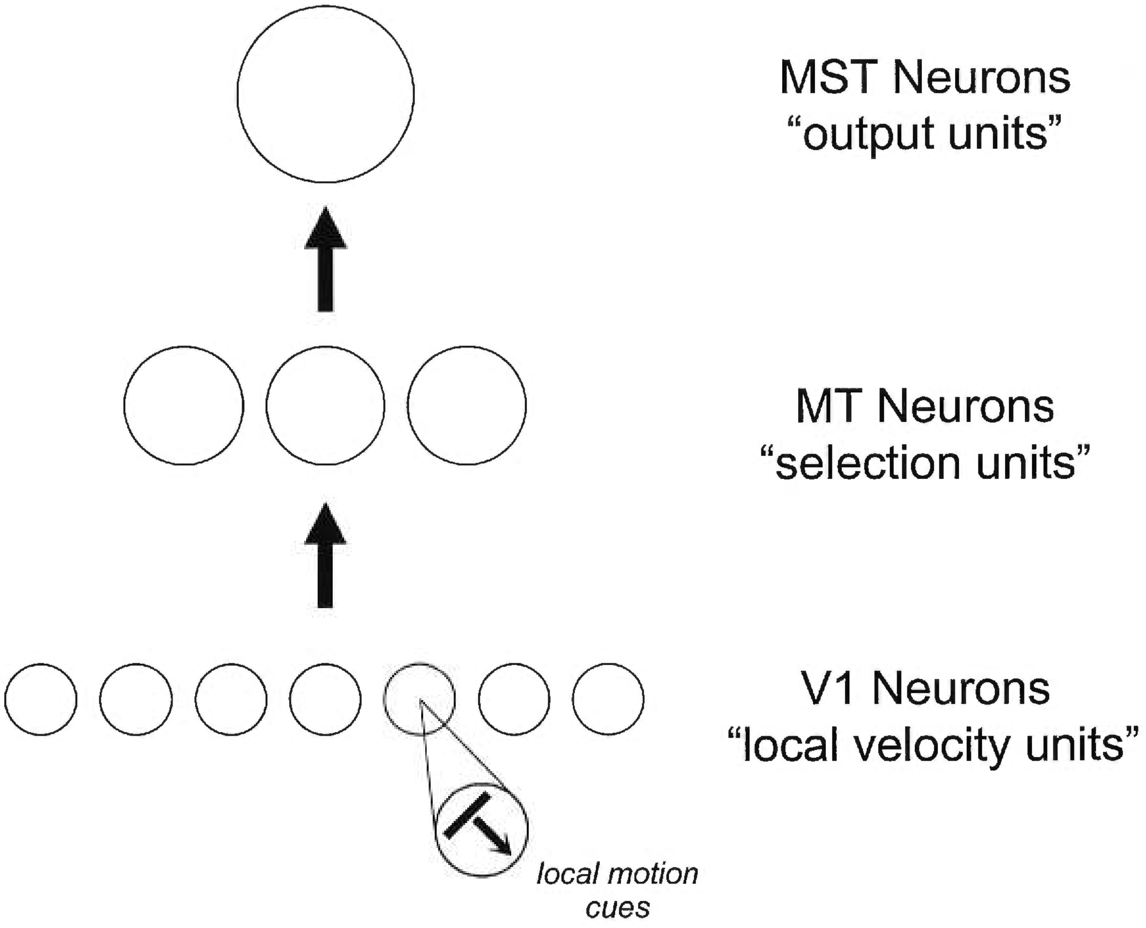

Figure 3. The selection model of motion processing. Schematic representation of the stages of motion analysis in primate visual cortex. The model suggests that local velocity units (i.e. V1) signal local motion cues. These signals converge onto selection units (area MT) that integrate local motion cues and signal the veridical direction of motion of an object. The final output stage (purported to be area MST) would combine the activity of selection units for subsequent processing of more complex and non-local motions such as optical flow fields. *Adapted from Sereno (1993), Nowlan and Sejnowski (1995).*

out in V1). These signals would subsequently be integrated within a second stage (area MT) to generate a coherent percept of the object in motion. The model is also extended to include a higher stage of integration (i.e. the medial superior temporal area; MST) as an output level for the integration of more complex non-local motions such as optical flow fields and three-dimensional rotations. Thus, at each stage of the model elementary and local motion information is combined to compute more complex and global motion signals. To date, these steps of motion integration have been attributed uniquely to cortical networks, as have all forms of higher-order processing.

1.4 The Role of Cortico-thalamic Loops in Information Processing

Classically, visual perception (i.e. object recognition) has been regarded as a “bottom-up” process. According to this influential doctrine, elementary features detected in "lower" visual structures converge upon “higher” cortical areas where successive levels of abstraction and integration are carried out in hierarchical fashion until a final percept is achieved (Hubel and Wiesel, 1968; Barlow, 1972; Marr, 1982; Maunsell and Newsome, 1987; Cavanagh and Mather, 1989; Maunsell, 1995). In this view, the role of the thalamus has been described as one of a relay of information *en route* to the higher-level processing in the cortex according to the state of vigilance (Macci et al., 1996; Miller, 196; Sherman and Guillery, 1996). Alternatively, the thalamus has also been viewed as mediating attention, serving to engage and shift (Crick, 1984; Posner and Petersen, 1990) or expand and contract attentional windows (Olshausen et al., 1993).

The purported relay function of the thalamus has generally been attributed to the fact that unlike the cortex, the thalamus does not possess a substantial population of intra-thalamic collaterals and/or local inhibitory inter-neurons (Jones, 1985; Garey et al., 1991). Thus, the thalamus appears to lack the computational machinery necessary to carry out high levels of abstraction and analysis characteristic of associative cortical areas (Koch, 1987; Mumford, 1991; Gilbert, 1998).

These notions notwithstanding, there remains the important fact that the visual cortex, as a functional whole, sends massive feedback projections to the thalamus in accurate topographical register. This organisation, referred to as the "principle of reciprocity" (Diamond and Hall, 1969; Jones, 1985), states that cortical areas receiving inputs from a projecting thalamic nucleus, will project extensively back to that nucleus. In a sense, the thalamus represents essentially a "7th layer" intimately tied with the cortex in a neuronal loop (Mumford, 1991). Viewed in this way, the largest input of sensory information to that thalamus is not the sensory periphery, but rather the *cortex itself* (Jones, 1985; Mumford, 1991;

Guillery, 1995). Thus, if the thalamus represents a mere relay station as it is classically assumed, it is pertinent to pose the following questions: 1) why does the thalamus receive such a massive reciprocal drive from the cortex and 2) why does the thalamus project to higher-order associative cortical areas? (Mumford, 1991). Furthermore, this pattern of organisation is not unique to the visual system nor to the primate brain and is particularly evident in all mammals with highly developed sensory systems (Jones, 1985; Creutzfeldt, 1988; van Essen et al., 1992). It would thus be reasonable to assume that this uniformity in organisational principle may embody a basic and versatile module of computation able to analyse sensory information and co-ordinate motor actions (Mumford, 1991).

While the existence of thalamo-cortico-thalamic loops is well established, the actual function of the cortico-thalamic feedback component has remained rich in theory and poor in evidence. The first attempts in elucidating the role of cortico-thalamic loops have concentrated (not surprisingly) on the lateral geniculate nucleus (LGN) and its reciprocal relationship to the primary visual cortex (V1). In the cat, extensive reciprocal cortico-thalamic projections outnumber forward thalamo-cortical inputs by an order of magnitude of 10 and are 40 times greater than the input from the retina (Jones, 1985). Despite this massive feedback, receptive field (RF) properties in the LGN resemble more those of retinal ganglion cells than they do cortex. For example, RFs in LGN are circular and concentrically arranged rather than being rectangular and elongated (see Hubel, 1988). Furthermore, cells in LGN are non-selective to stimulus orientation and direction[2] (see Hubel, 1988).

Early studies investigating the effects of cortical feedback on LGN neurons have produced mixed conclusions. For example, Kalil and Chase (1970) have shown that reversible deactivation of cat area 17 reduces light-evoked responses of most thalamic relay neurons, however facilitatory responses have also been reported by other groups (see Jones, 1985). More recently, Sillito and colleagues (1994) have found that cortical feedback may be essential in amplifying geniculate responses thereby increasing the probability that cortical cells in turn will fire. On the whole however, studies of the striato-geniculate system have been unsuccessful in elucidating the role of cortico-thalamic projections (Jones, 1985; Garey et al., 1991). It is possible that this lack of clear cortical influence on geniculate RF properties is masked by the retinal input this particular thalamic area receives and the network of inhibitory inter-neurons therein (Jones, 1985; Casagrande and Norton, 1991). Furthermore, it has been argued that the preservation of retinal RF properties in LGN is essential for its role in regulating the strength of visual signals to the cortex (see Casagrande and Norton, 1991).

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[2] Certain studies (e.g. Soodak et al., 1987) have indicated that LGN cells in cat show a certain degree of orientation and directional "bias". However, this selectivity is not anywhere as pronounced nor comparable to that observed in cortex.

1.5 The Thalamus as an "Active Blackboard"

It has been proposed that the thalamus could play a more integrative role in visual processing rather than a simple passive relay station. Projections through this region could represent a rapid and secure pathway that not only convey "raw" sensory data, but also processed and refined information from which salient features are enhanced and irrelevant information suppressed (Koch, 1987; Mumford, 1991; Singer, 1994; Miller, 1996).

Mumford (1991) has proposed that the role of the thalamus could be one of an "active-blackboard" reflecting the higher-order computations being carried out at the level of the cortex. In this model, the thalamus would serve as a blackboard where the results of ongoing cortical analyses could be stored and shown to other cortical areas involved in the computation. The *active* aspect of the model refers to the idea that the contents of the blackboard are continuously changing and dynamically reflect the latest computational decisions. Viewed as such, thalamo-cortical projections would convey the results of ongoing computations to all cortical areas concerned, while cortico-thalamic projections would transmit additional calculations and revisions back to the thalamus. Thus, visual processing represents a concurrent and iterative process implicating constant feed-forward and feedback loops within the entire hierarchical circuit of the visual system. By mediating ongoing cortical analyses and incoming sensory data, the thalamus would be strategically positioned to “select” or “group” appropriate signals for further processing allowing for cortical assemblies to “lock” onto relevant stimuli and enhance feature detection and saliency (Koch, 1987; Sillito et al., 1994; Singer, 1994; Miller, 1996). The idea that the cortex and thalamus have to work together interactively has been proposed in other theoretical models such as Koch (1987), Harth and co-workers (1987; Alopex Algorithm), Singer (1994, 1995), Miller (1996), and Grossberg (1999; Adaptive Resonance Theory).

For such models to be plausible, a candidate thalamic nucleus would have to exhibit reciprocal interconnections not only with extrastriate associative areas, but also receive inputs from subcortical structures and primary sensory cortices in order to mediate in-coming sensory data and ongoing cortical computations (Mumford, 1991). Furthermore, and most importantly, neurons on *both* sides of the cortico-thalamic loop would have to show similar higher-order response properties. That is to say, the results of integrative cortical computations should also be present at the thalamic level. To date, there has been no demonstration of a subcortical structure (of any kind) able to respond to higher-order visual stimuli.

1.6 The Extra-Geniculate Visual System: The LP-pulvinar Complex

1.6.1 The LP-pulvinar as a Candidate

The pulvinar region may represent a likely candidate as a higher-order thalamic area involved in the analysis of complex visual scenes. The pulvinar represents the largest thalamic nucleus in the human brain (Chalupa, 1991) and has exhibited a marked evolutionary increase in size and differentiation particularly in close association with the expansion of the parietal and temporal cortices (Jones, 1985; Chalupa and Abramson, 1988). In the cat, the lateral posterior (LP)-pulvinar complex remains the homologous structure to the primate pulvinar and occupies the majority of the dorsal half of the lateral thalamus (located medially and caudal to the LGN; Jones, 1985; Chalupa and Abramson, 1988; Garey et al., 1991). As with the primate brain, this nuclear group represents a higher-order nucleus since it receives its major input from layer V cortical neurons rather than a direct projection from retinal ganglion cells (Chalupa, 1991; Guillery, 1995). Furthermore, the LP-pulvinar is in reciprocal communication with virtually all visual and associative cortical areas and is firmly established as the predominant thalamic component of the extra-geniculate visual system (Hutchins and Updyke, 1988; Chalupa, 1991).

As a final note, using the cat model in the investigation of cortico-thalamic function is appropriate since it is in this species that it has been the most thoroughly studied (Jones, 1985). Furthermore, the general organisation of the extrastriate thalamo-cortical system is comparable in different mammals (especially in the cat and monkey) and the organisational principles found therein are likely to extend to numerous other species including primates (Jones, 1985; Creutzfeldt, 1988).

1.6.2 Neuroanatomy and Connectivity

The LP-pulvinar complex of the cat is subdivided into at least three regions[3] (each with their own representation of the visual field) forming characteristic "slabs" identified by differential staining to reveal acetylcholinesterase (AChE) enzymatic activity (Graybriel and Berson, 1980). These are: the medial region of the lateral posterior nucleus (LPm, or tecto-recipient zone), the lateral region of the lateral posterior nucleus (LPl, or striate-recipient zone) and finally, the pulvinar proper (Chalupa, 1991). In terms of connectivity, the LPm receives a predominant subcortical input from the superior colliculus (SC) and is reciprocally connected with the lateral bank of the suprasylvian visual areas and to the

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[3] According to Hutchins and Updyke (1989), the LP-pulvinar may contain as many as five separate representations of the visual field.

anterior ectosylvian visual (AEV) area. In contrast, the LPl is characterised by a strong cortico-striate input (area 17) and exhibits reciprocal connections with areas 18, 19 and the medial bank of the suprasylvian cortex (most notably the posteromedial area; PMLS). Finally, the pulvinar component of the complex receives projections from the optic tract and represents the only subdivision that receives a direct retinal input[4] (Symonds et al., 1981; Tong et al., 1982; Abramson and Chalupa, 1985; Jones, 1985; Chalupa, 1991). Figure 4 illustrates the subdivisions of the LP-pulvinar and its connectivity relations to subcortical and cortical areas. Note that LP establishes reciprocal relations with extrastriate cortical areas known to be involved in motion analysis most notably, the posteromedial lateral suprasylvian (PMLS) and anterior ectosylvian visual (AEV) cortices (Mucke et al., 1982; Norita et al., 1986; Rauschecker et al., 1987a; Rauschecker, 1988; Spear, 1991; Norita et al., 1996).

Based on it connectivity patterns, the LP-pulvinar complex appears to be strategically placed from an anatomical standpoint (i.e. directly between the geniculo-cortical and retino-tectal pathways). Furthermore, what has been classically viewed as two independent streams of visual information (Schneider, 1969), one for detection of form and the other for

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[4] Guillery and co-workers (1980) have argued that the retino-recipient part of the pulvinar region represents an extension of the medial intra-laminar nucleus; both of which comprise the “geniculate wing”. However, more recent investigation of this matter by Hutchins and Updyke (1989) re-establish this region as the pulvinar component of the LP-pulvinar complex.

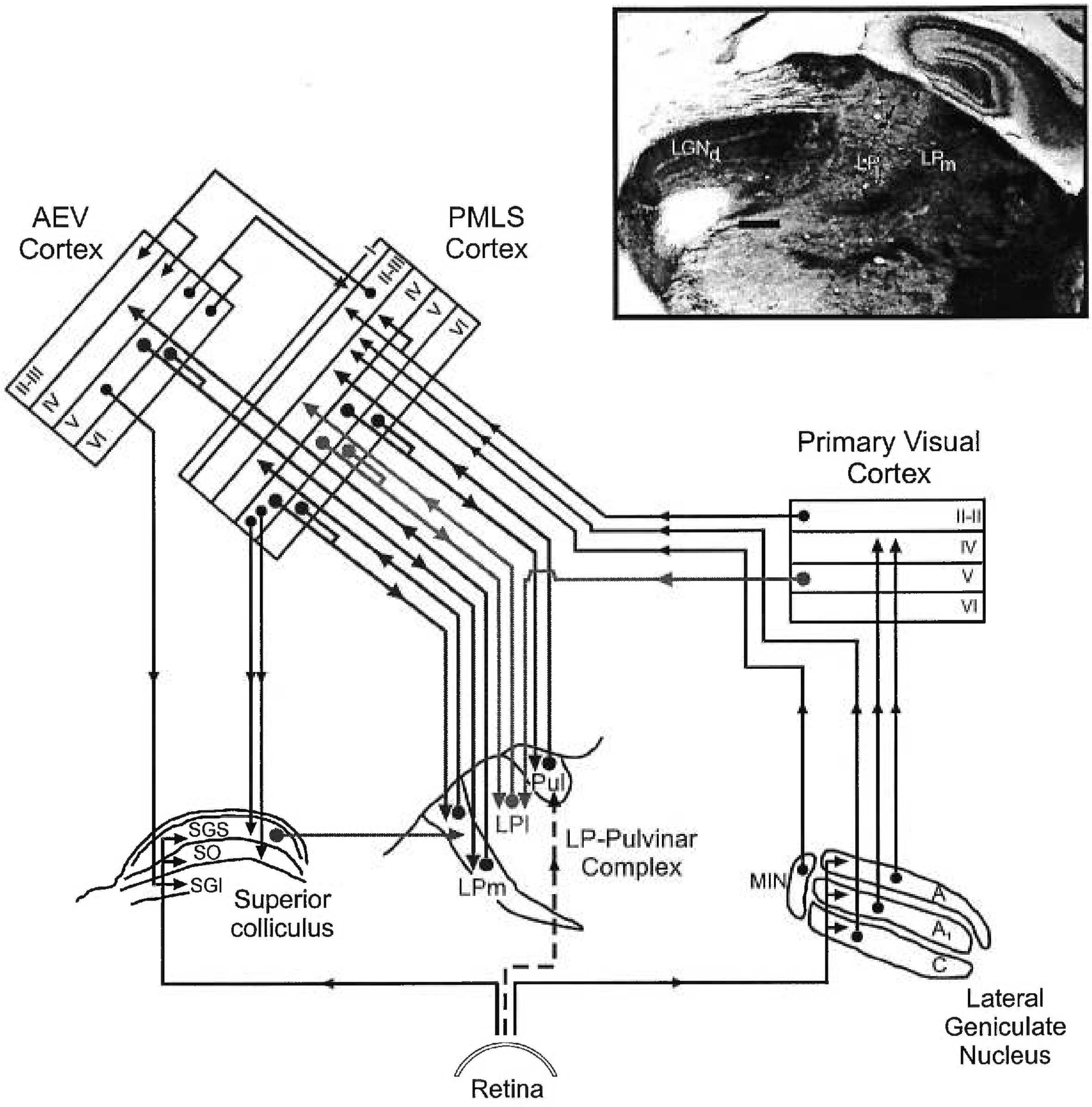

Figure 4. Schematic illustrating the subdivisions of the LP-pulvinar complex and the visual pathways investigated in this study. Besides receiving both striate cortical (area 17) and subcortical (superior colliculus) inputs, the LP-pulvinar complex establishes reciprocal relations with both the extrastriate PMLS and AEV motion areas. Inset figure shows a coronal section through the thalamus revealing the AChE coloration technique. The lateral portion (striate-recipient zone, LPl) shows a weak staining compared to the medial portion (tectal-recipient zone, LPm). Abbreviations: AEV: anterior ectosylvian visual area, LGNd: dorsal lateral geniculate nucleus, MIN: medial interlaminar nucleus, LPl: lateral portion of the lateral posterior nucleus, LPm: medial portion of the lateral posterior nucleus, PMLS: posteromedial lateral suprasylvian cortex, Pul: pulvinar region, SGI: stratum griseum intermediale, SGS: stratum griseum superficiale, SO: stratum opticum. For clarity, note that some projections (e.g. area 17 to LGN) have been omitted.

the orientation of gaze, seem to communicate and/or interact via the LP-pulvinar (Bender, 1988; Robinson and McClurkin, 1989).

1.6.3 Neurophysiological Response Properties

The function of the LP-pulvinar has often been associated with visual attention and visually guided movement (Fabre-Thorpe et al., 1986; Acuna et al., 1990; Robinson and Petersen, 1992), but for the most part its precise function has remained speculative (Bender, 1988; Chalupa, 1991). Unlike the LGN, the physiological response properties of LP-pulvinar cells resemble those of their cortical and subcortical inputs (Chalupa and Abramson, 1988; Casanova et al., 1997). For example, the majority of cells in LP are orientation and direction selective, can be binocularly driven and are sensitive to retinal disparity (e.g. Chalupa and Abramson, 1988, Casanova et al., 1989). As with cortical cells, units in LP are tuned to temporal and spatial frequencies and respond to drifting gratings with unmodulated discharges (Casanova et al., 1989; Casanova et al., 1997). With regards to motion sensitivity, LP cells have been shown to respond to a wide range of stimulus velocities. They respond robustly to moving texture patterns, and also code the relative motion between an object and its background (Casanova and Savard, 1996a,b). In addition, RF size in LP is typically quite large (i.e. encompassing those of area 17, Chalupa and Abramson, 1988) and exhibit a spatial organisation ideal for the processing of optical flow fields (Rauschecker et al., 1987b). The fact that RFs in LP are typically large is worth of mention and hints towards the integrative role this area may play. It has been argued that the generation of large RFs (typical of extrastriate areas) reflects an increase in complexity arising from integration of signals from different visual areas and concomitantly, a sampling of information from larger representations of the visual field (Zeki and Shipp, 1988; Sereno, 1993).

1.7 Extrastriate Motion Areas of the Cat

As mentioned in the previous sections, the LP-pulvinar complex establishes reciprocal relations with extrastriate cortical areas involved in motion analysis. Two extrastriate regions of interest in this study are the posteromedial lateral suprasylvian (PMLS) and anterior ectosylvian visual (AEV) cortices. Figure 5 shows the location of these two regions in relation to other visual cortical areas of the cat brain.

Rostral to area 17, the lateral and medial banks of the lateral suprasylvian (LS) sulcus contain visually responsive neurons and are generally subdivided into six sub-regions (referred to also collectively as the Clare-Bishop area). Of the six subdivisions, the PMLS region has been the most extensively studied (see Spear, 1991; Payne, 1993 for reviews).

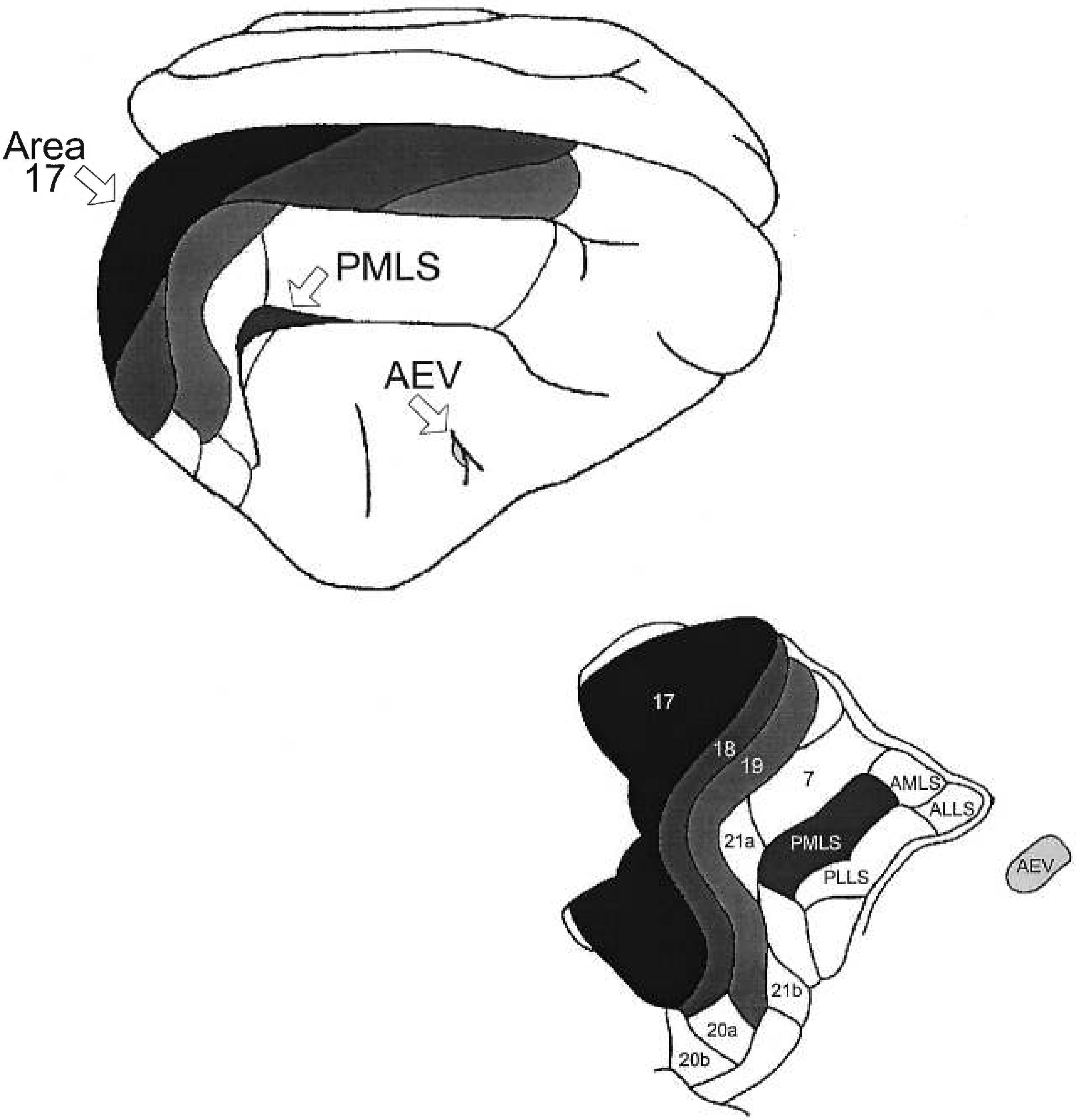

Figure 5. Location of visual cortical areas in the cat brain. Top figure shows a dorsolateral view. Arrows identify the location of the cortical areas investigated in this study. Bottom figure represents a flat-mounted view showing the neighboring relations and relative size of each cortical area. Abbreviations: AEV: anterior ectosylvian visual, PMLS: posteromedial lateral suprasylvian, AMLS: anteromedial lateral suprasylvian, PLLS: posterolateral suprasylvian, ALLS: anterolateral suprasylvian. *Adapted from Sereno and Allman (1991), Spear (1991).*

PMLS cortex has received considerable attention in terms of its purported role in motion analysis based on anatomical, physiological and behavioural evidence. Furthermore, this area has often been regarded as the functional analogue of primate area MT (see Payne, 1993). PMLS receives convergent inputs from the retino-geniculate pathway (predominately Y and W-cell types) and the extrageniculate pathway (of which the LPl is the predominant thalamic input) (Rauschecker et al., 1987a; Norita et al., 1996). Receptive fields of PMLS neurons show a clear retinotopic organisation and are generally much larger than those of areas 17,18 and 19. The majority of cells in this area are orientation selective and are binocularly driven, but by far the distinguishing characteristic of PMLS neurons is the fact that the overwhelming majority (approximately 80%) are direction selective to stimulus motion (e.g. Morrone et al., 1986; Minville and Casanova, 1998). Furthermore, cells respond preferentially to moving rather than stationary targets and are selective to rapid stimulus movement (as high as 200°/sec) and over a wide range of velocities (Spear, 1991). The RFs of certain PMLS cells possess an inhibitory surround component (referred to as "double-opponent") ideal for the coding the relative movement of a object with respect to its background (von Grünau and Frost, 1983). Directional selectivity of PMLS cells show a RF organisational bias towards centrifugal directions of motion (i.e. away from the area centralis) such as that produced by forward locomotion through the environment (Rauschecker et al., 1987b). Finally, behavioural studies using lesioning and reversible cooling techniques have shown that deactivation of PMLS creates velocity discrimination deficits similar to those observed in primate MT (Pasternak et al., 1989; Lomber et al., 1996; Rudolph and Pasternak, 1996;). This later evidence suggests that both PMLS and MT make similar contributions with regards to motion processing.

Mucke and co-workers (1982) were first to report the existence of a visually responsive area located within the anterior ectosylvian sulcus. This region, referred to as the anterior ectosylvian visual (AEV) area, is unique in that it is surrounded by entirely non-visual cortical areas. Furthermore, unlike most extrastriate visual areas, the main inputs of AEV do not arise from areas 17,18 and 19 nor the LGN. The major cortical projections originate from PMLS and PLLS while thalamic inputs are primarily from the medial part of the LP (LPm) as well as the suprageniculate complex (Symonds et al., 1981). Receptive fields in AEV show a crude topographic organisation with an overrepresentation of the lower visual field (see Scannell et al., 1996). Like PMLS, the large majority of AEV units are binocularly driven and direction selective, and prefer moving rather than stationary stimuli. However, neurons in this area respond to motion of much higher velocities. Optimal velocities as high as 1000°/sec have been reported for some units while maintaining their direction selectivity (e.g. Olson and Graybiel, 1987). Recently, Scanell and colleagues (1996) have reported that pattern-selective responses exist in the AEV (similar to those found in primate MT). To date, AEV is the only area known to possess pattern motion cells in the cat visual cortex.

2. *Hypotheses and Purpose*

On the basis of response properties of neurons in the LP-pulvinar complex and its reciprocal relations with areas involved with motion perception, we raise two main hypotheses regarding the participation of this thalamic region in complex motion analysis: 1) the LP-pulvinar complex should possess higher-order properties in response to complex motion stimuli. In addition, these properties should be comparable to those found in extrastriate cortical areas of which it exhibits reciprocal relations (i.e. PMLS and AEV) and 2) Deactivation (reversible and irreversible) of either LP or its reciprocally communicating cortical areas should disrupt neuronal operations along the cortico-thalamic loop in response to complex motion stimuli.

The purpose of this neurophysiological study is two-fold: The first, is to investigate the responses of neurons in PMLS cortex to 2-dimensional moving texture patterns (“visual noise”, see figure 6). Texture patterns have been used extensively in both psychophysical and

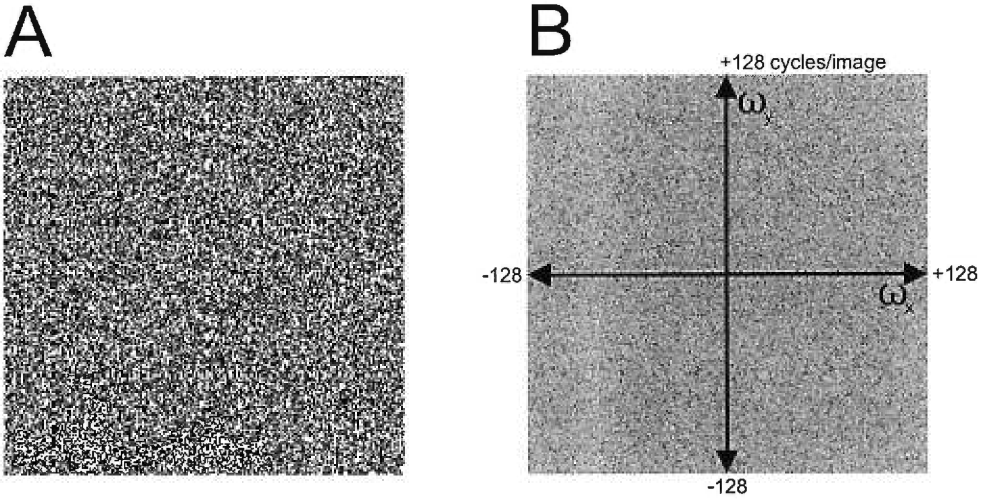

Figure 6. (A) Sample of the 256 x 256 pattern used in this study. (B) Fourier power spectrum of the stimulus. Note that the power spectrum shows that all spatial frequencies and orientations have the same amount of power up to 128 cycles/image in both frequency axes.

neurophysiological studies to simulate the short and complex contours that comprise natural scenes and assess the sensitivity of motion systems (Julez, 1971; Cavanagh and Mather, 1989; Olavarria et al., 1992; Casanova et al., 1995). The responses of PMLS neurons to moving texture patterns will be compared to those found in LP (the principle thalamic drive of PMLS cortex, Norita et al., 1996) in terms of texture sensitivity, including directional tuning and selectivity to speed. The findings of this part of the study will attempt to establish a functional commonality in terms of motion processing on both sides of the PMLS-LP cortico-thalamic loop.

In the second aspect of the study, we will investigate the functional relationship between LP and extrastriate cortical motion areas in response to more complex moving stimuli. Preliminary results in PMLS (Merabet et al., 1997) and previous studies in LP (Casanova and Savard, 1996b) have shown that neuronal responses to drifting sinusoidal gratings in both these areas can be modulated by the motion of a texture background. Further, reversible deactivation of LP (injection of GABA) influences the ability of PMLS neurons to code the relative motion between a figure and its background (see Preliminary Results).

These observations have provided the impetus for investigating the role of cortico-thalamic loops in the processing of higher-order visual stimuli (e.g. “plaid” patterns). Specifically, if LP-pulvinar participates in the analysis of global motion in conjunction with higher-order cortical areas, one would predict that cells in this area should also possess "pattern-selective" responses as described earlier in primate area MT. For this part of the study, we have shifted our attention to the reciprocal relationships between LP and the AEV cortex since to date, this region is the only cortical area shown in the cat to possess pattern-selective cells similar to those reported in area MT (Scannell et al., 1996). As a final part of the study, we wished to determine the contribution of the AEV cortex on these higher-order properties in LP by carrying out experiments involving reversible and irreversible cortical deactivations.

The results of this investigation are presented in the form of two articles, preliminary results (Preliminary Results section), and a recent review submitted for publication (Annex 1). The conclusion of this study will attempt to address the role of the thalamus and cortico-thalamic loops (as computational modules) involved in motion analysis and sensory perception.

3. Overview of Methodology

Experiments were carried out in anaesthetised normal adult cats prepared in classical fashion for electrophysiological studies (e.g. Casanova et al., 1997). Varnished tungsten microelectrodes were used to record single-unit activity in subcortical (LP) and cortical visual areas (PMLS, AEV, area 17) investigated in this study. Neuronal responses were fed to a PC computer for peri-stimulus time histogram (PSTH) acquisition. Visual stimuli (drifting sinusoidal gratings, moving texture patterns, and plaid patterns) were computer generated (Picasso Image Synthesizer, Innisfree) and presented on a CRT presented in front of the animal. Figure 7 shows a schematic of the recording experimental protocol used in this study.

In a few cats, reversible deactivation experiments were carried out. A glass recording-injecting microelectrode filled with γ-aminobutyric acid (GABA; 200 µM, stained with 1% Chicago Sky Blue) was descended in the AEV cortex using stereotaxic co-ordinates and visual response cues. Neuronal activity in LP in response to visual stimuli was recorded prior to, during, and following pharmacological deactivation of the extrastriate visual area.

In another set of experiments, the effect of acute lesioning of specific extrastriate visual areas on responses of LP neurons was investigated. Following resection of the dura, the overlying grey matter of the cortical area(s) targeted was aspirated and the cavities were filled with sterile gelfoam. The lesion experiments were subdivided into three parts: 1) bilateral resection of the AEV cortex (including the entire anterior

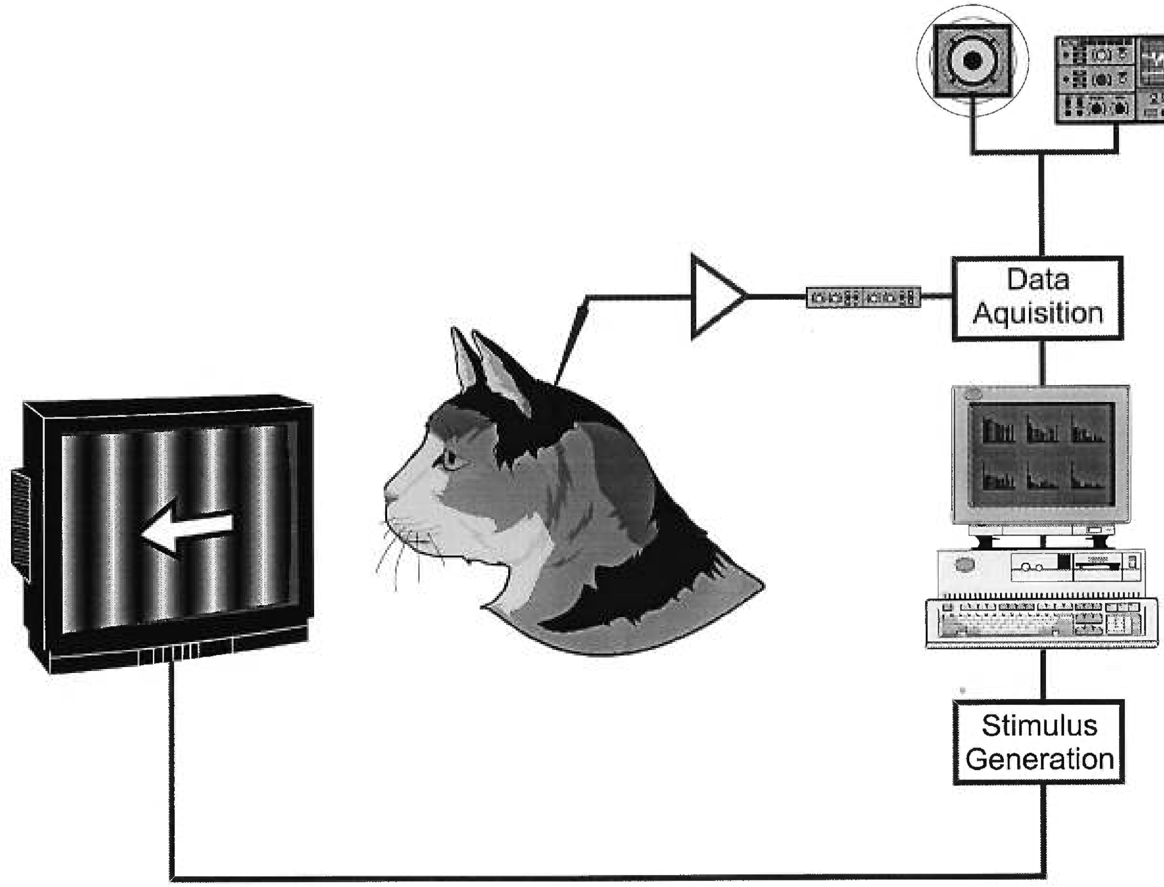

Figure 7. Schematic of experimental protocol. Visual stimuli (e.g. gratings, moving texture patterns, and plaids) are computer generated and presented on a CRT placed in front of the animal. Recorded neuronal activity in response to visual stimuli are fed into a PC-computer for data acquisition (PSTH form) and played back on an audio monitor and oscilloscope.

ectosylvian sulcus). 2) bilateral resection of the AEV cortex in conjunction with the PMLS cortex. 3) bilateral resection of the AEV in conjunction with the entire medial and lateral banks of the suprasylvian sulcus. Recordings in LP were carried out following a 12-16 hour recovery period. Prior to recordings in LP, control recordings in LGN, SC and area 17 were carried out to ensure that the trauma associated with the surgical procedures did not cause a general depression of brain activity.

Electrolytic lesions were made along recording tracks. At the end of each experiment, the brain was removed and fixed in buffered formalin for subsequent histological analysis. Serial sections of the brain were cut and stained with Cresyl Violet to confirm the position of electrode tracks, and to determine cortical laminar positioning of recorded cells, and the location and extent of inactivation injections and cortical resections. For recordings carried out in LP, alternating brain sections (100 µm) were stained to reveal acetylcholinesterase (AChE) activity (in order to distinguish the subdivisions in LP-pulvinar) and matched against sections stained with Cresyl Violet to confirm positioning of recorded cells.

Article 1: "Responses of Neurons in the Cat Posteromedial Lateral Suprasylvian Cortex to Moving Texture Patterns"

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Submitted to: *European Journal of Neuroscience*

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25 April 1999

Dear Dr Everitt,

I have enclosed a manuscript entitled "*Responses of neurons in the cat posteromedial lateral suprasylvian cortex to moving texture patterns* " that we would like to be considered for publication in *European Journal of Neuroscience.*

The data presented here addresses a long-standing problem regarding texture sensitivity of cells in the PMLS cortex.

Please note that this paper has not been submitted to other scientific journals. All authors have approved the enclosed version of the manuscript.

Sincerely yours,

[redacted]

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Responses of Neurons in the Cat Posteromedial Lateral Suprasylvian Cortex to Moving Texture Patterns

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Summary

The posteromedial lateral suprasylvian (PMLS) cortex represents a point of convergence between the geniculo-striate and extra-geniculo-striate visual pathways. Given its purported role in motion analysis and the conflicting reports regarding the texture sensitivity of this area, we have investigated the response properties of cells in PMLS to moving texture patterns ("visual noise"). In contrast to previous reports, we have found that a large majority of cells (80.1%) respond to the motion of a texture pattern with sustained discharges. Generally, responses to noise were more broadly tuned for direction compared to gratings, however direction selectivity appeared more pronounced in response to noise. The majority of cells were selective for drift velocity of the noise pattern (mean optimal velocity: 26.7°/sec). Velocity tuning was comparable to that of its principle thalamic input, the lateral-posterior pulvinar nucleus (LPl). Generally, responsiveness of cells in PMLS increased with increasing texture element size, although some units were tuned to smaller element sizes than the largest presented. Finally, the magnitude of these noise responses was dependent on the area of the visual field stimulated. In general, a stimulus corresponding to roughly twice the size of the receptive field was required to elicit an equivalent half-maximal response to that for gratings. The results of this study indicate that the majority of

PMLS cells can be driven by the motion of a drifting texture field, and highlight the importance of this area in motion analysis.

Introduction

The posteromedial lateral suprasylvian (PMLS) cortex of the cat has been associated with the analysis of motion on the basis of neural response properties and behavioral observations (Morrone et al., 1986; Blakemore and Zumbroich, 1987; Toyama et al., 1985; Kim et al, 1997; Brosseau-Lachaine et al., 1998; Kiefer et al., 1989; Krüger et al., 1993; Rudolph and Pasternak, 1996, for review see Spear, 1991). Thus, one would predict that most PMLS cells should strongly respond to the motion of 2-D texture patterns (visual noise). Such stimuli have been used extensively in both neurophysiological and psychophysical studies to simulate the complex contours and surfaces comprising natural scenes, and the changes in the flow of visual information perceived by an observer moving through the environment (Gibson, 1950; Julesz, 1971; Gulyàs et al., 1987; Cavanagh and Mather, 1989; Ollivaria et al. 1992; Casanova et al., 1995; Scase et al., 1996). Surprisingly, few laboratories have investigated the sensitivity of PMLS cells to moving texture patterns and the overall findings are contradictory. For example, von Grünau and Frost (1983) reported that a cell's discharges in response to a moving bar could be modulated by the presence of a moving texture pattern, but the same neurons were unresponsive to the motion of the texture pattern *alone*. On the other hand, Hamada (1987) found that the majority of PMLS cells

(73%) could be driven by the motion of a texture pattern, but only if the stimulus was composed of large-sized elements (i.e. 1.6-4.8° of visual angle). More recently, in a comparative study between areas PMLS and 21a, Dreher and colleagues (1996) showed that approximately half (46%) of PMLS cells in their sample were sensitive to the motion of visual noise. This is in direct conflict with the findings of von Grünau and Frost (1983) because the noise pattern used by both groups was similar. Further, Dreher and colleagues (1996) and Hamada (1987) have reported that the majority of the discharges elicited by visual noise were sporadic in nature. The absence of robust discharges is surprising because this region receives direct and prominent cortical and subcortical inputs (Symonds et al., 1981; Abramson and Chalupa, 1985; Lowenstein and Somogyi, 1991) from areas known to respond vigorously to the motion of texture patterns (*see Discussion*, Skutton et al., 1988; Casanova et al., 1995; Mason, 1978; Casanova and Savard, 1996a).

In light of the discrepancies between the previous findings, we have re-investigated the responses of PMLS neurons to the motion of 2-D texture patterns. We have systematically investigated issues that were not addressed in previous studies, namely the effect of stimulus velocity, density, and size of the noise pattern. Direction selectivity, tuning, and response profiles were also assessed. Further, we employed a texture pattern similar to that used previously in our laboratory to study texture-sensitivity in area 17 and LP-pulvinar complex (Casanova, 1993; Casanova et al., 1995, Casanova and Savard, 1996a; Casanova and Savard, 1996b). In contrast to the previously cited studies in PMLS, our stimulus was computer-generated, presented in randomly interleaved fashion, and regenerated at each trial. As a result, this stimulus configuration would abolish any phase sensitive responses related to the aggregation of elements in the pattern and alleviate any sporadic or variable firing caused by habituation (see Spear, 1991). Preliminary results have been published elsewhere in abstract form (Minville et al., 1996).

Methods and Materials

Animal Preparation

Experiments were carried out on normal adult cats (2.5-4.5 kg). All animals were treated in accord with the guidelines of the Canadian Council on Animal Care. The animals were premedicated with an injection (s.c.) of acepromazine (1.0 mg/kg) and atropine (0.2 mg/kg) and initial anesthesia was induced by inhalation of an O_2:N_2O (50:50) mixture with halothane (4-5% initially, and reduced to 2%). Oxygen saturation and pulse rate were monitored throughout preparatory surgery using an oxygen saturation meter (Nonin). Following cephalic vein cannulation and tracheotomy, the animal was placed in a stereotaxic frame. Lidocaine hydrochloride (2%) was applied at all points of incision and pressure. The animal was then paralyzed with gallamine triethiode (10mg/kg/h) and artificially ventilated (N_2O/O_2 :70%/30% and halothane 0.5%). End-tidal CO_2 partial pressure was monitored by a capnometer (Datex) and kept constant between 28 and 32 mmHg by adjusting the rate and stroke volume of the respiratory pump. Core temperature was maintained at 37.5° ±0.5° by a heating pad placed under the animal and the electrocardiogram (ECG) and electroencephalogram (EEG) were monitored throughout the experiment. The animal was continuously infused with a solution of 5% dextrose in Ringer and gallamine triethiode.

Pupils were dilated with atropine, and nictitating membranes were retracted with local application of phenylephrine hydrochloride (10%). The eyes were protected using contact lenses of appropriate power. Following a craniotomy overlying the PMLS region, the dura was incised and reflected exposing the lateral suprasylvian sulcus. The exposed cortex was covered with warm agar over which wax was melted to create a sealed recording chamber. The locations of the area centralis were estimated by determining the position of the optic disks via back-projection of the fundus (Bishop et al., 1962, Pettigrew et al., 1979).

Electrophysiolocal Recordings

Varnished tungsten microelectrodes (2-5 MΩ; A-M systems) were used to record single-unit activity in PMLS. Recordings were made between anterior 4 and posterior 2 (Horsley-Clarke coordinates) corresponding to the central representation of the visual field (Palmer et al., 1978; Updyke, 1986). Using an angle of descent of 40° ±1° with respect to vertical, the electrode was advanced roughly parallel to the surface of the medial bank of the lateral suprasylvian sulcus. Receptive fields (RF) of the recorded cells were located in the contralateral hemifield (occasionally extending into the ipsilateral field) and were generally situated between -2° and 20° in azimuth (on occasion extending as far as 40°) and –10° and +10° in elevation with respect to the area centralis. The signals were amplified, displayed on an oscilloscope, and played through an audio monitor. Neuronal activity of the recorded unit was isolated using a window discriminator (WPI) and fed to a PC computer for peri-stimulus time histogram (PSTH) and interval histogram (INTH) acquisition (binwidth 10msec and 1msec respectively). The RFs of the recorded units were plotted on a tangent screen facing the animal using stimuli presented with a hand-held projector and ophthalmoscope. Before data acquisition, a search program was used to evaluate the optimal parameters for the cell, after which various properties were then quantitatively studied.

Visual Stimulation

Stimuli were displayed on a CRT (DataCheck 5117; mean luminance of 14 cd/m^2) placed 57 cm in front of the animal and subtending 28° x 28° of visual angle. A dark circular window (8-15° diameter) appeared on the CRT on which a small light bar was projected and used to position the RF within the center of the screen. Cells were characterized using drifting sinusoidal gratings (generally 60% contrast) to quantify RF properties such as, orientation selectivity and direction selectivity, spatial and temporal frequency selectivity, and ocular dominance. The stimuli were generated by a Picasso Image Synthesizer (Innisfree, Cambridge) connected to a controller (CED 1708; UK) interfaced with a desktop computer. During each trial, the activity for a blank screen presentation was recorded (spontaneous activity level). Unless otherwise specified, each stimulus presentation (including blank screen presentation) lasted 4 sec and was repeated four times. Presentations were randomly interleaved and in most cases only the dominant eye was stimulated.

Orientation was varied over 360° in 12 steps of 30°. An orientation range of 360° also specifies the direction of motion. For example, 90° and 270° are both horizontal and denote opposite directions of motion. Cell responses at optimal orientation were also studied as a function of spatial and temporal frequencies. A modulation index (MI; Skottun and Freeman, 1984) calculated from the response of the cell to drifting sine-wave gratings (spontaneous activity level was subtracted) was derived as follows:

$$\text{MI} = \frac{\text{response at the first harmonic (AC component)}}{\text{mean firing rate (DC component)}}$$

Following characterization of basic response properties, each cell's responses to visual noise was studied. Under computer control, a full-screen 2-D moving random dot pattern was presented at different directions spanning 360°. The texture pattern was generated by a Dual Channel Velocity Field and Stereogram Generator (Innisfree) having a maximal density of 256 x 256 elements (refresh rate of 200 Hz). At the

Fig. 1 here

viewing distance of 57 cm, each element subtended 0.13° of visual angle and represented the outcome of an independent Bernoulli trial with equiprobable states. An example of the texture pattern used in the study is shown in figure 1A. The 2-D Fourier power spectrum of the texture frames showed that all spatial frequencies and all orientations had the same expected amount of power (fig. 1B). The preferred direction for noise was first assessed using a search program testing at various velocities (including the optimal velocity determined for gratings). Once a clear directional tuning was established, the velocity tuning function was assessed at the optimal direction. Criteria for determining the responsiveness of PMLS cells to the texture pattern were as follows: first, the optimal response had to be at least twice the spontaneous discharge rate and second, cells were regarded as tuned for noise direction when they responded to a specific range of directions (clear pattern of directional tuning). Consequently, their selectivity (optimal value) could be assessed quantitatively by measuring the bandwidth of tuning (quantified as half width measured at half height).

The direction selectivity of each unit was determined and quantified as follows:

$$DI = 1 - \left[\frac{\text{response in the non-preferred direction}}{\text{response in the preferred direction}} \right]$$

Cells with an index value greater than 0.5 were regarded as selective to the direction of stimulus motion (Minville and Casanova, 1998). We investigated the spatial organization of PMLS RFs with respect to noise directional preference to test for the presence of a bias towards centrifugal directions. Using a convention devised by Rauschecker et al. (1987b), the "axial direction preference" for each unit was determined by computing the difference between the conventional directional preference of the cell and the polar angle of the RF center (defined as the angle of the RF center in polar visual-field coordinates). A difference of 0° would correspond to a direction preference equal to the polar angle, suggesting a centrifugal preference (i.e. away from center of gaze), whereas a difference of 180° between the polar angle and direction preference would indicate a preference towards centripetal motion (i.e. towards the center of gaze) (Rauschecker et al., 1987b).

To quantify a unit's relative sensitivity to noise with respect to that of gratings, we computed a motion sensitivity index MRN/MRG (Casanova et al., 1995, Casanova and Savard, 1996a).

$$\text{MRN/MRG} = \frac{\text{mean response to noise at optimal direction}}{\text{mean response to gratings at optimal direction}}$$

An index value less than 1 denotes a cell that exhibits a stronger response to gratings compared to noise, and a value greater than 1 represents a cell showing a preferential response to noise compared to gratings.

To investigate the effect of texture density, a subset of cells were tested using patterns of increasing element size, and in a few cases, the screen was placed at 1.14m from the animal to determine the responsiveness to a fine texture field comprising elements 0.06° of visual angle. To study the responsiveness of PMLS cells as a function of the RF area stimulated (stimulus size), gratings and texture patterns (at the optimal direction and velocity) were presented within a circular aperture of varying diameter. The normalized diameter-response curves for both gratings and noise were generated to compare the responses as a function of stimulus size.

Histology

Electrolytic lesions were made along recording tracks. At the end of each experiment, the animal was killed by an intravenous overdose of Nembutal. The brain was removed from the skull and immersed in a solution of buffered formalin (10%). Eighty micron serial sections (coronal plane) were cut using a Vibroslice and stained with Cresyl Violet to determine the laminar position of the recorded cells.

Results

General Observations

A total of 206 cells have been recorded in PMLS cortex of which 191 were fully characterized for the purposes of this study. The general properties of the observed units were typical of those reported previously (Morrone et al., 1986; Blakemore and Zumbroich, 1987; Gizzi et al., 1990; Dreher et al., 1996; Minville and Casanova, 1998). For instance, the vast majority of cells were orientation selective (95%) and direction selective to the motion of a drifting grating (68%). The mean optimal spatial frequency was 0.21 ± 0.01 cyc/deg and the majority (69%) exhibited band-pass tuning (mean 2.04 ± 0.09 octaves) with the remaining 31% exhibiting low-pass tuning.

Comparison of Gratings and Texture Responses

The large majority of the cells fully characterized (153/191; 80.1%) responded to the motion of visual noise to varying degrees. The remaining cells were excluded from further study because they showed no evidence of a clear tuning function or they did not have a response that was superior or equal to twice the level of spontaneous activity. No obvious differences were observed with respect to RF size, location, orientation preference or spatial and temporal frequency tuning for the cells excluded from the study.

Fig. 2 here

A representative example of a texture-sensitive cell in PMLS is shown in figure 2. Panel A shows the response of a PMLS unit to sine wave gratings drifted in different directions (responses in PSTH form). The cell exhibited a clear direction preference at 30° (bandwidth = 32°). The cell responded with a low degree of modulation in its discharge (MI = 0.3) and was clearly direction selective (DI= 1.16). Panel B shows the response of the same unit in response to a moving texture pattern (texture element size 0.13°). The overall response strength was lower than that to gratings (54% difference in mean firing rate). Despite broader tuning, the unit showed an overall direction preference similar to that observed for gratings, as shown in panel C. There is a clear correspondence in the preferred directions of motion for the two types of stimuli. Panel D shows that 69% of the units had their optima within 30° for gratings and noise (corresponding to the interval size between directions used in our study). It is worth noting however, that approximately one third (31%) of the cells did not show a correspondence in the direction preference for the two types of stimuli. All directions were represented for both gratings and noise for the population of cells studied and there was no significant bias for horizontal, vertical, or oblique directions of motion with respect to stimulus type (χ^2= 18.6, p>0.05)

Bandwidth Tuning

Fig. 3 here

PMLS units generally responded to a broader range of drift directions for noise compared to gratings. This is illustrated in the above example (figure 2, panel C). Although the direction preference for both stimuli was similar, the unit showed broader tuning for noise drift direction (bandwidths of 64° for noise and 32° for gratings). Figure 3 A presents the distribution of bandwidth values for gratings and noise for cells responding to both stimuli (filled bars) and cells responding to only one type of stimulus (open bars). The range of bandwidth values were similar ranging between 10 and 60° for gratings and 10 to 100° for noise. Comparing bandwidth values for both types of stimuli showed that the means were significantly different (31.2° ± 1.1 vs. 47.3° ± 1.8, for gratings and texture patterns respectively; t-test; $p<0.001$). The mean bandwidth value for all visually responsive cells encountered for gratings was not significantly different from the population responding to both stimuli (gratings mean = 30.5° ± 1.1; t-test; $p= 0.67$). Similarly, the mean bandwidth value for all visually responsive cells for noise did not differ significantly from the overall population (noise mean = 46.8° ± 1.7; t-test; $p= 0.84$). The correlation between bandwidths computed from gratings and noise direction tuning curves is shown in figure 3 B. Clearly, there is a skewed distribution as the majority of cells are clustered above the line of perfect regression (r= 0.13, p= 0.13). This distribution reveals that bandwidth tuning was generally broader in response to the noise stimulus.

Direction Selectivity

Fig. 4 here

The direction selectivity of PMLS cells for both gratings and noise is compared in figure 4. Panel A shows the distribution of the DI for both gratings and noise. The DI values are within the same range for both types of stimuli (0.2 to 1.4), and indicate that the majority of the cells are direction-selective (cells to the right of 0.5). Comparing the mean index values revealed that cells showed a significantly higher DI for noise compared to gratings (0.83 ± 0.004 and 0.71 ± 0.02, respectively; t-test; p<0.001). This comparison reveals that PMLS cells exhibited a higher degree of direction selectivity when stimulated with noise compared to gratings. Panel B depicts the correlation between the DI for gratings and noise (r= 0.33, p< 0.0001). Despite some scatter, the cells appear to be clustered above the line of perfect regression suggesting again, that neurons were generally more direction selective to moving texture patterns compared to gratings. Using an arbitrary value of greater than 0.5 as an index of direction selectivity (Casanova et al., 1995; Casanova and Savard, 1996a; Minville and Casanova, 1998), the majority of the units (63 cells; 59.4%) were found to lie in the upper right-hand quadrant (i.e. direction selective to *both* gratings and noise). Interestingly, there was a substantial number of units (22) that were direction selective for noise and not for gratings (upper left-hand quadrant) compared to only 9 units showing a clear direction selectivity for gratings but not for noise (bottom right-hand quadrant). This latter difference is of interest, since it suggests that the mechanisms underlying direction selectivity may be different across the two types of stimuli. Finally, only a minority of cells (12 units) were not direction selective (i.e. DI less than 0.5) for either noise and gratings (lower left-hand quadrant).

Receptive Field Organization

We investigated whether the centrifugal bias in PMLS reported by Rauschecker and colleagues (1987b) was also evident when stimulated with visual noise, given that moving texture patterns can be considered a more accurate simulation of what is observed in optical flow fields during naturalistic viewing in locomotion (see Gibson, 1950). A distribution is said to exhibit a centrifugal bias when characterized by a uni-modal distribution with a peak centered at 0° (i.e., a predominance of cells showing a difference of zero between their conventional direction preference and the polar angle of the RF with respect to the area centralis; Rauschecker et al., 1987b). Figure 5 shows the distribution of axial direction preferences for PMLS cells assessed using moving texture patterns as a stimulus. The distribution appears weakly bi-modal, with preferences centered for

Fig. 5
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directions corresponding to +90° to +120° and -90° to -120°. The observed distribution does not appear to posses a clear directional bias towards centrifugal directions (Kolmogorov-Smirnov test for normality; z= 0.103, d.f.= 89, p= 0.021). In fact, the distribution of direction preferences appears to exhibit a bias for directions *orthogonal* to that predicted by the optic flow model. Further, in relation to the global organization of PMLS for optic flow processing, Rauschecker and coworkers (1987b) have indicated that velocity preference increases with eccentricity. No relation was observed in our study in terms of optimal velocity for texture drift and RF eccentricity (r= 0.109, p= 0.29). The absence of this eccentricity dependent relationship may arise because the large majority of cells were recorded within an eccentricity of 20° (central visual field).

Response Strength and Profile

Fig. 6 here

It was generally observed that the mean firing rate of PMLS cells was greater for gratings than for noise when comparing the responses at the optimal direction (see example figure 2 C). This relative sensitivity was quantified by computing the ratio of the mean responses at optimal direction for both stimuli (MRN/MRG). Figure 6 A shows the distribution of the MRN/MRG values. Most units (67%) had values less than 1 (mean value of 0.93 ± 0.09), indicating that the responses of the majority of PMLS cells were larger for the motion of drifting gratings compared to moving texture patterns. However, the remaining cells (33%) were shown to have an index greater than 1, indicating that a substantial proportion of cells showed a stronger response to moving texture patterns than to gratings.

In characterizing the responses of neurons to noise in various visual areas, previous groups have used the terminology “field” and “grain” in order to qualitatively describe the profile of discharges (Mason, 1979; Gulyàs et al., 1987; Dreher et al., 1996; Snowden et al., 1991). Field-type responses are sustained throughout the presentation of the stimulus. Grain-type responses are more erratic and characterized as mixed clusters of burst discharges and silent periods during the stimulus presentation. It has been proposed that this latter profile arises because the cell fires in response to an aggregation of discrete elements or phase relationships contained within the noise pattern (Gulyàs et al., 1987; Snowden et al., 1991). Based on these qualitative descriptions, it has been reported that the majority of responses to noise in PMLS were of the grain type (Hamada, 1987; Dreher et al., 1996). To quantitatively determine the nature of the discharge patterns and avoid any error in classification due to subjectivity, we assessed the interspike intervals (ISIs) from the noise response at optimal direction of PMLS cells. “Bursty” and erratic responses would be characterized by the presence of clustered spikes separated by silent periods (i.e. a long ISI; greater than

100 msec), so a predominance of ISIs of long duration would be characteristic of cells exhibiting a grain type profile response (Casanova et al., 1995). Figure 6 B illustrates the distribution of the ISI duration between 100 to 400 msec/ISIs between 1 to 400 msec. The distribution of ISI ratios shows that the majority of cells (68.8%; mean ISI ratio 0.11 ± 0.01) exhibited interspike intervals of very short duration (i.e. less than 100 msec) suggesting that PMLS neurons responded with relatively sustained discharges throughout the presentation of the stimulus.

Velocity Tuning Functions

Selectivity to velocity for drifting noise was assessed for 111 PMLS cells. The large majority of cells (81.3%) were band-pass tuned for velocity, while the remaining cells (18.6%) exhibited low-pass tuning (i.e. showing no attenuation in their responses at low velocities). Two units showed "high pass" profiles, in that their responses showed no attenuation at the highest velocities tested with our stimulation system. Examples of velocity band-pass and low-pass tuning profiles are shown in panels A and B of figure 7. Figure 7C shows the distribution of the preferred velocities to moving texture patterns. The mean optimal velocity was 26.74 ± 2.29°/sec with preferred values varying from 1 to 90°/sec. For units exhibiting band-pass tuning; the mean low and high cutoff values were 7.86 ± 1.75°/sec and 77.5 ± 3.19°/sec respectively. The mean high cut off

Fig. 7
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value for band-pass tuned cells was significantly higher (t-test; $p<0.001$) than that for low-pass tuned cells (mean 52.9 ± 5.43°/sec). The distribution of velocity bandwidth tuning is depicted in panel D. For band-pass cells, the overall mean bandwidth was 4.32 ± 0.34 octaves and ranged between 1.5 to 5 octaves. A high proportion of cells (59.8%) had their tuning width values clustered between 1.5-2.5 octaves suggesting that PMLS cells exhibit a relatively sharp selectivity for noise velocity.

The finding that a high proportion of cells exhibit sharp velocity selectivity suggests that this factor may be an important parameter when studying texture sensitivity in PMLS. In fact, if there is no careful evaluation of the optimal velocity, a weak response may be easily dismissed as being texture-insensitive. This statement is supported by the example shown in panel E. The cell shows a differential velocity profile depending on the stimulus used (low-pass tuning selectivity for gratings and a clear band-pass tuning profile when tested for noise; see additional tuning curves of figure 7 panel E). When direction selectivity for noise was tested at a velocity optimal for gratings (10°/sec; estimated by dividing the optimal temporal frequency by the optimal spatial frequency), the cell showed a directional tuning function barely above the level of spontaneous activity. However, after assessment of the velocity profile of the cell, it was found that its optimal velocity for noise was much higher (50°/sec). Drifting the noise at the optimal velocity yielded a clear response and a directional tuning function. Furthermore, the directional preference of the cell to moving texture patterns was not identical to that for gratings (as was the case for 31% of the cells in the study). Thus, the assumption that response properties for moving texture patterns (e.g. velocity or direction preference) are similar to those determined for gratings (or with a bar), could result in cells being incorrectly classified as texture-insensitive.

Influence of Texture Element Size

We tested the effect of increasing texture element size on the responses of PMLS neurons for a subset of 83 cells. The response to noise at optimal direction and velocity were recorded at four different texture element sizes. For the majority of the cells tested (63.8%), it was observed that discharge levels became more vigorous with increasing texture element size. This observation is illustrated in part 1 of Figure 8 A. The response of the cell gradually increased with increasing element size, reaching a maximal rate of discharge at an intermediate element size before saturating in its level of response. It is of note that the cell gave a measurable response to a drifting noise pattern comprising the smallest element size presented at optimal velocity and direction. A sub-population of cells (18.2%) responded with a similar rate of discharge regardless of the element size (see part 2 of figure 8 panel A). As shown in part 3, a few

Fig. 8 here

cells (14.4%) exhibited some degree of selectivity to element size in that the responses of the cell were attenuated at sizes inferior to or larger than an optimal element size. Finally, part 4 illustrates an example of a remaining group of cells (3.6%) exhibiting a maximal response at the smallest element size and an attenuation in responsiveness as the element size of the noise pattern increased.

For a subset of 27 cells showing a clear response to noise patterns with an element size of 0.13°, texture sensitivity was assessed by placing the CRT 1.14 m away from the animal (ie. halving the size of the elements within the texture pattern). Of the cells tested, 70.4% (19 cells) showed a clear response in directional tuning for the drifting noise pattern with texture elements as small as 0.06° (5 of the remaining 8 cells showed indications of response selectivity to the stimuli but responses were less than twice the spontaneous activity level). Figure 8 B shows an example of a cell's directional tuning in response to gratings and two moving texture patterns (element sizes: 0.13° and 0.06°). The cell showed a clear directional tuning to noise similar to that for gratings. Although the response of the cell was not as strong for the pattern with the smallest element size, it is clear that the unit could be driven by a very fine texture pattern.

To compare the profiles of the overall population as a function of texture element size, the responses of a given cell were normalized against its response to the largest element size used in the study (1.01°). Figure 8 C shows the distribution of normalized responses as a function of texture element size. Several conclusions can be drawn from this figure. First, there is an average increase in responsiveness with increasing texture element size. This is in accordance with the previous observation that the majority of cells (63.8%) exhibited an increase in their responsiveness with an increase in texture element size (see panel A, part 1). However, there are a large number of cells that exhibited a maximal responsiveness at sizes inferior to the largest element size used (data points above the 100 line). There were even a few cells (6 units) showing a response twice as great as their response to the pattern of largest element size (data above the 200 line). Finally, note that only a few cells (9.6%) were unresponsive to patterns comprised of the smallest element sizes (cells below the zero line).

Influence of Stimulus Size

For a subset of 15 cells, we determined the extent to which responses were dependent on the size of the pattern (i.e. the area of the visual field stimulated). The effect of stimulus size was assessed for both noise and grating stimulation by varying the diameter of the window containing the stimulus drifting at optimal speed and direction. Panel A of figure 9 shows a representative example of a diameter-response curve for

Fig. 9
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noise (open circles) in comparison to that for gratings (filled circles). In this example, note that the maximum response to gratings was attained at a stimulus size much smaller than that for noise (16° vs. 26°, respectively). The aperture size required to elicit a half-maximal response for the gratings (13°) was smaller than that for noise (19°). Further, an attenuation in response with increasing stimulus size is evident for the gratings but not for noise suggesting that differential mechanisms may be involved within and beyond the "classical" RF (see Discussion). Panel B, shows a unit where both the responses to gratings and texture increase with increasing stimulus size. As with the previous example, the size of the stimulus required to elicit a half-maximal response for noise was greater than for gratings (27° and 16°, respectively). Further, note that at an aperture size similar to the hand-plotted RF diameter (8°), a clear response is elicited for gratings but not noise. Finally, panel C shows an example where the aperture size required to elicit a half-maximal response was similar for both gratings and noise stimuli (14° and 16°, respectively). Cases where the diameter-response curves for both stimuli were similar were observed for 4 out of 15 cells.

Figure 9 D shows the distribution of the mean RF lengths (hand-plotted long axis) (mean ± SD: 8.93° ± 2.31) compared to distributions of the mean stimulus sizes necessary to elicit half-maximal responses for gratings and for noise (9.7° ± 6.31 and 17.34° ± 6.55, respectively).

Clearly, the stimulus size required to elicit the mean half-maximal response for gratings is comparable to that of the classical RF. Despite an overlap in the range of distributions, the mean diameter stimulus size necessary to evoke a half-maximal response for noise was significantly higher (t-test; $p<0.001$) and corresponded to roughly double the RF size.

Laminar Position

Fig. 10 here

We assessed the laminar position for 119 texture-sensitive cells to determine whether there was a relationship between responsiveness to visual noise and laminar position of the cells. Figure 10 shows the distribution of texture sensitivity indices as a function of cortical laminar position. Despite some sampling bias, the first observation is that texture-sensitive cells were observed in all cortical layers (ANOVA: $p=0.685$). Given the large tectal, thalamic, striate, and extra-striate inputs converging onto PMLS, and their reciprocal connections therein, one would expect a uniform distribution of texture-sensitive cells throughout all cortical layers in this area. Second, cells recorded in layer 4 showed a clear texture sensitivity (mean MRN/MRG: 1.01 ± 0.16), perhaps reflecting the strong extra-geniculate thalamic input of texture-sensitive cells this layer receives (i.e. LPl; Mason, 1981; Casanova and Savard, 1996a). Third, cells in supra-granular layers 2/3 were also texture-sensitive (mean MRN/MRG: 0.88 ± 0.14). This may be the result of a texture-sensitive input of striate origin (Casanova et al., 1995) and further suggests that texture sensitivity is also processed within communicating cortical areas. Finally, cells responding to noise were also distributed throughout infra-granular layers 5 and 6 (mean MRN/MRG: 1.17 ± 0.23 and 0.54 ± 0.15, respectively), in accordance with the fact that texture-sensitive cells have been documented in communicating subcortical structures namely; the LP (Mason, 1978; Casanova and Savard, 1996a), LGN (Mason, 1976) and SC (Mason, 1979). Investigation of preferred direction, optimal velocity, and tuning selectivity for noise showed no apparent correlation with cortical location (ANOVA; p= 0.308, p=0.525, p=0.794 respectively, results not shown). These latter findings are consistent with previous studies of striate cortex in our laboratory (Casanova et al., 1995).

Discussion

The results of this study indicate that a large majority of cells (80.5%) in PMLS could be driven by the motion of texture patterns comprised of fine elements (as small as 0.06° of visual angle in some cases). These responses varied as a function of drift direction, velocity, and with the size of the stimulus and elements comprising the texture pattern.

Comparison with Previous Studies

The proportion of texture-sensitive cells in PMLS cortex found in this study (80.5%) was much higher than those reported by previous groups [von Grünau and Frost, 1983: (0%); Hamada, 1987: (73%, using large element sizes); Dreher et al., 1996: (46%)]. Furthermore, the response profiles of texture-sensitive cells were predominantly characterized by discharges that were sustained throughout the presentation of the stimulus. The presence of sustained discharges is consistent with the fact that PMLS receives direct and prominent inputs from areas known to respond vigorously to the motion of texture fields; such as area 17 (Skutton et al., 1988; Casanova, 1993; Casanova et al., 1995), and the striate-recipient zone of the LP-pulvinar complex (i.e. LPl) (Mason, 1978; Casanova and Savard, 1996a).

The wide discrepancy in results across different studies could be related to a number of factors. The nature of the noise stimulus used is perhaps the most important of these. As already mentioned, the texture pattern used in the present study was computer-generated, refreshed at each trial, and responses of PMLS cells represented the average response of randomly interleaved presentations. Such a method of stimulation curtails any problems of weak sporadic firing and habituation (Blakemore and Zumbroich, 1987; Spear, 1991) that would result in an underestimation of responsiveness and ultimately, the proportion of texture-sensitive cells. Furthermore, their may have been a misclassification of cells based on their response properties. For example, the selectivity of a given cell was not necessarily identical for gratings versus noise stimuli in terms of directional preference and/or velocity. Therefore, using the same direction and/or velocity determined with gratings (or bars) would be an inaccurate assumption, and could generate a response to texture that is non-optimal (see example in figure 7 panel E). Also, the fact that responses of PMLS cells vary with both texture element size and overall stimulus size could further lead to the production of a weak response and subsequent wrongful classification of the cell as being texture-insensitive.

Directional Tuning

Comparison of direction preferences for both gratings and noise indicated that the majority of the cells (69%) had their directional optima within 30° of each other. This finding suggests that the circuitry for directional preference may be common for both types of stimuli. However, the fact that a substantial number of units (31%) showed very different direction preferences depending on the type of stimulus suggests that the mechanisms are not necessarily coupled for all cells in PMLS. Although it has been suggested that noise and gratings could share a common directional mechanism (Skottun et al., 1994), a directional anisotropy between these two stimuli has been previously reported in area 17 (Bauer and Jordan, 1993). The texture patterns used in the latter study however, were composed of very large elements (1.6° and 4.8°). An explanation for the observed anisotropy may be that at large element sizes, low spatial frequencies become more prevalent (Casanova et al., 1995) and thus, may have contributed to the differences in tuning found.

PMLS cells generally showed a broader tuning function for noise than for gratings. This finding is consistent with results for other visual areas obtained from our laboratory (Casanova et al., 1995, Casanova and Savard, 1996a). This broader tuning function can be explained if one considers both gratings and noise stimuli in the frequency domain. A grating pattern has a unique spatial frequency and orientation, whereas the power spectrum of a fine texture pattern reveals that it is composed of energy at all spatial frequencies and orientations (see figure 1). Therefore, one might expect a broader directional tuning for a cell responding to noise because elements moving at off-orientations contain spectral components contributing to the overall response of the cell (see Casanova et al., 1995; Casanova and Savard, 1996a). At a more intrinsic level, one might expect that the convergence of cortical and subcortical inputs on PMLS cells would result in a broadening of the noise tuning in this area. This was not the case, because PMLS neurons showed noise tuning functions and directional selectivity indices that were strikingly similar to their direct subcortical (LP) and striate inputs [mean bandwidth PMLS: 46.7°, LP: 49.3°, area 17: S cells: 43° and Cx cells: 47.6°; mean DI: PMLS: 0.86, LP: 0.92, area 17: S cells: 0.81 and Cx cells: 0.74 (Casanova et al., 1995; Casanova and Savard, 1996a)]. A likely explanation could be related to intrinsic cortical processing and/or the possibility that target cells in PMLS receive their cortical and subcortical afferent information regarding directional tuning in register; thus analyzing within the same tuning envelope (Casanova et al., 1995).

It is likely that the anisotropy for directional preference and selectivity between gratings and moving texture patterns (see above) are the result of differential directional inputs and stimulus-sensitivity. For example, converging afferent inputs from non-direction selective cells may render a target cell non-direction selective when stimulated with gratings. However, these same converging cells could also be responsive to moving texture patterns (each with a broad tuning function), with the result that the pooled inputs render the target cell direction selective in response to moving texture patterns. There is evidence that direction selectivity in PMLS is the result of afferent inputs rather than intrinsic computation, and these inputs are likely to originate from cortical rather than subcortical loci. Spear and Baumann (1979) have reported that removal of areas 17,18, and 19 leads to a reduction in the proportion of direction selective cells in PMLS. On the other hand, direction selectivity was not altered by deactivation of the LPI (Minville and Casanova, 1998). Furthermore, behavioral studies have shown that removal of PMLS (and the posterolateral bank; PLLS) does not produce a deficit in motion detection of simple sinusoidal gratings despite the strong direction selectivity of neurons in this area (Pasternak et al., 1989).

Rauschecker and colleagues (1987b) have reported that the RF spatial arrangement of PMLS cells exhibits a bias towards centrifugal directions of motion and is ideally suited for the analysis of expanding flow fields. In our study, we did not observe a clear centrifugal bias using noise to assess direction selectivity. In fact, the obtained distribution reflected a bias towards *orthogonal* directions of optic flow. This lack of agreement could have been produced by numerous factors. First, the observed centrifugal bias was determined using more conventional visual stimuli (i.e. bars) [Rauschecker et al., 1987b]. Thus, the fact that cells do not necessarily show identical direction preference for all stimuli may have contributed to the absence of a clear centrifugal bias for moving texture patterns. Second, the large majority of RFs mapped in the present study were localized in the central visual field representation. The same group has reported that this bias is particularly evident when assessing cells with eccentricities as far out as 40° (see also Albright , 1989, for a similar study in MT). Third, and perhaps most important, is the fact that Sherk and colleagues (1995) have reported that PMLS contains two subregions of cells: one group located in the anterior division showing a clear bias for optic flow (centrifugal) directions; and a second group located posteriorly, where directional preferences appear to be orthogonal to optic flow directions. This group has also suggested that the anatomical division between the two populations corresponds to a break in the representation of the lower vertical meridian. The majority of electrode penetrations in the present study were around or posterior to the coordinates corresponding to this region of the visual field, so it is possible that the distribution in axial preferences observed in our study represents a mixed sampling of these two populations of cells.

Selectivity to Noise Velocity

Previous assessments of the responsiveness of PMLS with bars and gratings revealed that cells were often tuned to a wide range of velocities (e.g. Morrone et al., 1986; Dreher et al., 1996). This finding is also confirmed when cells were tested with moving texture patterns (mean high cut-off: 71.9°/deg) and lends further credence to the purported role of this area in motion analysis.

PMLS cortex receives a strong excitatory Y-type input which likely underlies the preference of this area for high velocities (Rauschecker et al., 1987a; Dreher et al., 1996). However, it is unknown if the wide range of velocities represented in PMLS are the result of massive convergence of cortical and subcortical afferents or intrinsic cortical computation. There is evidence suggesting that velocity tuning in PMLS reflects the convergence of inputs onto this area. For example, despite a massive striate projection, it has been shown that the large indirect tectal input this extrastriate area receives is responsible for the low temporal frequency attenuation of PMLS cells (Smith and Spear, 1979).

The Effect of Texture Element and Stimulus Size

In general, we found that responses of PMLS cells increased with increasing element size. Nonetheless, cells could be driven with texture patterns composed of elements as fine as 0.06°. This finding is of particular importance, because Hamada (1987) reported that only patterns composed of texture element sizes between 1.6° and 4.8° were effective in driving cells. In the present study, only a minority of cells (38 out of 191) could not be driven by noise patterns comprised of elements as small as 0.13°. In addition, the maximal responses for a cell were not always limited to the largest texture element size used in the study. A certain number of cells (14.4%) exhibited a preference for an intermediate element size, and a further subset of cells (3.6%) exhibited an attenuation in their responses as the size of the texture elements increased. The mechanisms involved in producing selectivity with respect to texture element size are unknown and are worth further investigation.

The results of this study also indicate that the responses of PMLS cells vary as a function of the size of the stimulus. It was observed that most cells did not respond to the moving texture pattern if the latter covered an area equal or inferior to the cell's RF. A stimulus size corresponding to roughly twice the RF size was necessary on average, to elicit a half maximal response. These findings are also congruent with observations in area 17 (Casanova, 1993). This increase in responsivity as a function of stimulus size could result from the recruitment of neighboring cells integrating information over a much larger area than that of the classical RF (conceivably via long-range horizontal connections: Lowenstein and Somogyi, 1991; Norita et al., 1996; Gilbert, 1998). The differential profile observed between diameter-response curves for noise versus grating stimuli indicates that distinct mechanisms could be involved within and outside the classical RF depending on the “contextual relevance” of the stimulus. It has been suggested that the mechanism underlying PMLS receptive field structure (e.g. double-opponency) is the result of complex local circuitry and the convergence of afferent inputs (von Grünau and Frost, 1983; Dreher et al., 1996). For example, responses to stimuli within the RF center could be mediated by an orientation-dependent input from area 17 simple cells. The surround effects on the other hand, are likely to be the contribution of cortical complex cells and tecto-thalamic input (von Grünau and Frost, 1983). It is also possible that a direct LP projection may contribute to the surround effects in PMLS. RFs in LP are large (encompassing those of PMLS cells) and these cells also show modulatory effects in association with stimulus interactions (Casanova and Savard, 1996b; Minville and Casanova, 1998).

Functional Considerations

Rauschecker (1988) has proposed the notion of a LP/LS subsystem representing a unique thalamo-cortical loop important for complex motion analyses such as figure-ground discrimination and optical flow field detection. Specifically, the lateral portion of LP (LPl) and PMLS could represent such a module of analysis. Anatomically, these regions are reciprocally connected (Norita et al., 1996), and both areas have similar proportions of texture-sensitive cells and overall texture sensitivity (PMLS: 80%, LP:87%; mean MRN/MRG: PMLS: 0.93; LP: 0.78). More importantly with respect to motion analysis, the range of velocities represented within both areas is similar (27.5°/sec for LP and 26.7°/sec for PMLS; Casanova and Savard, 1996a), suggesting that both areas are analyzing motion within a similar velocity envelope. Such an organization would allow for cortical motion computations to be carried out in parallel, with subcortical structures (e.g. LP) analyzing, transforming, refining, and finally, re-routing visual information through various visual areas in an iterative and dynamic matter (Rauschecker, 1988; see also Merabet et al., 1998).

Numerous groups have proposed that the PMLS cortex of the cat represents the functional analogue (or homologue) of the middle temporal area (MT) of primates (for review see Payne, 1993). Although a complete survey and comparison of both areas is beyond the scope of this study, the basis for this conclusion stems from anatomical (Payne, 1993), physiological (Blakemore and Zumbroich, 1987, Wang et al., 1995) and behavioral evidence (Pasternak and Merigan, 1994; Lomber et al., 1996) suggesting that both these areas make similar contributions with regards to the processing of complex motion stimuli.

Studies at both the physiological and theoretical levels have proposed that motion perception involves a two-stage process; one involving the detection of local motion signals and a second stage, involved in the integration of local information into global motion signals (e.g. Adelson and Movshon, 1982). The finding of "pattern-selective" cells capable of signaling the veridical direction of a moving plaid pattern in MT has reinforced notions that this area is important for global motion processing (Movshon et al., 1985, Stoner and Albright, 1992). To date, however, similar studies in PMLS have not been able to demonstrate the existence of pattern-selective responses (Gizzi et al., 1990; Merabet et al., 1998). Given the present results, it is possible that PMLS neurons make a greater contribution to local motion integration than previously suggested, and provide the necessary input for other areas processing global motion (for example; providing the component input to the anterior ectosylvian visual cortex (AEV) and/or LP nucleus where pattern-selective cells have been reported: Scannell et al., 1996; Merabet et al., 1998). It is also possible that other areas of the LS cortex [e.g. the posterolateral (PLLS) and anterolateral (ALLS)] possess pattern-selective responses. If further experiments in these areas reveal this to be the case, it would perhaps more appropriate to consider the *entire* LS cortex as the MT homologue.

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Abbreviations

AEV	anterior ectosylvian visual cortex
Cx	complex cell
deg	degrees
DI	direction index
ISI	interspike interval index
LGN	lateral geniculate nucleus
LP	lateral posterior nucleus
LPl	lateral part (striate recipient zone) of the lateral posterior nucleus
LPm	medial part (tectal recipient zone) of the lateral posterior nucleus

LS	lateral suprasylvian cortex
MI	modulation index
msec	milliseconds
MRN/MRG	mean response to noise at optimal direction/mean response to gratings at optimal direction
PMLS	posteromedial lateral suprasylvian cortex
S	simple cell
SC	superior colliculus
Sp/sec	spikes per second
RF	receptive field

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FIGURE LEGENDS

Figure 1. (A) Example noise pattern used in this study. For description see text. (B) Fourier power spectrum of the stimulus. Note that the power spectrum shows that all spatial frequencies and orientations have the same amount of power in both frequency axes (up to 128 cycles/image).

Figure 2. Responses of a PMLS cell to drifting gratings (A) and noise pattern (B). Results are shown in PSTH form (duration 4 sec). (C) Corresponding tuning curves showing the responses as a function of drift direction for gratings (filled symbols) and noise (open symbols). Arrows indicate spontaneous activity levels and error bars represent SEMs. (D) Distribution showing the optimal direction difference between the two stimuli.

Figure 3. (A) Distribution of the bandwidth tunings for gratings and for noise. The unfilled bars represent the distribution for all PMLS cells encountered in the study. Filled bars represent the cells showing a clear tuning for *both* gratings and noise. (B) Correlation between bandwidths computed from responses to gratings and noise. Note that the majority of the data points are skewed above the line of perfect regression.

Figure 4. (A) Distribution of the direction indices for gratings and for noise. (B) Correlation between direction indices. Dashed lines represent criterion used in this study to establish direction selectivity (DI=0.5). Shaded regions represent areas where cells were direction-selective to only one stimulus. Inset figure depicts number of cells in each quadrant. Note that the majority of the cells are direction-selective to both the gratings and noise stimuli.

Figure 5. Distribution of axial direction preferences for noise corresponding to the difference between the polar angle of the RF center and conventional direction preference.

Figure 6. Response strength and profile to visual noise (A). Distribution of MRN/MRG indices for PMLS cells. (B) Distribution of $ISI_{100-400}/ISI_{1-400}$.

Figure 7. Influence of noise velocity. Examples of band-pass (A) and low-pass (B) type velocity tuning. Arrows indicate spontaneous activity levels. (C) Distribution of optimal noise velocities. (D) Distribution of velocity bandwidths from cells in C). (E) Example showing the importance of testing response to noise at optimal velocity. The directional tuning curves to gratings (solid line), noise at a velocity comparable to that of gratings (open circles), and at optimal noise velocity (filled circles) are shown. Note

that the cell shows a clear response for noise only when tested at its optimal velocity. Arrows indicate spontaneous activity levels. The responses of the cell as a function of temporal frequency of the grating and the velocity for noise are also shown. ①Noise velocity corresponding to the velocity of gratings, ②Optimal noise velocity for the cell. Abbreviations: LP; low-pass; HP: high pass.

Figure 8. Effect of texture element size on responses of PMLS cells. (A) Representative examples of response profiles observed as a function of texture element size. The proportion of cells exhibiting a similar profile are shown in parentheses. Note that in all cases, the cells responded to noise patterns with the smallest element size. (B) Responses of a cell to a drifting noise pattern comprised of very fine elements (0.06°; grey circles) compared to a pattern of 0.13° (open circles) and to gratings (filled circles). (C) Responses for each cell at different texture element sizes are normalized with respect to the response at the maximum element size (1.01°). A normalized response of 100 indicates that the cell responded equally well to a pattern of a given element size as to its response the largest element size. Filled triangles indicate the mean responses for a given texture element size (mean ± SEM; 0.13°: 58.39 ± 5.65, 0.25°: 70.86 ± 6.24, 0.5°: 90.77 ± 6.80).

Figure 9. Effect of stimulus size on responses of cells in PMLS. (A-C) Example of the responses of three units as a function of window diameter containing gratings (filled circles) and noise (open circles). Insets depict the maximum response for each tuning curve (spikes/sec). Dotted lines represent the stimulus diameter required to elicit a half-maximal response. [long axis of the excitatory region of the "classical" RF: A: 6.4°; B: 8.1°; C: 9.3°] (D) Distribution of RF lengths (long-axis, hand plotted) and the diameter necessary to elicit a half-maximal response for gratings and for noise. Filled triangles represent mean diameter values (mean ± SD; RF long axis: 8.92° ± 2.31, Gratings ½ maximal: 9.71° ± 6.31, Noise ½ maximal: 17.33° ± 6.55) .

Figure 10. Noise responsiveness (expressed as MRN/MRG) of texture-sensitive cells in PMLS as a function of laminar position. Dashed line represents an equivalent response to both gratings and noise. Filled triangles represent mean MRN/MRG values [mean ± SEM (median); 2/3: 0.88 ± 0.14 (0.63), 4: 1.01 ± 0.16 (0.73), 5: 1.17 ± 0.23 (1.26), 6: 0.54 ± 0.13 (0.48). Ind: 0.89 ± 015 (0.60)]. Abbreviation: Ind; cells of indeterminate laminar position.

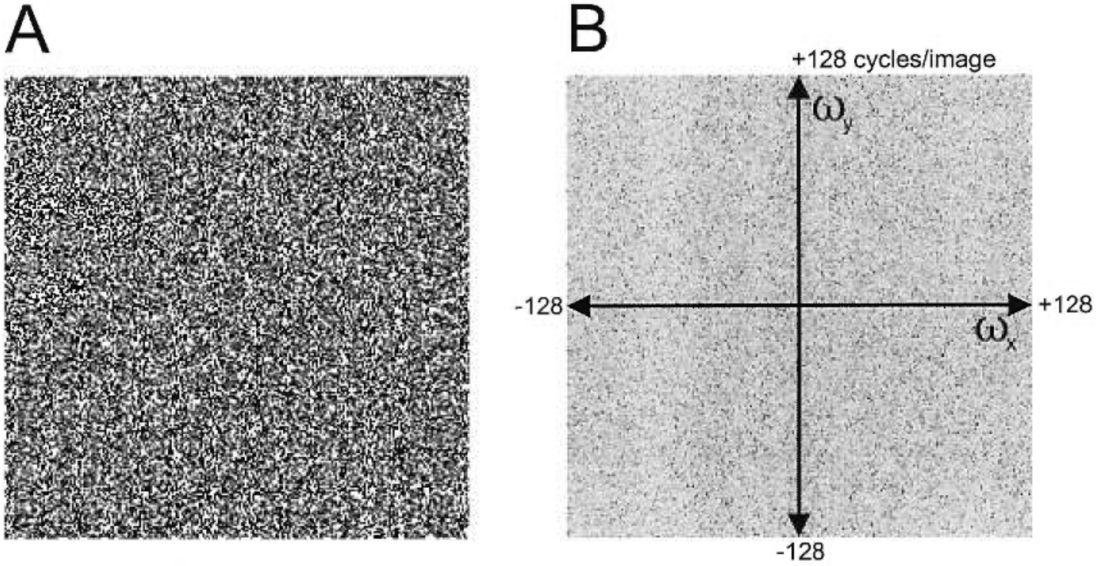

Figure 1
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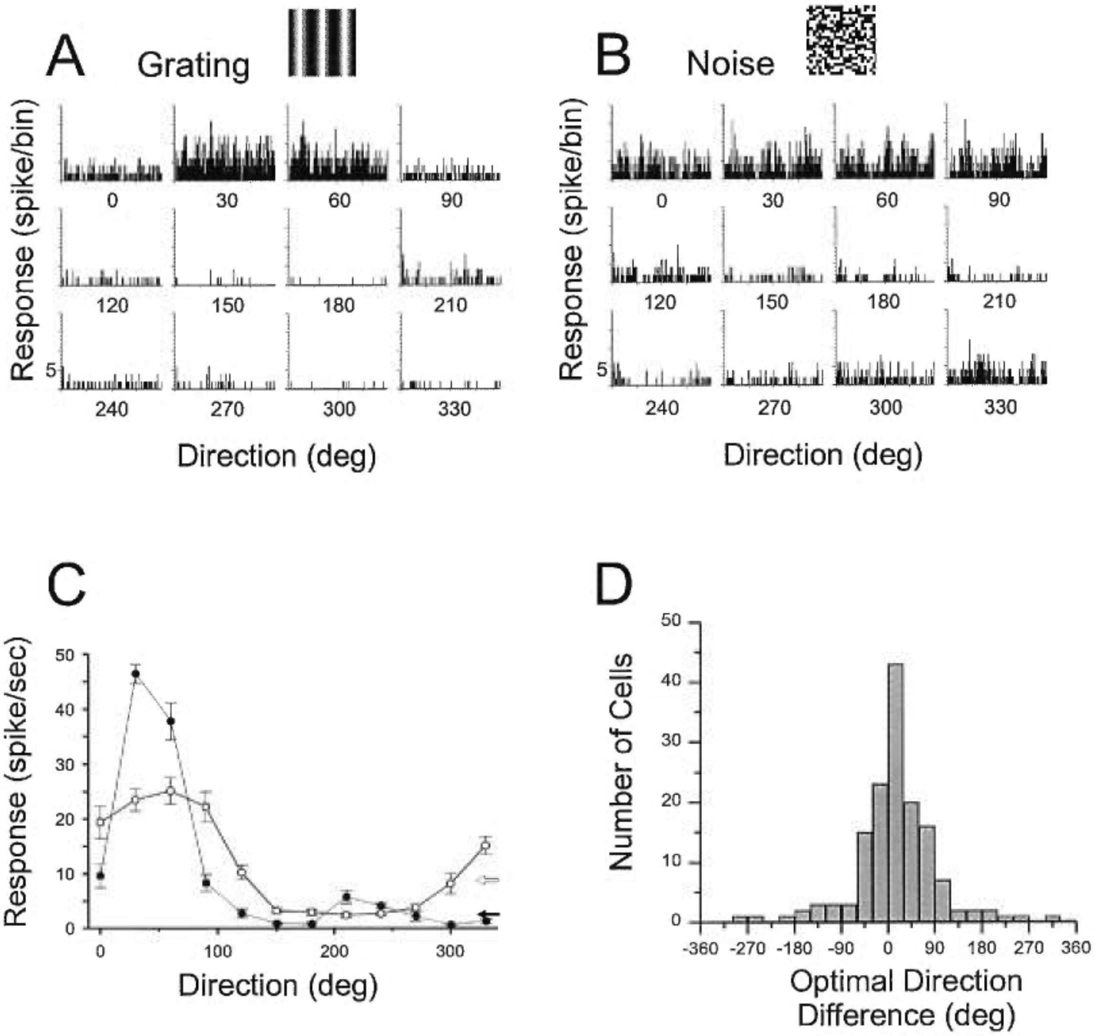
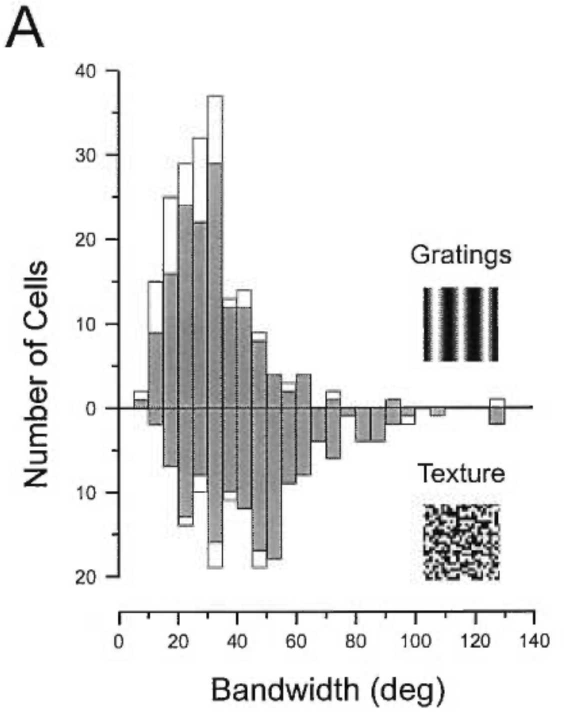


Figure 2
Merabet et al., 1999
Cell:Kz2506:1,8



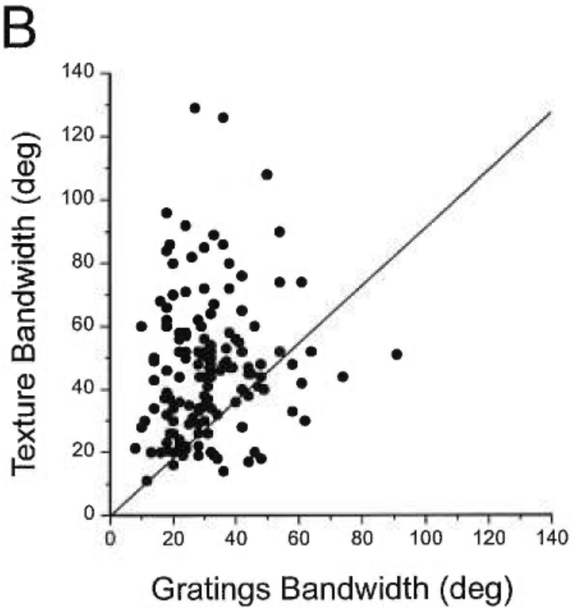


Figure 3
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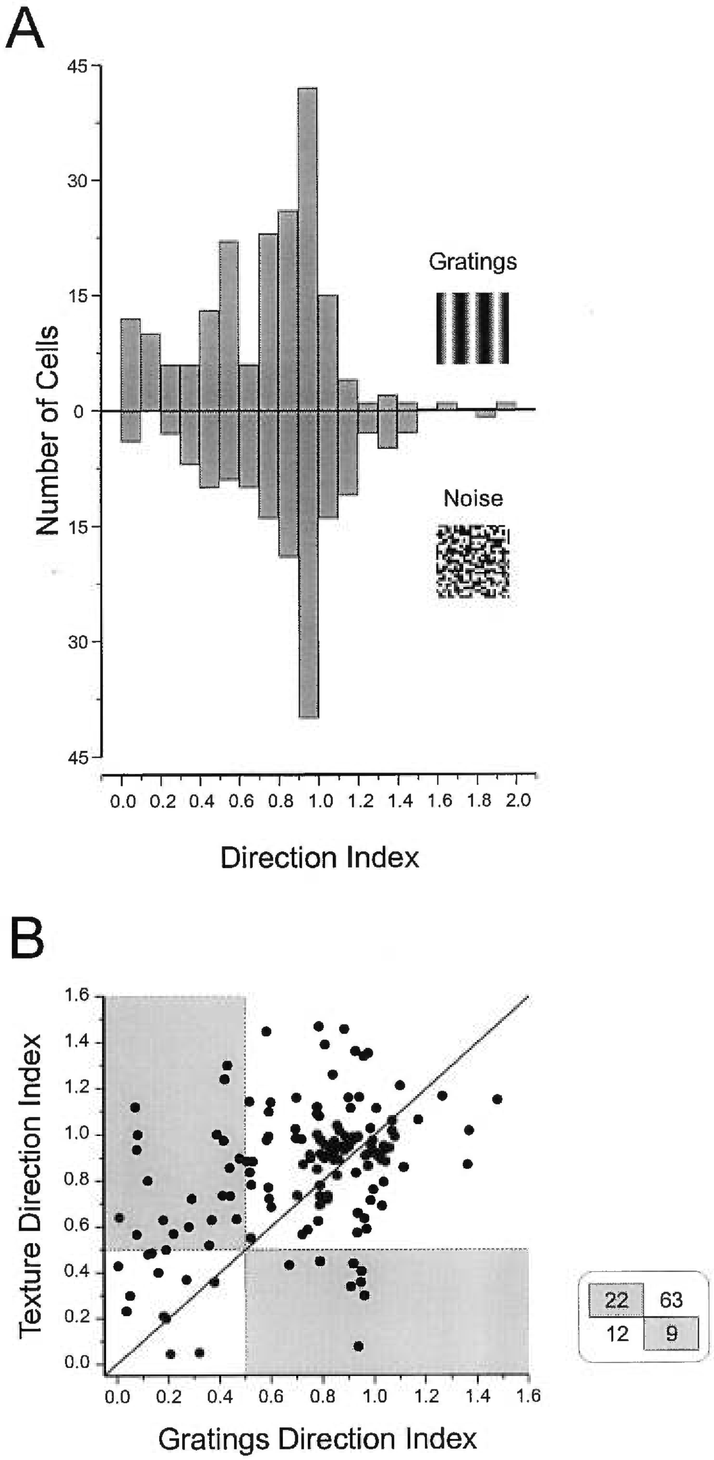

Figure 4
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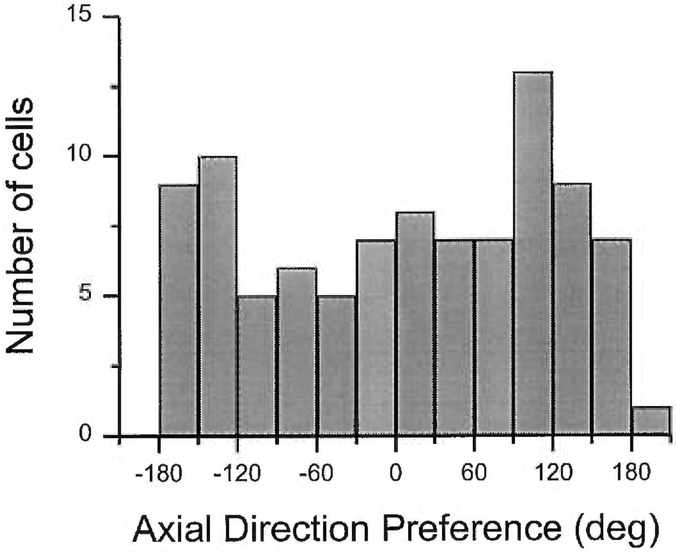

Figure 5
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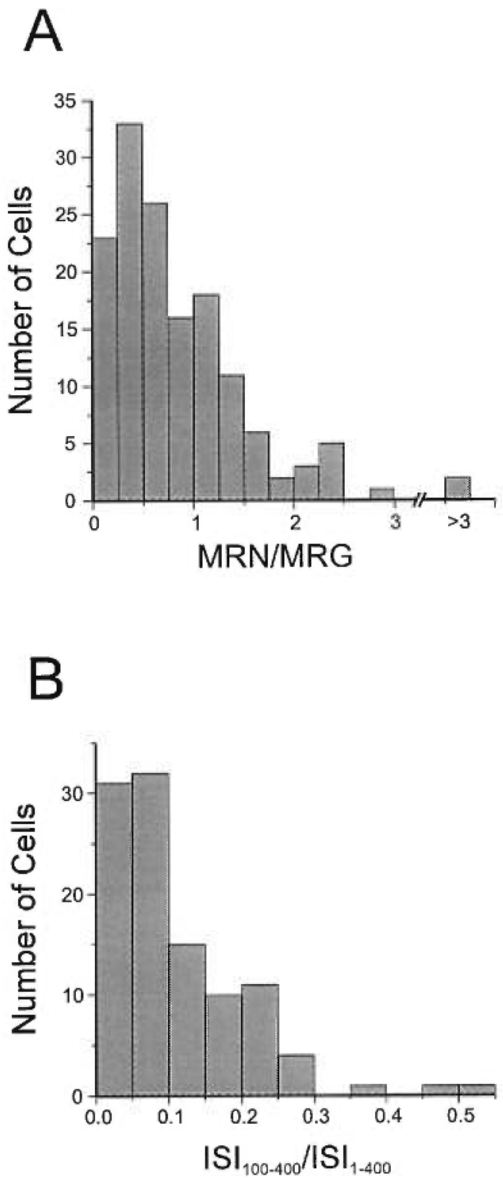

Figure 6
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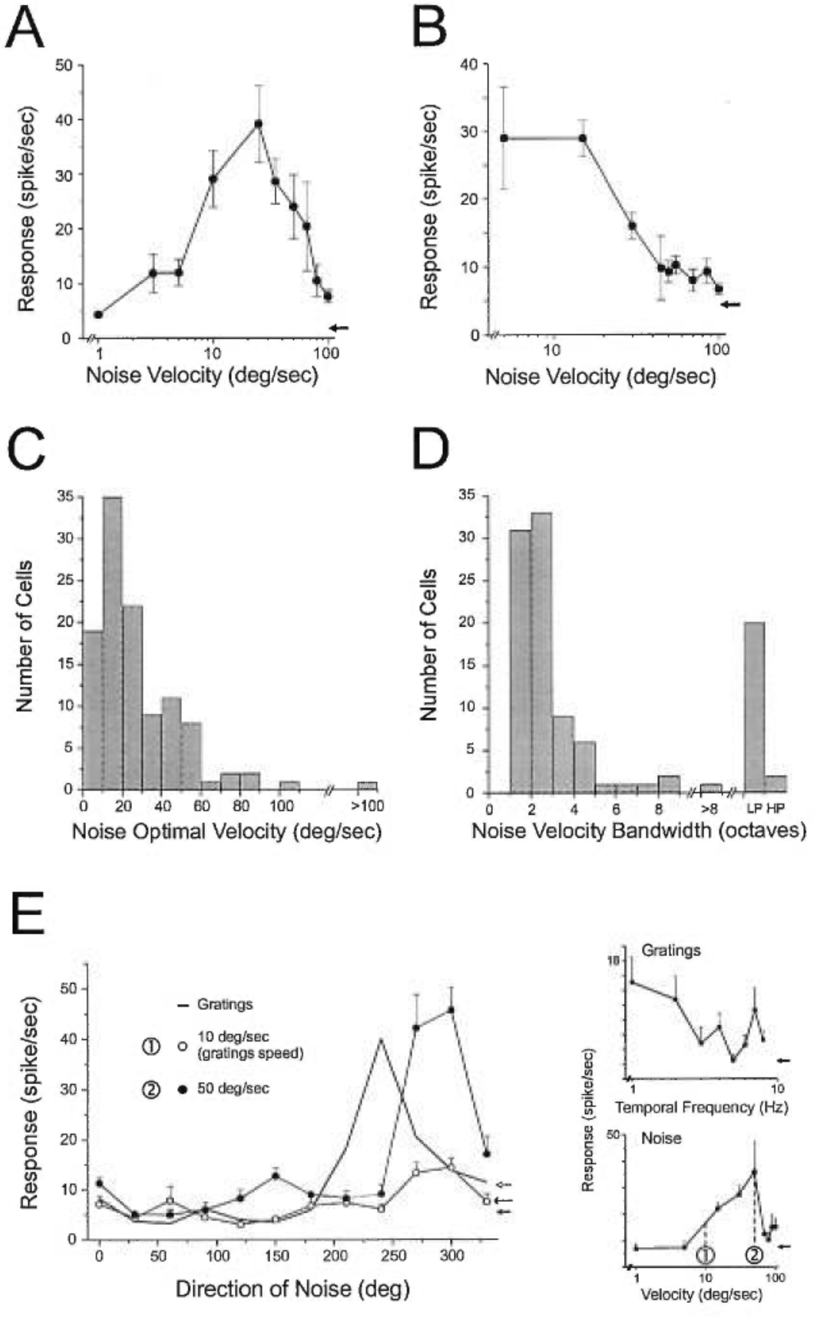

Figure 7
Merabet et al., 1999
Cells: A: Cz3004, B: Jz3001, E: Fz3004

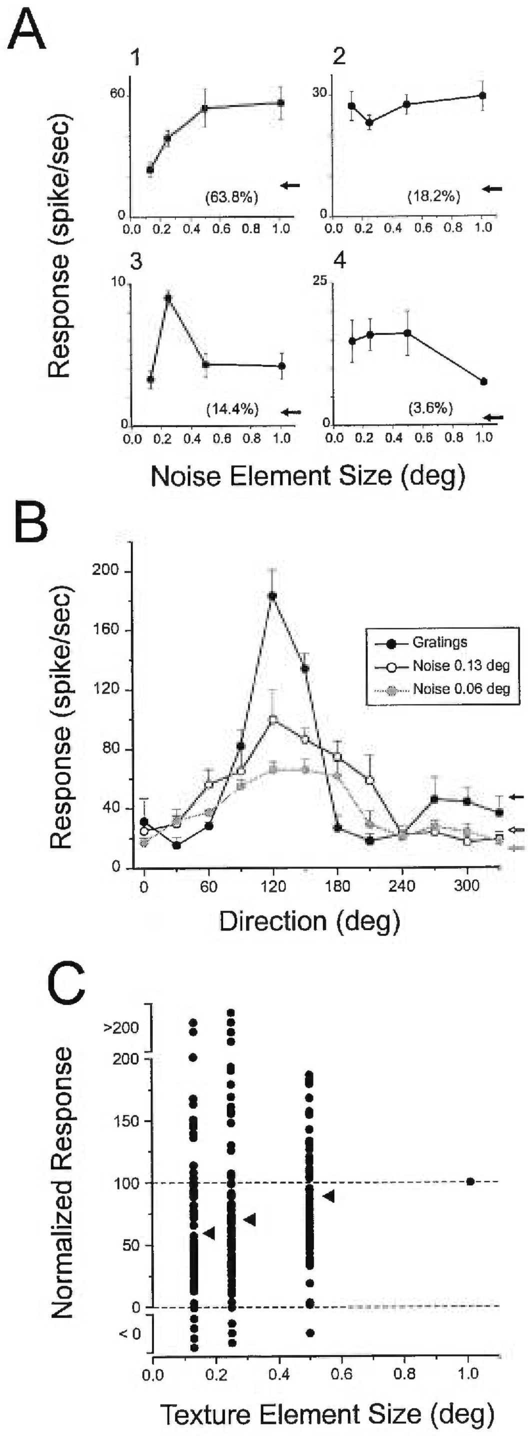

Figure 8
Merabet et al., 1999
Cells 1:Cz1302, 2:Cz3004, 3:Dz1303, 4:Jz2409

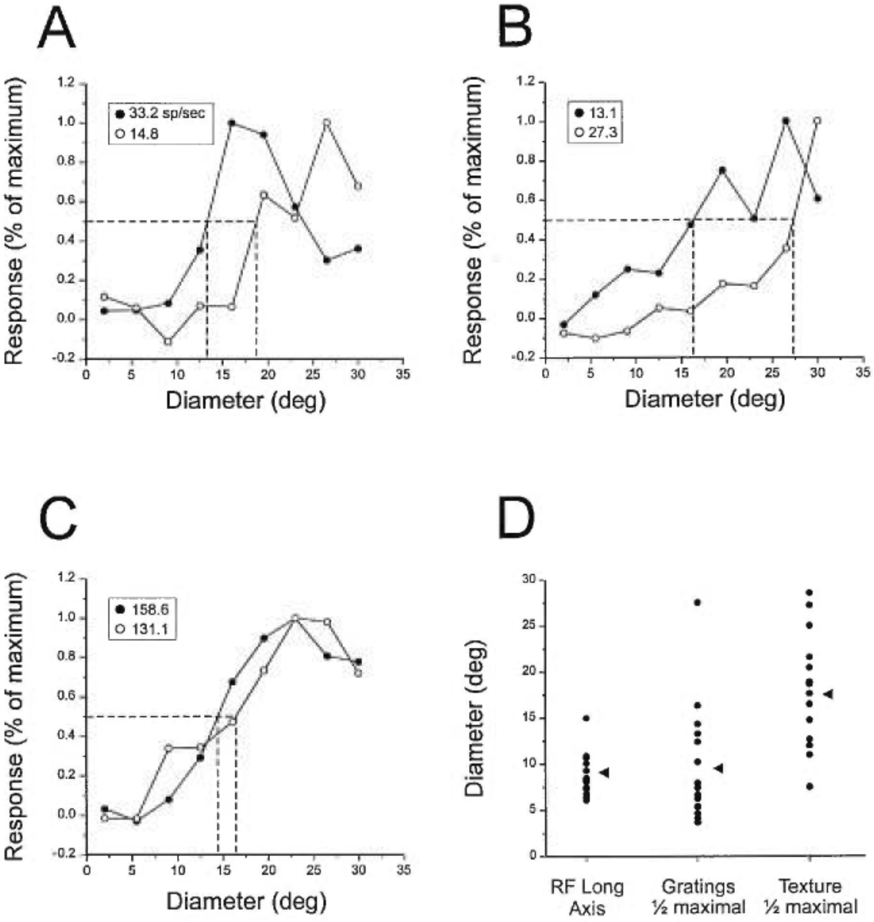

Figure 9
Merabet et al., 1999
Cells: A: Gz0312, B: Jz2409, C: Gz2210

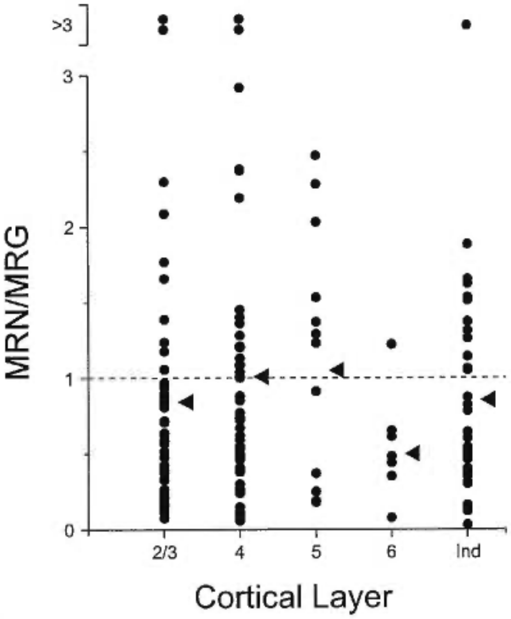

Figure 10
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Preliminary Results: Influence of Moving Texture Patterns on Responses of Cells in the Cat Posteromedial Lateral Suprasylvian Cortex

The anatomical connections and strong similarities in response properties between PMLS and LP support the notion that these two areas may be analysing similar aspects of a visual scene along a cortico-thalamic loop. In a preliminary attempt to investigate the properties of both these areas to a more complex motion stimuli, we have characterised responses of cells in PMLS cortex using a visual stimulus that differentiates between a figure and its background. These stimulus-interaction effects (defined by relative motion cues) have been previously reported in PMLS (von Grünau and Frost, 1983; Merabet et al., 1997) and in LP (Casanova and Savard, 1996b). We have employed a stimulus protocol used previously in LP and compared these results with responses found in PMLS. The stimulus used was characterised as follows: full-field drifting sinusoidal gratings are superimposed on a texture background that is moving either in the same direction (in-phase condition), opposite direction (anti-phase condition) or remaining stationary. Our results indicate that in general, PMLS cells show a strong facilitation in their response when the grating moves in the same direction and speed as the texture background (in-phase condition; mean increase in response of 74.4% ±16.2 SEM, see figure 8 A). Interestingly, comparison with results obtained in LP indicate that responses in this area are inhibited when the grating and texture pattern move in *opposite* directions (anti-phase condition) while responses to the in-phase condition remain unaffected (Casanova and Savard, 1996b).

This discrepancy may be related to the fact that both areas could be computing the relative movement of an object with respect to its background differently. The combined effect however, may allow for a more efficient and accurate global motion analysis (Casanova and Savard, 1996b).

As a continuation of the study, we investigated the effect of reversible deactivation of LP (injection of GABA) on PMLS responses to figure-ground stimulus interactions. At first, this study may appear counter-intuitive given that previous reports in our laboratory (using a similar deactivation protocol) have found that deactivation of LP does not affect the spatial and temporal frequency tuning nor direction selectivity properties of most cells in PMLS (Minville and Casanova, 1998). This finding was somewhat surprising given the strong anatomical connections between these two areas. Initially, this unanticipated lack of effect was attributed to the fact that the physiological link between PMLS and LP was not as robust as once believed. Furthermore, the properties of PMLS cells may perhaps be functionally more dependent on its striate rather than thalamic input (Spear, 1991). However, an alternative possibility may be that the function of the LP-PMLS loop is related to more complex aspects of motion analysis and that the contribution of LP can only be ascertained by investigating more complex motion analysis tasks (see Bender, 1988 for a similar discussion in primate). Figure 8 part B shows the effect of reversible LP deactivation on stimulus interactions in PMLS. In the control condition, the cell shows a facilitation in its response to the in-phase condition (see above). Following deactivation of LP, the cell was no longer able to discriminate between the in-phase and anti-phase conditions. This observation suggests that the LP input may be important in contributing to the analysis of relative motion between a figure and its background in PMLS. While these results are preliminary, they indicate that there is a functional relationship between LP and extrastriate cortical areas implicated in specific aspects of motion analysis.

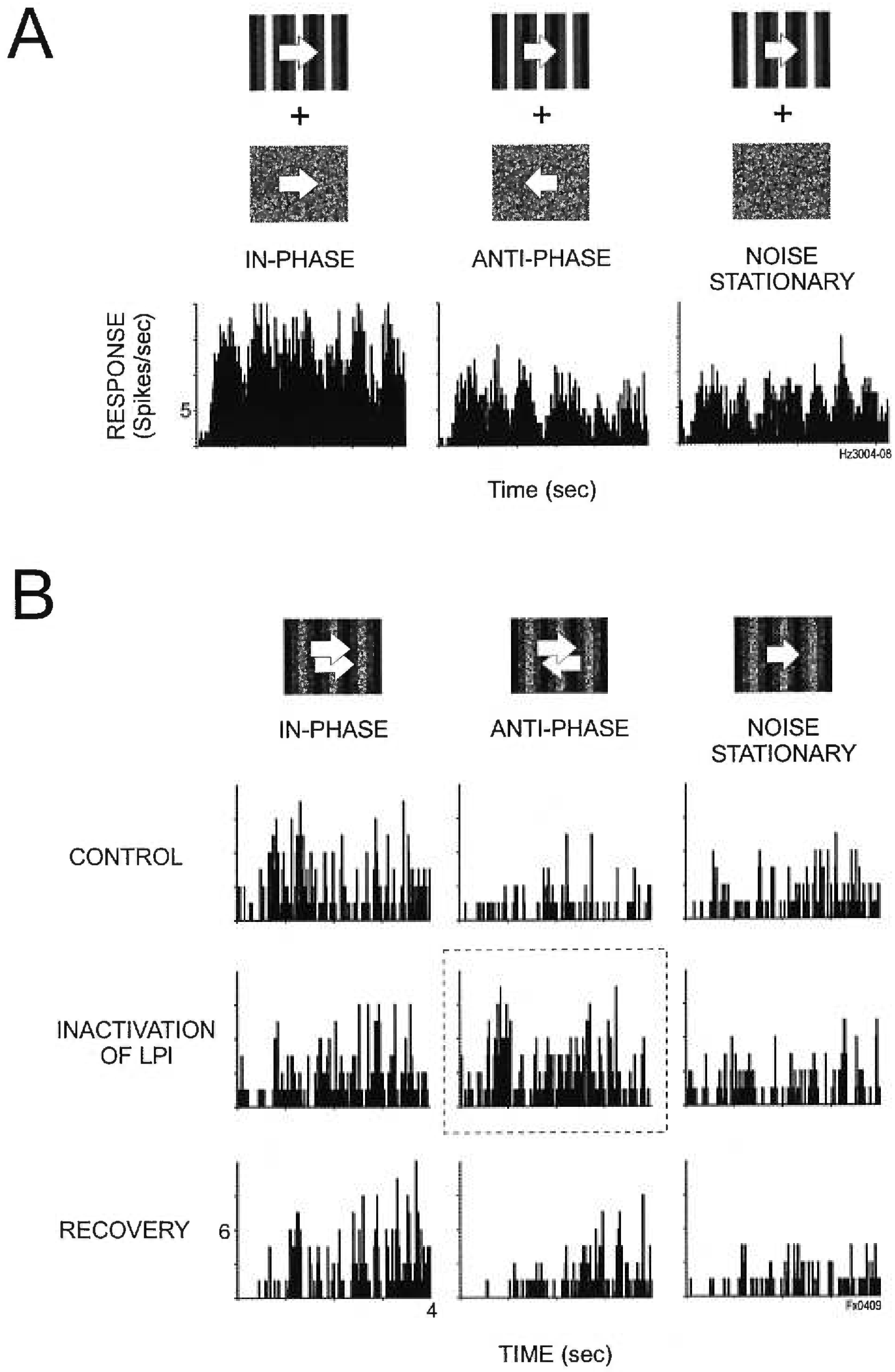

Figure 8. Preliminary Results: Modulatory effects of a moving texture pattern on the responses of PMLS cells. (A) Representative response of a cell in PMLS to drifting sinusoidal gratings superimposed upon a moving (in phase or anti phase) or stationary texture background. The cell shows a strong facilitation in its response when the gratings and texture background move in the same direction and at the same speed. (B) Effect of reversible deactivation of LPI on responses of a PMLS unit to stimulus interactions. During the control, the cell shows a facilitation in its response to the in phase condition. Following deactivation of the LPI (injection of GABA), the unit shows an increase in response to *both* the in phase and anti phase conditions (dotted line). This effect suggests that LPI contributes to the ability of PMLS cells to code the relative motion between an object and its background.

Article 2: "Motion Integration in a Thalamic Visual Nucleus"

Merabet, L., Desautels, A., Minville, K., Casanova, C.

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Dear Dr Casanova,

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September 30, 1998. ***Letters to Nature*** *Manuscript #C10759*

Motion Integration in the Thalamic Visual Nucleus

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Thalamic nuclei have long been regarded as passive relay stations for sensory information en route to the cerebral cortex, where higher level processing occurs. During the last decade, however, the role of the thalamus has been reassessed by physiologists and theoreticians alike, and they have proposed that thalamic nuclei may actively participate in the processing of specific information in conjunction with cortical areas[1,2,3,4]. In support of this conjecture, we report clear evidence that a subset of neurons in an extra-geniculate visual nucleus, the lateral posterior-pulvinar complex, can signal the true direction of motion of a plaid pattern, indicating that thalamic cells can integrate different motion signals into a coherent moving percept[5,6,7,8]. To date, only neurons in higher-order cortical areas have been shown to carry out such computations[5,6,9,10]. These findings suggest that extra-geniculate cortico-thalamo-cortical loops are implicated in the dynamic processing of image motion, and may in general, represent basic computational modules involved in the analysis of specific features of complex visual scenes.

Classically, the integration of motion signals has been considered a two-stage process[5,11]. The first stage involves the analysis of object features as one-dimensional components which are subsequently integrated at a second stage. It has been argued that the first stage is inherently limited in its coding of local motion signals (i.e., the aperture problem[5]) and the second stage combining the outputs from the first is necessary to generate a global percept of an object in motion. This analysis and all forms of higher-order processing, have been attributed to cortical networks. However, theoretical studies have proposed models in which thalamic nuclei participate in these processes in close relationship with the neocortex[1,2,3,4,12,13,14]. A common implication of these models is that cells on both sides of the cortico-thalamic loop exhibit similar higher-order response properties. To date, however, there has been no clear demonstration of sub-cortical neurons that respond to higher-order visual stimuli. In well developed visual systems, the pulvinar region represents a likely candidate for a sub-cortical counterpart to the cortex for the establishment of a loop involved in the analysis of moving objects. The pulvinar complex represents a higher-order nucleus because it receives its major input from layer V cortical neurons rather than directly from retinal ganglion cells, and it is in reciprocal communication with virtually all visual and associative cortical areas[15,16]. This region has often been associated with visual attention[17,18] and visually guided movement[19] but for the most part its function has remained speculative[15]. In cats, the physiological response properties in the lateral posterior-pulvinar (LP-pulvinar) complex suggest that these cells code attributes of image motion such as direction, velocity, and the relative motion between an object and its background[20].

On the basis of these response properties and connectivity patterns, we postulated that the LP-pulvinar participate in the analysis of the global motion of complex scenes. To investigate this hypothesis, we have studied the sensitivity of cells in the cat's LP-pulvinar to moving plaid patterns. This stimulus is composed of two superimposed drifting gratings differing only in orientation. A human observer perceives a single rigid pattern moving unambiguously with a direction and velocity that is uniquely consistent with the constraints imposed by the motion of the individual components[5,7,8]. At the neuronal level, a cell that is selective for the global motion of the plaid pattern responds with a profile similar to that of a single grating moving in the integrated direction ("pattern" motion selectivity) rather than in the directions of the oriented components comprising the pattern ("component" motion selectivity)[5,6].

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We recorded from 67 direction-selective units in the LP-pulvinar and found a subset of 21 cells that responded unequivocally to the pattern motion of plaids. For the two cells illustrated in Figure 1A and B, there is a close correspondence between the directional tuning function computed from the responses to moving gratings and plaids, indicating that these neurons are able to signal the true direction of motion of the pattern. Another subset of 7 LP cells (10.5%) exhibited bi-lobed tuning curves with peaks roughly symmetrical to the peak obtained in the single grating experiment (Figure 1C). These responses closely match the predicted tuning curve for component responses, indicating that these neurons process the one-dimensional motion signals making up the plaid pattern. The remaining 39 units (58.2%) could not be grouped in either of the two categories (unclassified direction-selective cells, Figure 1D). We classified the cells' responses to plaids based on the calculation of partial correlation coefficients comparing the responses to plaids to the component and pattern motion predictions[8]. These values are plotted in Figure 2. The data shows that a substantial proportion of neurons (~31%) in the LP-pulvinar lie in the region determined as being selective to pattern motion. Component responses were also present indicating that both local and global information is processed at the thalamic level. As a comparison, the responses to moving plaid patterns were measured from cells in the primary visual cortex (area 17) and in the postero-medial part of the lateral suprasylvian (LS) cortex (a region often referred to as the functional analogue of the primate middle temporal (MT) area)[21]. We found that the majority of neurons in these areas were component motion selective and no pattern motion direction selective cells were found, consistent with previous reports[6,22].

Fig 2 near here

Histological reconstruction of the electrode tracks indicated that the majority of pattern motion selective LP-pulvinar cells (80%) were located in the medial part of the LP nucleus (LPm) while the remaining units were found in the lateral section (LPl) of this nucleus. The LPm corresponds to the tecto-recipient zone of the LP-pulvinar which receives a major input from the superior colliculus (SC) and establishes reciprocal connections with the anterior ectosylvian visual (AEV) cortex[15,23]. This extrastriate area is the only region so far described in the cat visual cortex possessing a population (~55%) of pattern motion processing cells[6] similar to those observed in primate area MT[8,9,10]. The presence of pattern motion selective cells on both sides of the AEV-LPm loop raises the possibility that this cortico-thalamic network represents a module specifically involved in the processing of motion information. Two sets of experiments were carried out to demonstrate a physiological link between these two regions. First, we measured the responses of 16 LP neurons to plaids before and after pharmacological deactivation of visuotopically corresponding regions of the AEV cortex. Eight LP cells were classified as pattern selective and half of them were affected by the cortical deactivation: for 3 cells, the plaid responses were strongly reduced (Figure 3) whereas the discharges of the fourth unit were enhanced. These results demonstrate that the LP and AEV cortex are functionally linked, and further, that this loop is likely to be involved in processing higher-order motion information. However, the finding that responses of 4 pattern motion selective units were not altered by the cortical deactivation suggests that pattern selectivity in LP does not solely depend on descending projections from the AEV (see below). Blocking the AEV

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cortex also reduced the responses to plaids for 3 out of 5 component cells and 2 out of 3 unclassified direction-selective units. The fact that component cells were affected by cortical deactivation is surprising given that virtually no such cells were found in the AEV[6]. One possible explanation is that local velocity signals from the LP are used by the AEV for the integration or comparison of local and global motion signals, or that deactivation of the AEV affects lower-level motion areas which in turn project to the LP nucleus. In addition, this finding may indicate that concurrent excitation of both regions is needed for the information to be processed along the cortico-thalamic loop[24]. In the present case, disrupting the feed-back input short-circuit the loop and decrease the probability of thalamic firing.

To determine whether or not pattern motion responses in LP depend solely on inputs arising from the AEV, we recorded in the extrageniculate thalamus of three cats that sustained acute bilateral ablation of the anterior ectosylvian cortex. In all animals, pattern motion selective responses could still be recorded (Figure 4). These data, together with the fact that half of the LP pattern motion cells were unaffected by cortical deactivation, suggest that LP-pulvinar cells can process pattern motion from inputs other than those provided by the AEV cortex. To test this hypothesis, we studied pattern motion sensitivity in the LP-pulvinar of cats that sustained ablation of the AEV in conjunction with

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the lateral suprasylvian (LS) cortex, which is generally considered to be the main motion area in cats[21] despite the fact that no pattern selective cells have been found yet in the LS subdivisions investigated[22]. Ablation of the two cortices yielded a global reduction in the visual responsiveness of LP cells and in the number of direction selective neurons. When tested with drifting gratings, only 3 of 16 units preferred a specific direction of motion. The responses to plaids were all characterized as unclassified direction-selective. Thus, the persistence of pattern motion selectivity in LP after removal of the AEV cortex appears to depend on the integrity of the LS cortex. These data suggest that there is a sub-population of LS neurons which can code the true direction of moving objects, as recently proposed[25]. It is also possible that intrinsic computations are taking place within the thalamus (e.g., integration of multiple component signals). Moreover, the absence of pattern motion cells indicates that sub-cortical inputs from the SC do not account for pattern selectivity in the LP-pulvinar. This observation is in agreement with previous reports showing that deactivation of the SC does not alter the responses in the LPm[15] and that this region does not contain pattern motion units[8].

The finding that LP neurons can code the integrated motion of plaid patterns strongly suggests that the LP-pulvinar plays an important role in motion integration. This finding also supports the theoretical notion that clusters of thalamic cells, in conjunction with cortical assemblies, participate in the analysis of complex percepts[1,3,4]. One possibility is that the sensory maps in AEV and LS are used to establish a "global" template in LP-pulvinar. Through feedback loops, these maps could be dynamically used to compare the first and second stages of motion processing of an image encoded at cortical levels with the information stored at the thalamic level[1,10]. In addition, successive iterations within the cortico-thalamic loops could help to refine the cortical image (e.g., segmentation from motion). Our findings may force a reconsideration of the computational steps involved in the analysis of moving scenes that to date have only been modeled at the cortical level[5,9,26]. While the current "two-stage processing" models have only been described in the primate visual system, there is evidence that such organization may also be present in the cat. Recent findings clearly demonstrate that higher-order motion computations do occur in the cat extrastriate cortex[6]. Furthermore, computer-based analysis of connectivity patterns have indicated that intermediate cortical stages of motion analysis[26] are likely to be present in areas of the LS cortex that have yet to be fully explored (e.g., PLLS, ALLS)[6,25]. It remains to be determined whether the same pattern of responses described here also exists in the primate thalamic visual areas. This may very well be the case because there are reciprocal connections between the pulvinar and area MT[27] and there are strong similarities in the organization of cat and primate extrageniculate pathways[28]. Such a finding would suggest that these cortico-thalamic loops represent a common module of computational organization in these species. In conclusion, the demonstration that higher-order properties are analyzed outside the neocortex is of fundamental importance to the reassessment of the role of the thalamus and cortico-thalamic loops[1,3,4,8,9,13]. The fact that neuronal responses to pattern motion can be found in the LP-pulvinar in anaesthetized preparations provides evidence that the function of thalamic nuclei goes beyond the mere relaying of sensory information in relation to the state of vigilance. We propose that the LP-pulvinar represents a unique platform upon which specific aspects of an image are processed and integrated in close relationship with the visual cortex.

Methods: Cats were initially anaesthetized with acepromazine (1.0 mg/kg) and atropine (0.2 mg/kg) and general anesthesia was carried out using a gaseous mixture of halothane (1-3%) and N_2O/O_2 (50/50%). The animal was paralyzed via intravenous injection of gallamine triethiode (10mg/kg/h) and artificially ventilated (N_2O/O_2:70/30% and halothane 0.5%). Core temperature, electrocardiogram and electroencephalogram were continuously monitored. Pupils were dilated with atropine and nictitating membranes were retracted with phenylephrine hydrochloride (2.5%). The eyes were protected using contact lenses of appropriate refractive power. Animals were treated according to Canadian Council for the Protection of Animals guidelines. Varnished tungsten microelectrodes were used to record single-unit activity in the LP. Neuronal activity was fed to a PC-compatible computer for peri-stimulus time histogram acquisition. Stimulation was carried out using drifting sinusoidal gratings and plaid patterns (Picasso image synthesizer; frame rate of 200 Hz) presented on a CRT (Data Check 5117; mean luminance of 14 cd/m^2, Z-axis gamma correction) placed 57cm in front of the animal and subtending 28 x 28° of visual angle. Plaids were generated by a frame interleaved method and composed of two superimposed sine-wave gratings differing in orientation (120°) and of identical spatial frequency, temporal frequency and contrast. Both plaids and gratings were presented for at least 4 complete trials consisting of 12 interleaved directions of motion in 30° increments.

Responses to plaids were classified as pattern selective (PM) or component selective (CM) by calculating partial correlations using the following equation[8]: $R_p=(r_p-r_c r_{pc})/[(1-r_c^2)(1-r_{pc}^2)]^2$. R_p represents the partial correlation coefficient for the pattern prediction, r_c is the correlation coefficient of the plaid response calculated from the component model, r_p is the correlation coefficient for the plaid response from the pattern model, and r_{pc} is the correlation coefficient for the two models. Similarly, R_c is the partial correlation defined for the CM prediction and is calculated by exchanging r_p with r_c in the equation. A cell is considered as pattern motion selective when the value of R_p is significantly greater than either R_c or zero[8]. Electrolytic lesions were made along recording tracks and cell localization was determined.

Deactivation Experiments. In eight experiments, a glass microelectrode filled with γ-aminobutyric acid (GABA, 200µM, stained with 1% Chicago Sky Blue) was lowered into the AEV. It was inserted in the headstage of a nanopump (WPI) modified to allow simultaneous recording. Placement of the electrode in AEV was determined on the basis of stereotaxic coordinates and visual cues. The deactivation procedure was performed only if there was a visuotopic correspondence between the receptive fields (RF) in LP and AEV cortex. All LP RFs were located between +12 and -15° for elevation and –5 and +20° for azimuth. The cortical activity was continuously recorded prior to, during, and after the injection. The deactivation solution was injected and continuously delivered at a rate ranging between 80-90 nl/min for the first two minutes and maintained at 20-30nl/min throughout the testing period. The mean ± SD volume injected was 460 ± 140 nl, and the mean ± SD diameter of these injections inferred from the CSB staining[29] was 1.2 ± 0.2 mm. The tested LP cells were kept for further analysis only if the injection of GABA yielded a clear suppression of the AEV multi-unit activity and if the location and extent of the injection site could be determined. For each cell a blocking index (BI) was calculated by dividing the mean response of the LP unit during deactivation by the mean control response recorded prior to the blocking. Indices of 0 and 1 would indicate, respectively, that the cell discharges were totally abolished or not affected. Details of the deactivation technique are given elsewhere[29].

Cortical Ablations. In three experiments, we recorded from the LP-pulvinar in cats with acute bilateral lesioning of the anterior ectosylvian sulcus, including the entire visual area, i.e., the AEV. The dura was resected and the cortex was removed by aspiration of the grey matter lying along the ventral bank of the anterior ectosylvian sulcus and overlying the claustrum[23]. In two additional experiments, the LS cortices were also removed in conjunction with the AEV. The cortex located in the medial and lateral banks of the suprasylvian sulcus (the six subregions defining the LS[30]) was ablated by aspiration. The cavities were filled with sterile gelfoam and sealed with warm agar and wax. Recordings in the LP-pulvinar were made after a 12-16 hour period of recuperation following the surgical procedures. In order to determine if the trauma associated with the destruction of both the AEV and LS cortices may have caused a general depression of brain activity, we first recorded from a few neurons in the lateral geniculate nucleus, superior colliculus and primary visual cortex. In all of these regions, cells exhibited properties similar to those observed in intact animals.

Figure legends

Figure 1. Polar graphs illustrating the responses of LP-pulvinar neurons to gratings (solid line) and plaid patterns (dashed line) drifted in 12 directions of motion. The response to gratings alone is considered as the predicted profile for a truly pattern direction selective unit. The dotted line represents the predicted response to plaids for a component-direction selective unit. Panels A and B are examples of pattern-motion selective neurons. Panel C presents the response of a component motion direction selective cell. Panel D shows the discharges of an unclassified direction-selective cell. The small central circles represent spontaneous activity levels.

Figure 2. Scatter plot in which the partial correlation for pattern and component selectivity are plotted against each other for neurons in the LP-pulvinar (filled symbols), area 17 (open circles), and PMLS cortex (open squares). Each direction-selective unit was classified by quantifying the degree of correspondence between the response to plaid and the responses predicted from the pattern (responses to the grating alone) and the component models (i.e., shifting the grating responses by 60° in both directions and summing the resulting curves around the clock). The data space is divided into 3 statistical regions. Cells falling in the upper left and lower right areas are respectively pattern and component motion selective. The points lying in between represent unclassified direction-selective cells.

Figure 3. Effect of deactivating the AEV on a LPm pattern motion neuron. During cortical deactivation, a strong suppression of the cell's overall response and a concomitant loss of its ability to signal direction of the drifting grating (solid line) and plaids pattern (dashed line) was observed [BI of -0.25 and -0.4, respectively]. In each polar graph, data points within

the shaded region represent cell discharges below spontaneous activity levels. The inset shows the location of the RF of the thalamic neuron in reference to the AEV scotoma.

Figure 4. A. Coronal sections showing the site and extent of the cortical ablations of one cat at various rostro-caudal H-C coordinates. Inset: lateral view of the two hemispheres showing the location of the lesions. B. Distribution of partial correlation coefficients of LP-pulvinar neurons of cats that sustained bilateral ablation of the AEV cortex. Note the presence of all cell types and particularly the pattern motion selective units. Abbreviations: A, anterior; AEs, anterior ectosylvian sulcus; Ls, lateral sulcus; P, posterior; Ss, suprasylvian sulcus.

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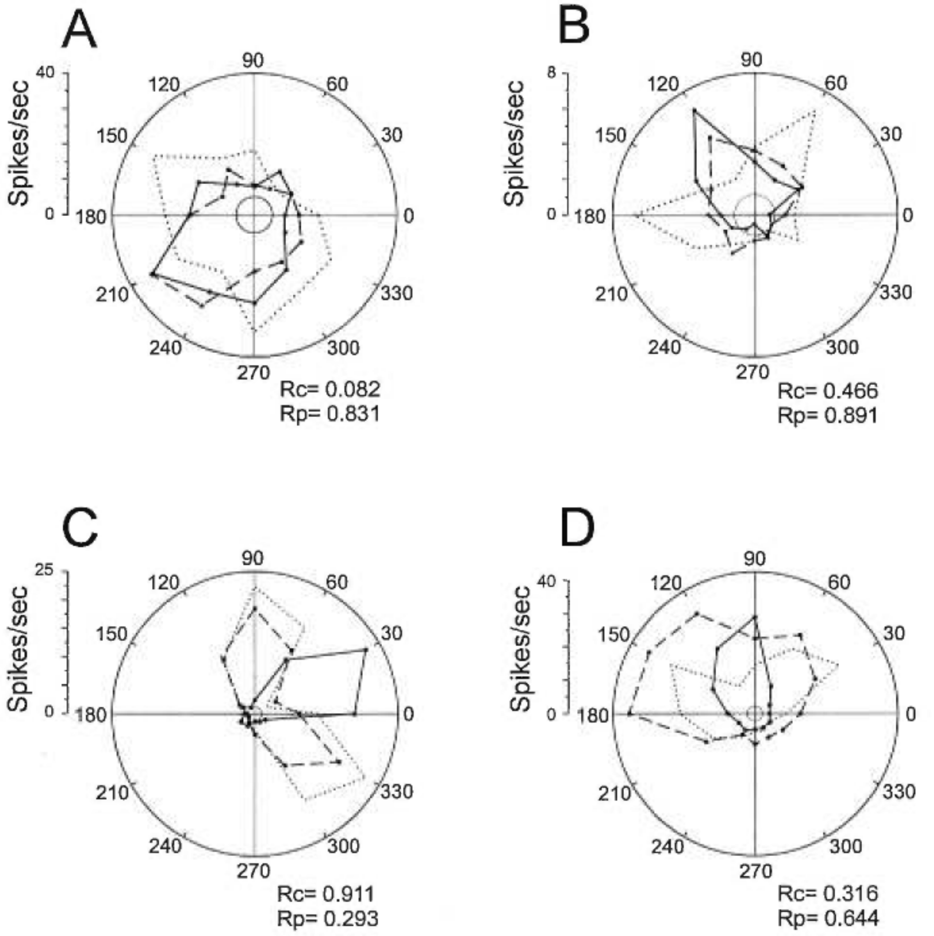
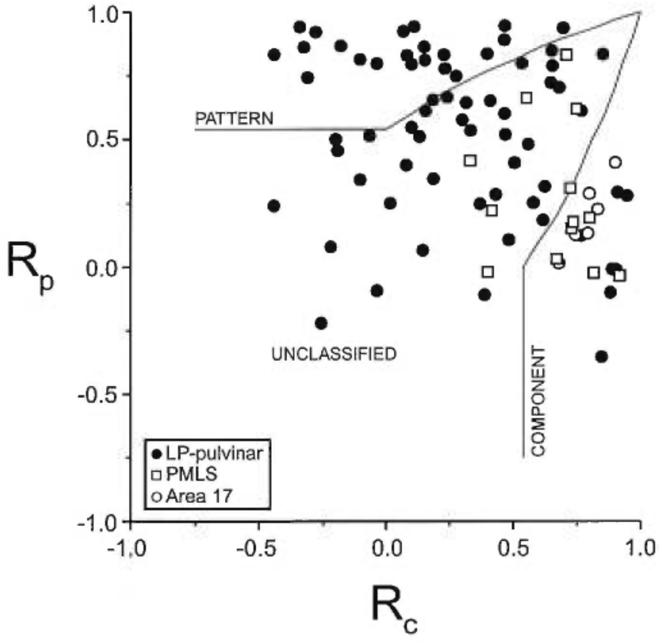


Figure 1.
Merabet et al., 1998



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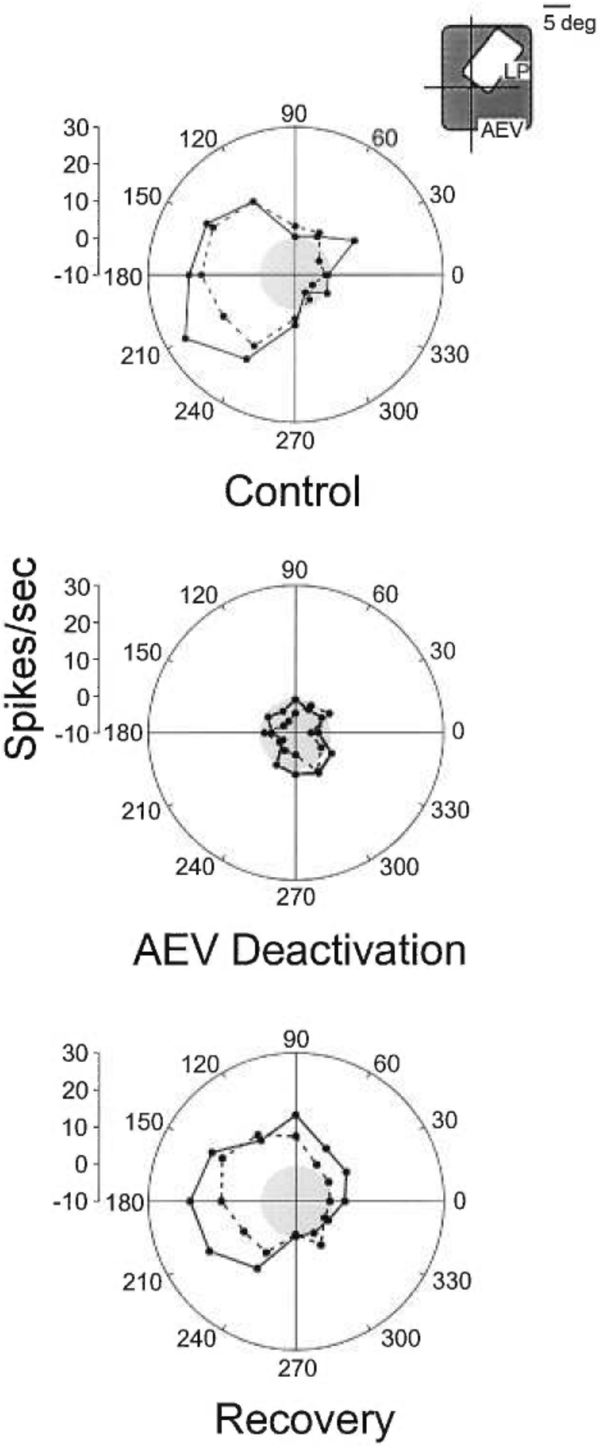

Control

AEV Deactivation

Recovery

Figure 3
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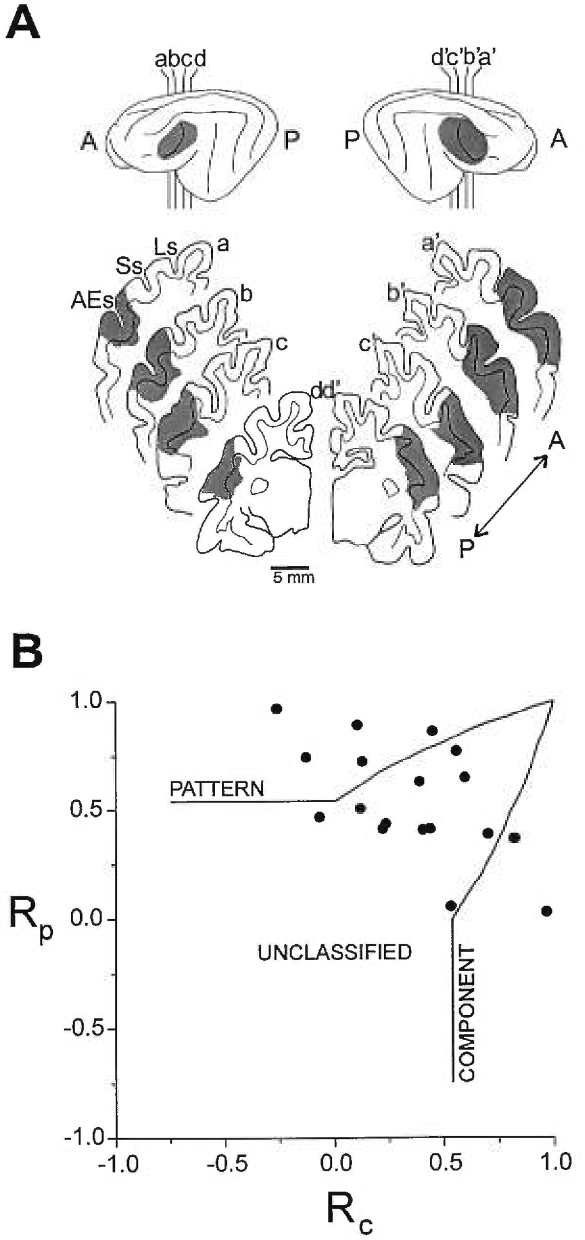

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7. Discussion

7.1 Summary of Findings

7.1.1 Motion Perception in and along the Extra-Geniculate Pathway: Responses to Moving Texture Patterns

In the first part of the study, we investigated the responses of PMLS neurons to moving texture patterns ("visual noise"). The results from this study have shown that a large proportion of cells in PMLS (approximately 80%) are sensitive to the motion of a texture pattern. Furthermore, the majority of cells were selective for the drift direction and velocity of the stimulus. Comparing the responsiveness of PMLS cells with texture sensitive units in LP revealed that texture sensitivity, optimal velocity, and range of velocity tuning were comparable in both these areas (Casanova and Savard, 1996a). These results serve to establish that both LP and PMLS exhibit similar properties in response to moving patterns such as visual noise. Furthermore, these findings suggest that both subcortical and cortical components of the LP-PMLS loop respond to motion within a similar envelope of analysis.

7.1.2 Stimulus Interactions in PMLS: Effect of Reversible Deactivation of LP

The findings in the first part of the study (article 1) are important as a first step in establishing that similar response properties regarding motion analysis exist on both sides of a cortico-thalamic loop. However, this study somewhat fails to capture the essence of higher-order processing in that responses to visual noise do not encompass the notion of integration of motion signals. Furthermore, in order to establish that LP and PMLS are functionally linked, it would have to be demonstrated that deactivation of one component of the loop disrupts the responses of the other counterpart.

The results presented in the preliminary study (Preliminary Results) serve to initially address these two issues. We have found that like in LP, responses of PMLS neurons to drifting gratings can be modulated by the presence of a moving texture background. Furthermore, both PMLS and LP neurons can code the relative movement of objects and use motion cues to discriminate between a figure and its background. Finally, reversible deactivation of LP disrupts the ability of PMLS cells to carry out these operations. This latter finding demonstrates that these two areas are physiologically and functionally linked with regards to specific aspects of motion analysis within a visual scene.

7.1.3 Motion integration in LP: Responses to Plaid Patterns

We have studied the sensitivity of cells in LP using plaid patterns to determine whether neurons in this thalamic region can integrate motion information. The results of this study show that a subset of cells (31.3%, 21 out of 67 units) exhibit pattern-selectivity indicating that these neurons are capable of signalling the global direction of a plaid pattern. Another subset (7 units) responded only to the component motions comprising the plaid pattern (component-selectivity). The fact that both pattern and component responses were present at the thalamic level is of importance because it suggests that both global and local information are processed in LP. For comparison, we also investigated the responses of cells to plaid patterns at the cortical level [i.e. primary visual cortex (area 17), PMLS and AEV cortices]. In agreement with previous studies, we found that pattern selective neurons were present only in the AEV cortex (Scannell et al., 1996).

The fact that pattern-selective responses exist at the thalamic level is of importance for three reasons: First, it demonstrates (for the first time) that higher-order properties exist outside extrastriate cortical areas. Second, these results firmly establish that the LP-pulvinar complex plays an important role in motion integration. Finally, these findings lend credence to the aforementioned theoretical models proposing that specific thalamic nuclei participate in more complex aspects of sensory processing (e.g. Mumford, 1991; Miller, 1996).

It is possible that pattern responses in LP may be the result of a "top-down" influence from AEV cortex. We attempted to address this issue in two ways; by recording neurons in LP in response to plaids following reversible deactivation of the AEV cortex and after irreversible destruction of AEV (alone and in conjunction with other cortical areas involved in motion analysis). We have found that reversible deactivation of the AEV cortex (micro-injection of GABA) can suppress LP responses to plaids. This demonstrates that the LP-AEV loop is active in the processing of higher-order motion information. Following acute bilateral ablation of AEV alone and also in conjunction with PMLS cortex, pattern selective responses were still present in LP. The persistence of pattern-selective responses suggests that LP-pulvinar cells can process pattern motion from inputs other than those provided by the AEV and PMLS cortices. Only upon destruction of AEV in conjunction with the entire LS cortex were pattern responses completely abolished. Consequently, other areas of the LS cortex (putatively the posterolateral and anterolateral regions: PLLS and ALLS) may be necessary in providing pattern motion signals to LP. Another possibility (though not mutually exclusive) could be that intrinsic computations are being carried out within the LP generating an integrated signal at the thalamic level.

It is possible that the absence of pattern-selective responses in LP following irreversible massive cortical deactivation (AEV and PMLS) is due in part to a general depression of cortical activity. While this factor cannot be ignored, control recordings in LGN, SC, and area 17 insured that visual activity (and in particular, directional selectivity in area 17) was intact within these remaining inputs to LP. Alternative techniques however should be considered in future investigations. For example, irreversible deactivation by chemical lesions (e.g. ibotenic acid; Newsome et al., 1985; Rudolph and Pasternak, 1996) could circumvent the trauma associated with such massive surgical resections. In addition, reversible deactivations of superficially exposed cortical areas could be accomplished using cooling techniques (e.g. cryogenic blockade; Lomber et al., 1996; Casanova et al., 1997) in order to ensure a more widespread deactivation effect.

To clearly establish the origin of these pattern-selective responses in LP, further experiments must be carried out. These investigations should entail exploration of cortical areas such as PLLS and ALLS in order to confirm whether or not pattern-selective responses exist within the LS cortex. Furthermore, the effect of reversible deactivation of LP on pattern responses in extrastriate cortex (e.g. AEV) should also be investigated. These latter studies are essential in order to establish the thalamic contribution of these responses at the cortical level, and are currently underway in our laboratory.

7.2 Inter-relations between LP and Extrastriate Cortical Areas Involved in Motion Processing

The concept that the LP-pulvinar complex is involved in motion processing in relation to extrastriate visual areas is not a novel one. Based on functional connectivity and common RF properties (such as narrow directional and velocity tuning, binocular facilitation, and RF organisation for optic flow processing (Rauschecker et al., 1987b), Rauschecker (1988) has proposed the existence of a "LP/LS subsystem". The author suggests that the extensive feedback projections from cortical areas (such as the LS cortex) onto LP lead to the formation of cortico-thalamic loops that may be important for global motion processing. Putatively, these loops could be involved in motion analyses by carrying out computational transformations between the primary visual cortex and extrastriate areas (Rauschecker, 1988).

The results of the present study represent an extension of these ideas with respect to three points. First of all, our findings suggest that the specificity and degree of computational analysis being carried out at the thalamic level (and more specifically, along cortico-thalamic loops) has been underestimated. The fact that PMLS and LP show similar response characteristics to moving texture patterns illustrates that both these areas process motion information in parallel and within the same envelope of analysis. Furthermore, the finding of pattern-selective responses in LP demonstrates that this thalamic nucleus is participating in not only rudimentary, but also higher-order aspects of motion perception.

Secondly, our preliminary findings (Preliminary Results) have shown that reversible deactivation of LP disrupts the ability of PMLS neurons to code the relative movement between an object and its background. These results suggest that these areas are functionally linked and that functional integrity of both components of the loop is necessary to carry out certain aspects of motion analysis.

Finally, we propose that the establishment of cortico-thalamic loops in motion analysis goes beyond the LS cortex and LP. The fact that reversible deactivation of AEV cortex alters pattern-selective responses in LP suggests that other cortico-thalamic loops (i.e. LP-AEV) also exist.

In the cat visual system, the LP-pulvinar complex may serve to integrate multiple aspects of motion analysis carried out along multiple cortico-thalamic loops. With regards to the cortical areas investigated in this study, the LP-pulvinar complex appears to be strategically placed between one computational loop implicating PMLS (through the LPl sub-region) and another implicating the AEV cortex (through the LPm) (see figure 9). It is conceivable that LP serves as a “global template” integrating

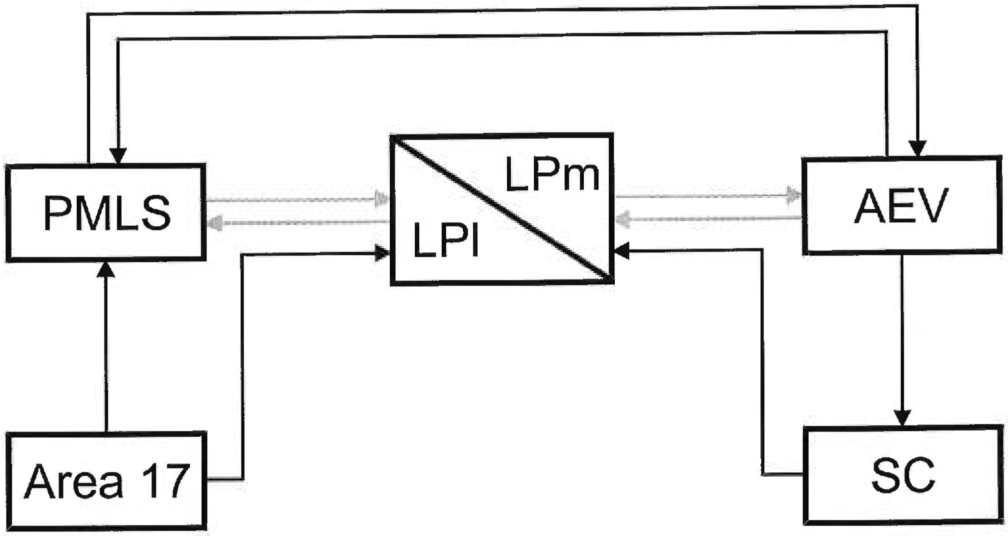

Figure 9. Schematic showing the LP-pulvinar complex in relation to cortical motion areas investigated in this study. Through the establishment of cortico-thalamic interrelations (shown in grey), LP could mediate local motion analyses carried out in the PMLS-LPl loop and global motion analyses at the level of the AEV-LPm loop (the SC, largely under cortical control, could also putatively contribute directional signals to LPm). In such a scheme, the LP-pulvinar complex could conceivably coordinate analyses carried out within multiple cortical assemblies and represent a site of integration between the two motion analysis streams.

component motion analyses (implicating area 17 and PMLS) and the pattern motion analyses (in relation to the AEV cortex). The recursive transmission of cortical computations back to LP would allow this area to compare multiple ongoing stages of motion processing. Alternatively, LP could also be mediating separate aspects of motion analysis. For example, global motion analysis in conjunction with AEV cortex and figure-ground discrimination in relation to PMLS and area 17. Again, the results of these integrative operations would be continuously present in LP and made available for other cortical areas.

The advantage of "storing" these results at the thalamic level are two-fold. First, the computational results of cortical analyses could be continuously updated and refined in an iterative and dynamic manner. This recursive operation allows for the continual refinement of the perceived image, for example in scene segmentation or in the grouping of common features of an object. Secondly, through reciprocal connections between LP and all visual cortical areas, the results of these ongoing computations could be redirected and made available to other areas for further processing and/or the planification of an appropriate behavioural response.

7.3 The Role of Cortico-thalamic Loops and the Pulvinar Revisited

There is clear evidence that the visual system is composed of multiple, anatomically segregated and functionally specialised areas. Furthermore, information processing appears to be carried out in a parallel and distributed fashion (Zeki and Shipp, 1988; Tonini et al., 1992; van Essen et al., 1992). Yet, the visual world we perceive appears unified, coherent and perceptually stable. Computational models of vision have emphasized that analysing the attributes of a visual scene in their entirety would represent a formidable task (e.g. Marr, 1982; Tonini et al., 1992; Ulman, 1995). Clearly, the visual system must employ strategies for efficient information processing within the anatomical constraints imposed by its circuitry (van Essen et al., 1992). In order to accomplish such a task, the flow of information within and between visual areas must be controlled to allow the computational flexibility necessary to respond to the dynamic world that surrounds us (Zeki and Shipp, 1988; Tonini et al., 1992; van Essen et al., 1992; Singer, 1994; Singer, 1995).

Figure 10 contrasts two approaches as to how information processing could be carried out within the visual system. Part A represents the traditional "bottom-up" view regarding object recognition. In this model, elemental features of an image are extracted, recombined in successive and hierarchical steps, and compared with previous

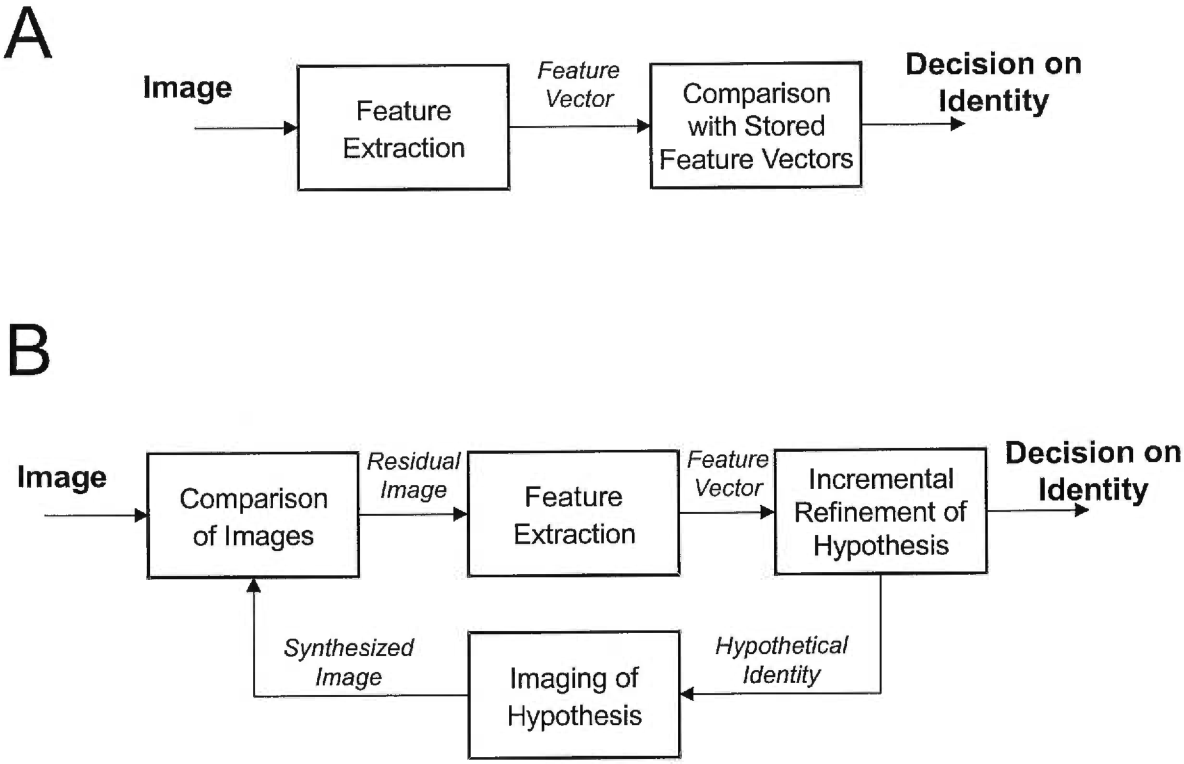

Figure 10. Theoretical models of object recognition. (A) Classical "bottom-up" view. Features of an image are extracted in serially organized steps and results are compared with stored memories in order to generate a perceptual decision. (B) Iterative view of object recognition implicating a recursive loop (Pattern Theory) where feedback projections allow for the continual adjustment, refinement, and updating of ongoing analyses. *Adapted from Mumford, 1994*

experience to form a perceptual decision. An alternative view (part B) suggests that visual perception is an iterative process (referred to as Pattern Theory; Mumford, 1994) and implicates a continual exchange between “bottom-up” and “top-down” processes. Feed forward (bottom-up) projections represent feature extraction routes while recursive (top-down) pathways would activate “template-like patterns” that continuously adjust, refine, and update ongoing analyses (Mumford, 1994; see also van Essen et al., 1992; Singer, 1994). These transformations may be of the form of filtering of irrelevant information, identification of salient features or grouping operations (van Essen et al., 1992, Mumford, 1991, Mumford, 1994; Singer, 1994; Singer, 1995).

Along the same lines of thinking, cortico-thalamic feedback projections may very well represent the neurophysiological substrate as to how the visual system maintains explicit control over its own computations (van Essen et al., 1992). Ascending thalamo-cortical pathways extract features of a visual scene and relay information throughout the hierarchy of the visual system. Cortico-thalamic pathways on the other hand, may be essential in regulating the inflow or re-routing of information to new targets and computational areas (van Essen et al., 1992). The advantage of such a recursive architecture is that it allows for an adaptive and flexible mechanism to co-ordinate computational structures for optimal utilisation of incoming data (Tonini et al., 1992; Ulman, 1995). Furthermore, the generation of a coherent and unified percept could occur within a parallel and distributed processing network without the implementation of a supra-ordinate centre, thus solving the so-called "binding problem" (Tonini et al., 1992; Tononi, 1994).

While cortico-thalamic feedback may provide the neuro-physiological substrate to co-ordinate computations within this processing system, the pulvinar may serve to mediate operations within and between computational areas. This is not to say that the pulvinar represents a supra-ordinate area. Rather, given its anatomical disposition, physiological response properties (particularly to higher order stimuli), and its purported role in attentional mechanisms (e.g. Robinson and Petersen, 1992), this thalamic nucleus is strategically positioned to mediate ongoing computational analyses throughout multiple levels of the visual hierarchy. This mediation may be of the form of grouping operations allowing for a flexible recombination of hard-wired computational pathways (Singer, 1995). Furthermore, the dynamic re-routing of signals activates various neural assemblies allowing for continual refinement of current computational results (Mumford, 1991; van Essen et al., 1992; Miller, 1996). Thus, through a process iterated over multiple processing stages, computational analyses of cortical assemblies could be enhanced and the results made available throughout the visual processing hierarchy via interactions through the pulvinar. Continuous recursive signalling through a thalamic region has the advantage of allowing computational flexibility and versatility in that relations of ever-increasing complexity can be brought together to generate a unified percept (Singer, 1995) .

It would be perhaps premature at this stage to draw immediate comparisons between the function of the LP-pulvinar complex of cats and the primate pulvinar. However, the presence of higher-order properties at the thalamic level should force a re-evaluation of the computational steps involved in motion processing. Figure 11 proposes the selection model of motion processing in primates (introduced earlier) incorporating the pulvinar nucleus. In this updated scheme, the pulvinar is in immediate relation with computations carried out at each cortical level. By possessing neurophysiological properties common to all stages of the hierarchy, this thalamic area can contribute to each integrative step. For example, the pulvinar may group appropriate neural assemblies in V1 carrying out local motion analyses (i.e. related to a particular object or aspect within the visual scene). By integrating these local attributes (e.g. component motions) in parallel with the next combinatorial step (MT), the pulvinar may provide for a “secure” or enhanced computational pathway (Miller, 1996). Consequently, the results of a given stage can re-enter a previous processing level thereby grouping pertinent neural assemblies. Alternatively, results can be fed to subsequent levels (i.e. MST) in order to contribute to current analyses carried at higher or within multiple levels of

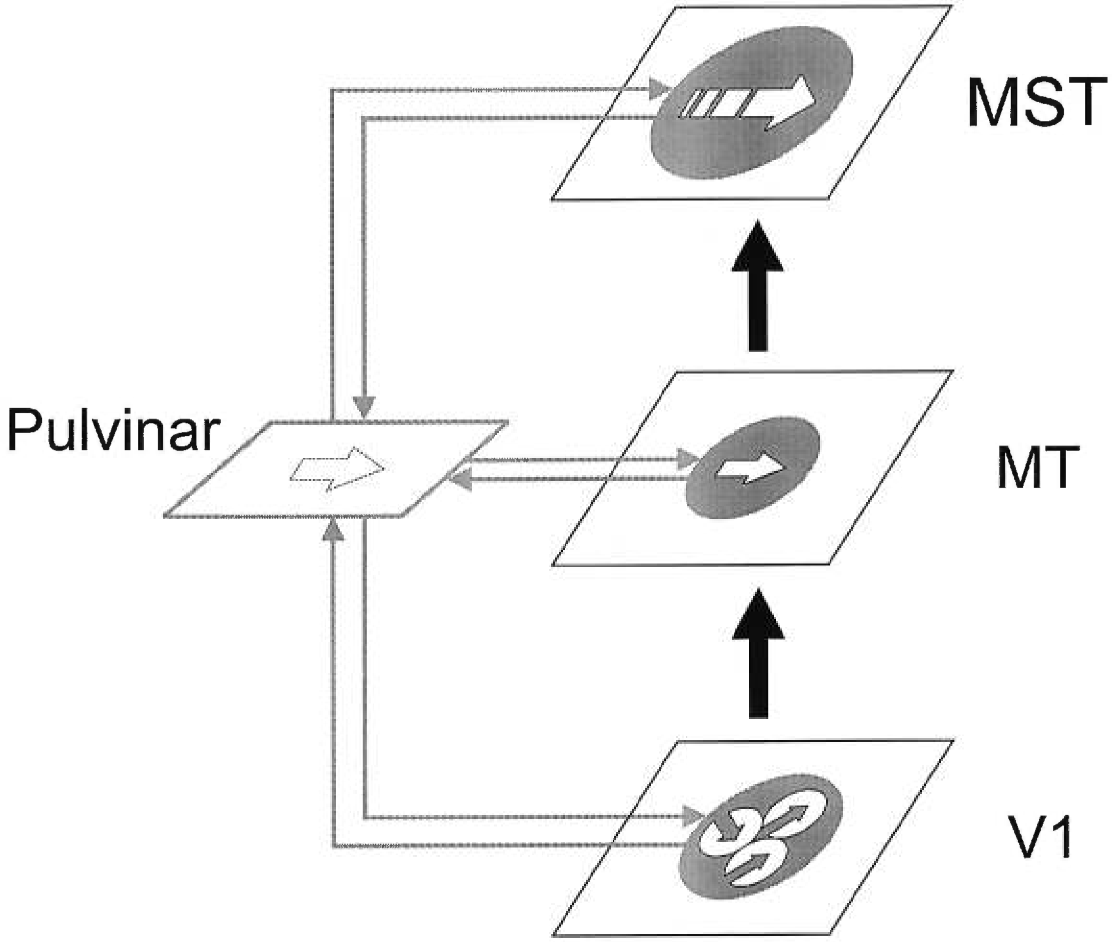

Figure 11. Implication of the pulvinar in the selection model of motion processing (in primates). Through reciprocal connections with each cortical stage (grey arrows), the pulvinar could mediate grouping operations at each level, enhancing the analyses of cortical assemblies throughout the hierarchy (see text for explanation).

the processing hierarchy. This “security of operation”, implicating recursive signalling through the thalamus, could be essential in refining the perceived image by rendering appropriate features of a visual scene more salient (Mumford, 1994; Sillito et al., 1994; Miller, 1996). In addition, temporarily representing the results of ongoing analyses through the thalamus frees previously recruited cortical assemblies allowing them to participate in different assemblies as the visual scene changes. The ability to dynamically enhance the computations of neural assemblies and temporarily store representations of their results, allows multiple analyses to occur in parallel. Furthermore, this processing scheme greatly reduces the number of representational units required to analyse a complex and dynamic visual scene (Singer, 1995).

To date, support for the notion that the cat LP-pulvinar complex and primate pulvinar carry out comparable functions stems more from anatomical similarities (Creutzfeldt, 1988) rather than neurophysiological evidence. Anatomical studies have confirmed that the primate pulvinar exhibits strong reciprocal relations with all the cortical structures implicated in the aforementioned model (Maunsell and van Essen, 1983c; Boussaoud et al., 1992; Cusick et al., 1993). However, it is unknown if higher-order properties (such as pattern-selective responses) are also present within the pulvinar and if the disruption of cortico-thalamic loops influences motion perception in any way in primates.

It is hoped that the results obtained in this present study will lead to further investigations in other animal models (such as primates), and renew interest in the importance of the thalamus and cortico-thalamic loops in sensory processing.

8. Conclusions

The results of this study may force us to reconsider the role of the thalamus and cortico-thalamic loops in general. The demonstration of pattern-selective responses in the LP-pulvinar complex is of considerable importance. To our knowledge, the findings of the present study represent the first demonstration that integrative sensory computations occur outside higher-order cortical areas. Furthermore, these results may require a re-evaluation of current notions regarding motion processing (see figure 11). Finally, the fact these higher-order properties can be found in the LP-pulvinar complex in anaesthetised preparations goes against classical notions that the thalamus merely relays unprocessed sensory information in relation to the state of vigilance of the animal.

The anatomical disposition and neurophysiological response properties found in LP satisfy theoretical notions (e.g. Rauschecker, 1988; Mumford, 1991) that certain thalamic nuclei participate in the analysis of complex visual scenes. We propose that the LP-pulvinar complex represents (via the establishment of cortico-thalamic loops) a unique platform working in close relation and in co-operation with the visual cortex allowing the adjustment, refining, and updating of specific visual attributes of a complex visual scene.

While the results of this study have concentrated on only one aspect of visual perception namely motion processing, other higher-order properties may very well exist at the thalamic level (e.g. “face cells” as observed in inferior temporal cortex; see Creutzfeldt, 1988). Furthermore, given the common reciprocal arrangement between the thalamus and the entire sensory cortex, there should also be evidence of cortico-thalamic relations across sensory modalities. Evidence of functional cortico-thalamic links have been recently reported in the somatosensory and auditory systems (see Rauschecker, 1998 for a recent review). Recently, Ergenzinger and co-workers (1998) have shown that tactile RFs within the ventroposterior (VP) thalamic nucleus of monkeys are grossly enlarged following chronic treatment of the primary somatosensory cortex with APV (a NMDA receptor antagonist). These results are particularly interesting with regards to plasticity changes in the adult brain and challenge theoretical views that this is strictly a bottom-up process. Yan and Suga (1996) as well as Zhang and colleagues (1997) have found that reversible deactivation (lidocaine injection) of cortical auditory neurons in bats reduces the auditory responses of thalamic neurons in the medial geniculate nucleus (MGN). Furthermore, this inhibitory effect was specific to neurons with the same frequency tuning whereas the responses of neurons tuned to different frequencies were enhanced. Conversely, electrical stimulation of cortical neurons increased and sharpened the responses of certain thalamic neurons in the MGN.

The results of these investigations are in line with those obtained in the present study. It appears that cortico-thalamic projections serve to enhance responses and/or suppress irrelevant information. Furthermore, cortico-fugal control appears to be precisely correlated with its reciprocally connected thalamic targets. That is to say, restricted to comparable areas of somatic representation (as observed in the somatosensory system) or to tuning properties within the same envelope of analysis (as shown in the auditory system and in the results of this study).

In conclusion, cortico-thalamic loops may represent a basic computational module common to all organisms with highly developed sensory systems. Furthermore, the organisational principles found therein are likely to lead to a generalised scheme regarding sensory processing and contribute to our understanding as to how they mediate our perception of the world around us.

9. Acknowledgements

I once read somewhere that the point of graduate studies is to learn more and more about less and less, until you know everything there is to know about nothing. There is perhaps some truth in this…in fact, it's ironic that in these past few years, I have probably learned more about myself than I could ever hope to learn about the visual system or the role of cortico-thalamic loops.

I have learned…
…that graduate school has more to do with perseverance and sacrifice than it does with intelligence and talent.

I have learned…
…that not all families are biological.

I have learned…
…that arguments rarely decide who's right, just who's left.

I have learned…
…that we don't need to change friends, if we understand that friends change.

I have learned…
…that you are never as good or as bad as people say you are.

I have learned…
…that you can keep going long after you think you can't.

I have learned…
…that background and circumstances may have influenced who we are, but ultimately we are responsible for who we become.

While I am grateful to those who have opened the door and showed me the way; it is to those who stood by me throughout the most difficult parts of the journey that I am forever indebted.

J'espère qu'un jour, chacun d'entre nous arrivera à sa destination…

Salem,

lotfi

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Annex 1: Un nouveau rôle pour le thalamus?

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Cher docteur Casanova,

Nous accusons réception et vous remercions pour votre manuscrit intitulé :
Un nouveau rôle pour le thalamus ?
que vous nous soumettez pour publication dans la revue **médecine/sciences**.

Votre manuscrit sera expédié à des arbitres et leurs commentaires vous seront transmis dès réception.

Nous vous prions de croire, cher docteur Casanova, à l'expression de nos sentiments les meilleurs.

[redacted]

Martine Deshaies pour :
Dr Jacques Drouin
Rédacteur en chef adjoint

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UN NOUVEAU RÔLE POUR LE THALAMUS ?

(A NEW ROLE FOR THE THALAMUS ?)

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Hormis l'olfaction, toutes les informations sensorielles (c'est-à-dire la vue, l'ouïe, le goût et le touché) transitent par le thalamus avant de parvenir aux aires néocorticales du cerveau. De façon générale, les noyaux thalamiques sont considérés comme des structures «relais » qui transmettent l'information périphérique vers le cortex où ont lieu les opérations complexes menant à la reconnaissance et à l'interprétation des stimuli sensoriels. Ainsi, le thalamus est en quelque sorte la porte d'entrée des voies sensorielles vers le cortex, porte dont l'ouverture dépend du degré de vigilance de l'animal. Cette image conventionnelle du thalamus est de plus en plus remise en question [1]. La première indication que cette région du cerveau jouerait un rôle qui dépasse celui d'un strict relais repose sur l'organisation anatomique des voies nerveuses. La relation entre le thalamus et le cortex est telle que les régions corticales qui reçoivent des signaux des noyaux thalamiques se projettent à leur tour vers ces mêmes noyaux. Il existe donc des connexions réciproques, sous formes de boucles thalamo-cortico-thalamiques, liant intimement l'activité des neurones du néocortex et du thalamus. Dès lors, ce dernier doit-il être vu comme faisant partie d'une voie strictement ascendante ou plutôt comme un partenaire actif du cortex dans le traitement de l'information?

Les neurones du thalamus peuvent-ils réaliser des opérations complexes?

Au cours des dernières années, plusieurs travaux d'ordres théoriques [2, 3] ont suggéré que le thalamus soit impliqué de façon dynamique, via les boucles thalamo-corticales, dans l'analyse complexe des signaux sensoriels, analyse jusqu'à présent associée uniquement au cortex. Qu'est-ce qu'une opération complexe pour un neurone? Prenons l'exemple des cellules nerveuses du système visuel et de leur capacité à coder la direction du mouvement d'un objet. Chez les mammifères supérieurs, la plupart des neurones visuels corticaux peuvent déterminer la direction du déplacement d'un stimulus simple, comme l'un des réseaux de barre présenté à la figure 1A. Que se passe-t-il si l'on présente maintenant un stimulus plus complexe, tel qu'un plaid (figure 1B). Ce dernier, qui a l'apparence du motif d'une couverture écossaise, est constitué de deux réseaux identiques superposés mais qui diffèrent selon leur axe d'orientation. Au niveau perceptif, un observateur humain verra le plaid se déplacer vers le bas, dans une seule direction correspondant aux contraintes imposées par le mouvement des deux composantes du stimulus. En d'autres mots, le sujet ne voit pas chaque composante bouger dans des directions différentes (absence de cohérence, figure 1C), mais plutôt le mouvement harmonieux des intersections vers le bas (percept cohérent, figure 1B). Au niveau cortical, seules les cellules d'une aire extrastriée de haut niveau hiérarchique spécialisée dans l'analyse du mouvement [l'aire temporale médiane (MT) chez les primates et l'aire ectosylvienne visuelle antérieure (EVA) chez le chat], sont capables de coder la direction réelle du plaid [4, 5, 6]. Les cellules des autres aires corticales étudiées jusqu'à présent par les électrophysiologistes (incluant le cortex visuel primaire) sont inaptes à réaliser cette intégration et ne peuvent alors coder que le déplacement des deux composantes du plaid. La détection du mouvement réel du plaid nécessite donc des mécanismes neuronaux élaborés.

Un candidat de choix : le pulvinar

Cette analyse complexe peut-elle être effectuée par les neurones du thalamus visuel? Nous avons émis l'hypothèse que certains neurones du pulvinar en seraient capables. Le pulvinar occupe une large zone du thalamus postérieur dorsal et s'est considérablement développé et complexifié au cours de l'évolution, en parallèle avec le néocortex [7]. Cette structure a la particularité d'avoir des relations réciproques avec virtuellement toutes les aires visuelles du cortex, et en particulier avec l'aire MT des primates et l'aire EVA du chat. Compte tenu de la nature des propriétés des neurones du pulvinar (en particulier, leur sensibilité au mouvement) et de l'organisation de ses connexions afférentes et efférentes, nous avons proposé qu'il existe une boucle thalamo-corticale incluant le pulvinar, impliquée dans le traitement de haut niveau du mouvement des objets. L'une des prémisses des modèles mentionnés plus haut est que les neurones situés aux deux extrémités de la boucle soient capables de réaliser les mêmes algorithmes complexes. C'est-à-dire que pour qu'une telle boucle fonctionnelle existe, il est nécessaire que les neurones thalamiques soient capables de coder la direction réelle du plaid et c'est le cas. Nous avons en effet démontré [8] que le tiers des neurones de la partie médiane du pulvinar du chat codent la direction véritable du plaid (Figure 3). Plus encore, ces mêmes neurones peuvent réaliser cette analyse après l'ablation chirurgicale aiguë du cortex EVA. Il s'agit, à notre connaissance, de la première démonstration que des neurones situés dans des structures sous-corticales peuvent réaliser des opérations normalement attribuées au néocortex.

En conclusion, quels sont les impacts de cette découverte?

Ces résultats sont importants à plus d'un titre. Ils indiquent que le rôle du thalamus transcende celui de simple relais de l'information sensorielle vers le cortex en relation avec l'état de vigilance. Il est vraisemblable que le pulvinar représente une plate-forme où sont intégrés les différents aspects d'une image en étroite collaboration avec le cortex.

Nos données appuient aussi les notions théoriques selon lesquelles le thalamus, via les boucles thalamo-corticales, participerait de concert avec le cortex à l'analyse de percepts complexes. Dans ce contexte, il semble essentiel de réévaluer les modèles d'intégration sensorielle qui, pour la plupart, ne prennent en considération que les aires corticales (e.g., [9]). Plus encore, la découverte que les cellules du thalamus peuvent réaliser des opérations de haut niveau en conjonction avec les aires extrastriées est importante dans le cadre de l'origine des capacités visuelles qui persistent chez des sujets ayant subis une lésion accidentelle ou chirurgicale du cortex visuel primaire (V1). Les récents travaux de Ptito et collaborateurs [10] s'inscrivent dans cette ligne de pensée. Ces auteurs ont étudié les fonctions visuelles d'une patiente ayant eu une lésion de V1 à un âge précoce (avant l'âge de 8 ans) et qui a présenté une récupération fonctionnelle tout à fait remarquable. En effet, alors que la patiente, en son jeune âge, était totalement aveugle au niveau de l'hémichamp controlatéral à la lésion (hémianopsie), sa vision est réapparue après quelques années dans le champ visuel supérieur (quadranopsie). L'examen de l'activité cérébrale (par tomographie à émission de positron) évoquée par le mouvement d'une cible visuelle dans son champ préalablement aveugle a révélé que le pulvinar et certaines aires corticales extrastriées étaient activés lors de cette tâche, impliquant directement le thalamus extragéniculé dans les fonctions visuelles résiduelles des sujets cérébrolésés.

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Figure 1. Un plaid est formé par la superposition de deux réseaux de barre identiques sauf en ce qui a trait à leur orientation (A). Dans l'exemple présent, l'axe des deux réseaux diffère de 120 degrés. Dans des conditions normales, un observateur verra un seul mouvement vers le bas qui correspond à celui des intersections des stimuli (B) et non pas le mouvement des deux composantes (C).

Figure 2. Exemple de la réponse d'un neurone du pulvinar en fonction de la direction du mouvement du plaid. Les réponses sont illustrées sous la forme d'un diagramme polaire. La courbe d'accord indique que la cellule code la véritable direction du stimulus. Si ce n'était pas le cas, la courbe serait similaire à celle, hypothétique, présentée en lignes pointillées (courbe d'accord bilobée correspondant à la direction du mouvement des deux composantes du plaid). Abréviation : p.a. : potentiels d'action; sec : seconde.

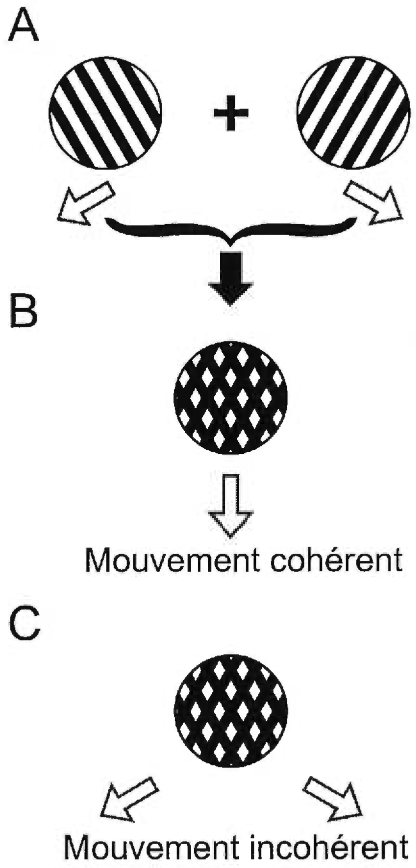

Figure 1. Casanova *et al.*

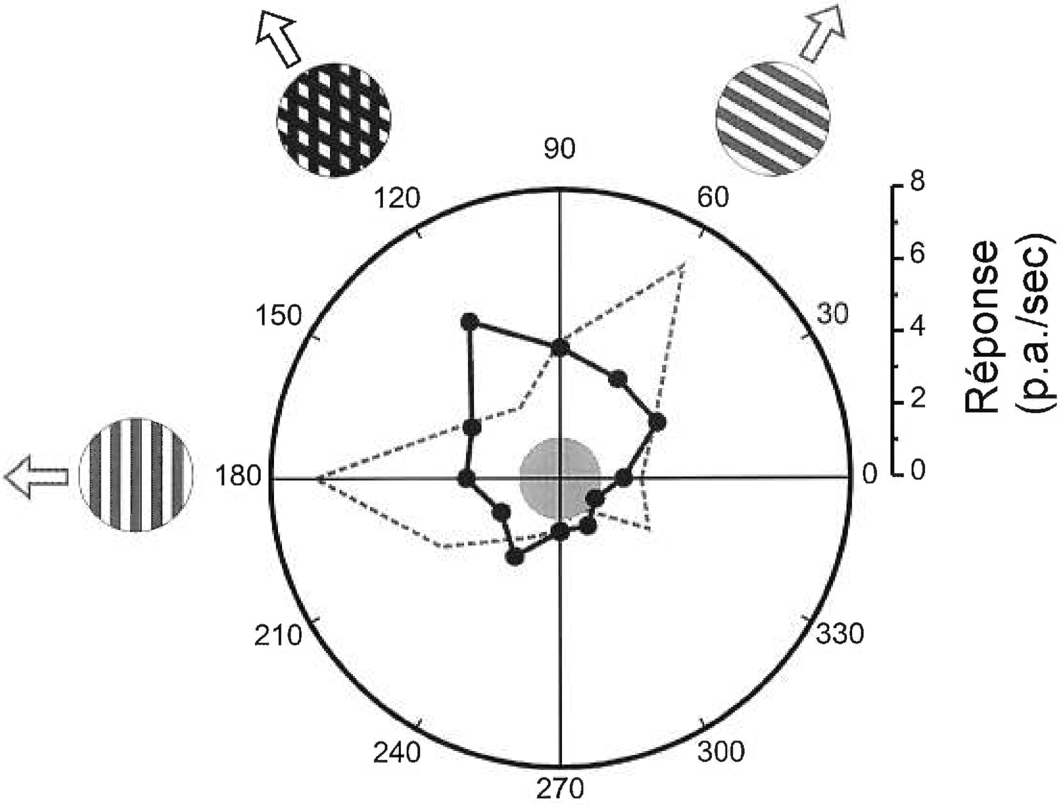

Figure 2. Casanova *et al.*