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Université de Montréal

Global Motion Processing by Neurons of Lateral Posterior-Pulvinar Complex

.

par

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Mémoire présenté à la Faculté des études supérieures
en vue de l'obtention du grade de
Maître ès sciences (M.Sc.)
en sciences neurologiques

Faculté des études Supérieures
Grade accordé à compter du
01 NOV. 2001
Université de Montréal

avril, 2001

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Page d'identification du jury

Université de Montréal
Faculté des études supérieures

Ce mémoire intitulé :

Analyse du mouvement global par les neurones du complexe noyau latéral postérieur-pulvinar

présenté par :

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a été évalué par un jury composé des personnes suivantes :

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Mémoire accepté le: ~~27 avril 2001~~ 20.09.2001

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Résumé

Afin d'avoir une perception juste du monde visuel dynamique, notre système visuel doit intégrer une multitude d'indices locaux parfois conflictuels a un *percept* cohérent. Les expériences neurophysiologiques ont démontré que le mouvement visuel est analysé par un sous-ensemble de neurones spécialisés dans la détection et l'intégration du mouvement. Des études classiques affirment que ces neurones seraient localisés dans différentes régions de cortex visuel. Les noyaux thalamiques étaient alors considérés comme une station de relais passive pour l'information sensorielle qui est traité au niveau cortical. Toutefois, chez le chat, notre laboratoire a démontré qu'un sous-ensemble des neurones du thalamus extragéniculé (complexe noyau latéral posterior-pulvinar: complexe LP-pulvinar) peut participer à l'analyse complexe des signaux visuels, analyse qui jusqu'à présent associée uniquement aux aires corticales. Le but principal de cette étude est de déterminer si les champs récepteurs de grande taille de cellules du thalamus extragéniculé serait capable d'intégrer les déplacements aléatoires des points (*random dot kinematograms*) dans une direction globale cohérente. Cette étude a été proposée afin d'étudier d'avantage la participation possible du complexe LP-pulvinar dans l'analyse des scènes visuelles complexes.

Les expériences ont été effectuées sur des chats adultes normaux anesthésiés. Des électrodes de tungstène ont été descendues afin d'enregistrer l'activité des neurones. La réponse neuronale à des stimuli définis par un patron des points aléatoires en mouvement simple et complexe et à des stimuli définis par des *plaids* ont été caractérisés pour étudier les mécanismes qui sous-tendent l'intégration du mouvement au niveau neuronal. Les résultats de cette étude se résument comme suit: 1) un sous-ensemble de neurones de LP-pulvinar est capable de coder la direction réelle du patron de points en mouvement complexe, démontrant que les neurones du thalamus extragéniculé peuvent intégrer le déplacement de multiples éléments en un percept global cohérent. 2) nous avons également constaté que la majorité de cellules sélectives au mouvement complexe de points ne sont pas systématiquement sélectives au mouvement réelle des *plaids.*

Ces résultats indiquent que les cellules du complexe LP-pulvinar du chat peuvent exécuter l'intégration spatio-temporelle de haute-niveau exigée pour détecter le déplacement global des objets dans une scène visuelle complexe. De plus, ces résultats fournissent l'évidence que le complexe LP-pulvinar participe à l'analyse spécifique des différents types de mouvement complexe, analyse qui se fait en collaboration avec des aires corticales de haut niveau.

Les résultats de cette étude sont importants pour supporter la nouvelle théorie au sujet du rôle du thalamus dans le traitement sensoriel. Par conséquent cette étude, renforce l'hypothèse que le complexe de LP-pulvinar du chat participe activement dans les mécanismes neurophysiologiques impliqués dans la perception du mouvement global.

Summary

The visual motion system performs numerous functions essentials for survival in a dynamic visual world. Neurophysiological experiments have demonstrated that visual motion is analyzed by a subset of neurons specialized in motion detection and interpretation. These neurons are thought to be localized in different regions of the visual cortex, and the thalamus has long been seen as responsible for relaying such this information on the way to the cerebral cortex.

Previous studies in the cat have shown that thalamic neurons in an extrageniculate nucleus, the lateral posterior-pulvinar complex (LP-pulvinar) could perform higher-order neuronal computations that had until then only been demonstrated in extrastriate cortical areas. The main purpose of the present study was to investigate whether neurons in the extrageniculate visual thalamus could integrate multiple displacements of random dot kinematograms into coherent motion information.

Experiments were carried out on normal adult anaesthetized cats. Varnished tungsten microelectrodes were used to record single-unit activity in the LP-pulvinar complex. Neuronal activity to drifting sine-wave gratings, complex random dot kinematograms (complex-RDKs), and “plaid patterns” were recorded in order to investigate the mechanisms underlying the global motion integration at the neuronal level.

The results of this study demonstrate: 1) A subset of LP-pulvinar neurons selective to moving complex-RDKs, suggesting that neurons in the LP-pulvinar complex can integrate the displacement of individual elements into a global motion percept. The results also indicate that the large visual receptive field of thalamic neurons permits the integration of motion for elements separated by large spatial intervals. 2) Almost all of the global motion selective units were not systematically pattern-motion sensitive when tested with plaid pattern motion. The results indicates that LP-pulvinar cells can perform the higher-order spatio-temporal integration required to detect the global motion displacement of objects in a complex visual scene. Furthermore, these results provide evidence that there may be specialized mechanisms for processing different types of complex motion within the LP-pulvinar complex.

The results of this study are important to support the new theory concerning the role of thalamus in sensory processing. Therefore this study, together with other results from our laboratory emphasize the hypothesis that the cat's LP-pulvinar complex is implicated in the neurophysiological mechanisms involved in motion processing to yield a global and coherent motion percept.

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Abbreviations list

AChE	Acethylcholinesterase
ALLS	Antero-lateral lateral suprasylvian area
AMLS	Antero-median lateral suprasylvian area
AEV	Anterior ectosylvian area
CM	Component-motion selective cell
D	Spatial interval between partner dots
DI	Direction selective index
Dmax	Maximal displacement of the dots
DLS	Dorsal lateral suprasylvian area
ISI	Interspike intervals
LGN	Lateral geniculate nucleus of the thalamus
LP	Lateral posterior nucleus of the thalamus
LPm	Medial part of the lateral posterior nucleus
LPl	Lateral part of the lateral posterior nucleus
LS	Lateral suprasylvian area
MRC	Mean response to complex-RDK
MRS	Mean response to simple-RDK
MST	Middle superior temporal area
MT	Middle temporal area
PLLS	Postero-lateral lateral suprasylvian area
PM	Pattern-motion selective cell
PMLS	Postero-median lateral suprasylvian area
Pmd	Dorso-lateral portion of the pulvinar

PSTH	Peri-stimulus time histogram
RDK	Random dot kinematograms
RF	Receptive field
T	Temporal interval between the appearance of partner dots
V1	Primary visual area
VLS	Ventral lateral suprasylvian area
VP	Ventral posterior nucleus of the thalamus

If asked what aspect of vision means the most to them, a watchmaker may answer "acuity", a night flier "sensitivity", and an artist "color". But to animals, which invented the vertebrate eye, and hold the patents on most of the features of the human model, the visual registration of movement was of the greatest importance.

GORDON WALLS (1942, p. 342)

1. Introduction

1.1. General introduction

Although our visual system provides us with a unified picture of the world around us, this picture has multiple facets. Objects we see have shape and color. They have position in the world, and often they move. For us to see each of these facets, neurons somewhere in the visual system must be sensitive to them. Moreover, because we have two eyes, we actually have two visual images in our brain, and somehow they must be merged.

Motion detection is one of the most ancient and important forms of vision (Walls, 1942). Perhaps this is because it is so important for survival (Anstis, 1980). Color vision and shape recognition are often effective in finding prey; however these systems alone would frequently

fail to detect prey or predators because they could be defeated by camouflage. While humans don't need movement perception to avoid predators, we do need it to avoid cars and other moving objects in our environment. How are we able to see moving objects? When thinking of vision it is natural to think first of the eye, where light is received by the organism. The eyes are only the beginning of a complex series of processing stages that carry visual information to the higher centers of the brain. A major aim of visual neuroscience is to explain subjective perceptions in terms of the properties of single neurons at these different processing stages (Van Essen and Gallant, 1994). Visual motion is thought to be analyzed by a specialized subset of neurons in the extrastriate cortex. However, a recent physiological study has shown that thalamic nuclei participate in motion processing interacting closely with the neocortex (Merabet et al., 1998).

1.2. The visual pathways

1.2.1. Primates

The visual pathway begins at the retina, the structure lining the rear of the eyeball that contains the photoreceptor cells. Animals with color vision have two types of receptors: rods and cones. Rods are inoperative

in bright light and function optimally at night, or wherever illumination is low. Cones, on the other hand, work best in bright light and have the pigments and neural connections that allow for the perception of color, for detailed vision or high visual acuity. Rods and cones, like other receptor cells, are the cells that actually receive photons from environmental stimuli and convert it into a neural impulse, that are transmitted to the second layer of retinal cells, the bipolar cells. Further the inputs converge at the third retinal level, the ganglion cells. The ganglion cells have been classified on the basis of such features as their cell body size and speed of conduction of their axons. There are two important types of ganglion cells. M-type ganglion cells (M from magno) are essentially color-unselective but fast conducting, with high contrast sensitivity and low spatial resolution. These cells are motion-sensitive. P-type ganglion cells (P from parvo) are color selective and sensitive to low contrast but have high spatial resolution. They generate action potentials that travel at a slower speed in the axon (optic nerve). These cells are more sensitive to the form and fine details of the visual stimuli.

According to a different organization of the afferents from the retina to visual thalamus, two visual systems were distinguished (Trevarthen, 1968) (see Figure1).

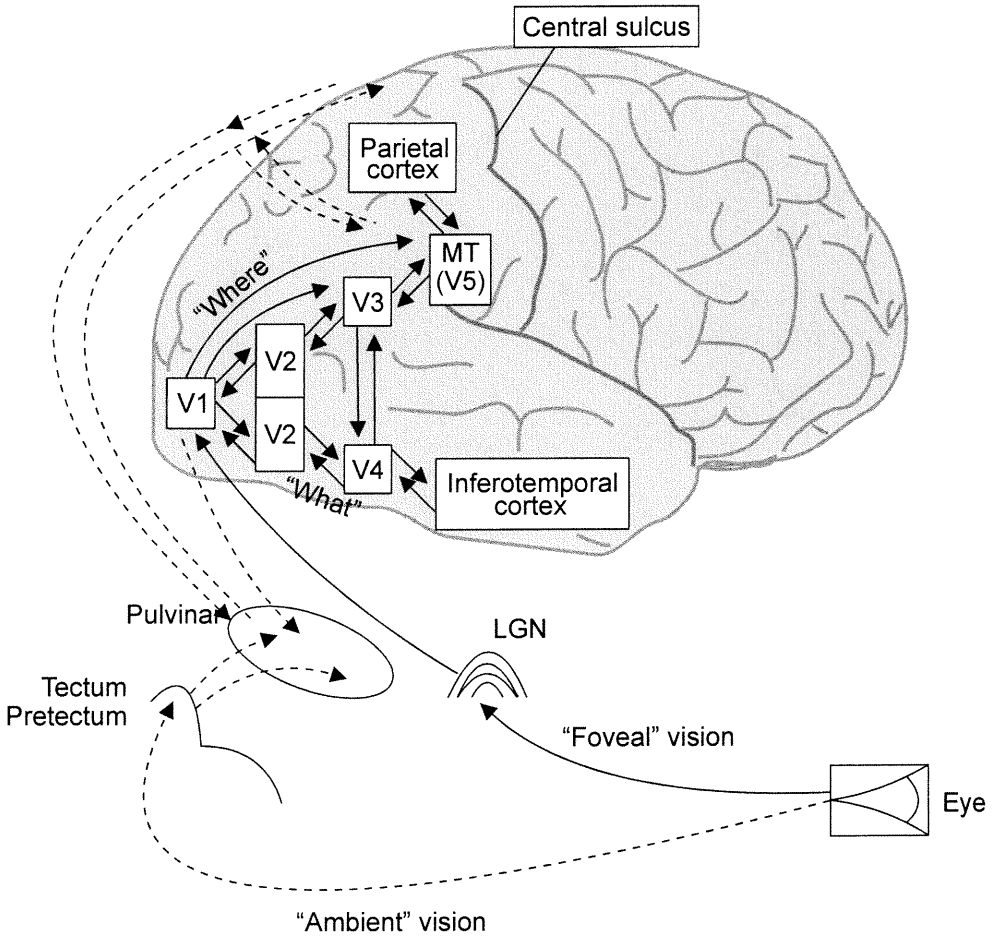

Figure 1. Two concepts of "two visual systems". Visual information reaches the cortex through the retino-geniculo-striate pathway ("foveal" vision) and is transmitted to the extrastriate cortex through intercortical association connections. These connections are later divided into two main streams, one responsible for form processing in the temporal association cortex ("what" pathway) and another for motion perception in the parietal association cortex ("where" pathway). The retino-collicular pathway ("ambient" vision) transmits the information to the extrastriate visual cortex through extageniculate thalamic nuclei (e.g. pulvinar). Adapted from Creutzfeldt, 1988

1.2.1.1. The retino-geniculo-striate system

The two main cytologically distinguishable subdivisions of ganglion cells in the primate retina are segregated in their projections to the thalamus, where they terminate selectively in the parvocellular (P) and magnocellular (M) layers of the lateral geniculate nucleus (LGN). The LGN is located in the most lateral and inferior region of the thalamus. In primates, it is composed of six layers, with the ipsilateral eye projecting to layers 2, 3 and 5 and the controlateral eye projecting to layers 1,4 and 6. The two ventral layers, layers 1 and 2, contain the larger magnocellular cells receiving projections mainly from the M-type ganglion cells, while the four dorsal layers, layers 3 through 6, contain smaller parvocellular cells receiving projections from mainly the P-type ganglion cells. The magnocellular and parvocellular geniculate outputs reach primary visual cortex (area V1).

The so-called visual cortex contains many visual areas in the occipital lobe (the primary and some extrastriate visual cortices), and in the temporal and parietal lobes (higher extrastriate visual areas). These visual areas are specialized to process different aspects of visual information and they form two major pathways, the dorsal (from V1 to parietal lobe) pathway and the ventral pathway (from V1 to the temporal lobe). Each pathway can be considered as a hierarchy, consisting of many

levels of visual information processing stages. The dorsal pathway is also called the "where" pathway as it is mainly for processing information regarding location and motion, while the ventral pathway is the "what" pathway involved mainly in processing information regarding the form and identity of visual objects (Ungerleider and Mishkin, 1982).

Thus the temporal visual areas may represent the continuation of the parvo system, and the parietal areas the continuation of the magno pathway (Livingstone and Hubel, 1988).

1.2.1.2. The retino-colliculo-extrastriate system

The superior colliculus is a mesencephalic structure that receives direct input from the retina. The superior colliculus projects to the pulvinar complex in the thalamus (Harting et al., 1972; 1980; Benevento and Fallon, 1975), which in turn has connections with association areas of the occipital, parietal and temporal lobes (Benevento and Rezeak, 1976; Ogren and Hendrickson, 1976; Rezeak and Benevento, 1979). There are reciprocal connections between virtually all visual cortical areas and the pulvinar (Ogren and Hendrickson, 1976) suggesting that similar visual processing is taking place along cortico-thalamo-cortical loops (Mumford, 1991; Miller, 1996; Crick and Koch, 1998). Thus, a second visual pathway was distinguished, and it includes structures on different brain levels,

midbrain, thalamus, and cortex. This extrageniculate pathway could explain the residual visual capacity in patients with lesions of the primary visual cortex (Mestre et al., 1992; Ptito et al., 1999).

1.2.2. Cats

The ganglion cells in the cat's retina have been classified on the basis of their morphological and functional features. X-type retinal ganglion cells have small receptive field centers, respond relatively poorly to fast moving stimuli and have medium calibre axons, which are slow conducting; these cells are form selective. Y-type retinal ganglion cells have large receptive fields and respond well to fast-moving stimuli. Furthermore, Y-cells have large calibre, fast-conducting axons; these cells are motion selective. W-cells are more heterogeneous in both their morphological and functional properties. The majority of retinal ganglion cells project to LGN, but about 10% of axons have connections with the superior colliculus (for reviews see Sherman and Spear, 1982; Garey et al., 1991).

1.2.2.1. The retino-geniculo-striate system

The two most important subdivisions of ganglion cells (X and Y-types) in the retina are segregated in their projections to the LGN. The LGN is located dorsolaterally, separated from dorsal thalamus by the medial ramus of the optic tract. It is composed of three laminae, with the controlateral eye projecting to the most dorsal lamina (A) while the more ventral lamina A1 receives the input from the ipsilateral retina. X-cells project mainly to the A laminae from where LGN medium neurons relay information to primary visual area (Leventhal, 1979; for review see Sherman and Spear, 1982). Y-cells project to the A laminae, the magnocellular part of lamina C from where LGN neurons project to cortical area 18, although some of them seem to project to cortical area 17 (Stone and Dreher, 1973; Sherman and Spear, 1982; Garey et al., 1991). Both striate areas (17 and 18) project to the medial bank of the lateral suprasylvian sulcus, a visual area that was first described by Clare and Bishop in 1954 (Kawamura, 1973; Gilbert and Kelly, 1975; Ferrer et al., 1992;). This area also receives direct inputs from the C laminae of the lateral geniculate nucleus (Le Vay and Gilbert, 1976; Naito and Kawamura, 1982). Analyses of the hierarchy of visual areas (Scannell et al., 1995) has shown that a small visual area coined the anterior ectosylvian area (AEV) located in the fundus of the anterior ectosylvian

sulcus receives projections from the lateral suprasylvian cortex. Figure 2 shows the location of these regions in relation to other cortical areas of the cat brain.

The geniculo-striate system mainly signals the shape and form of an object ("foveal vision"), while the retino-colliculo-extrastriate system is closely related with active visual exploration of world around us, or "ambient vision" (Trevarthen, 1968; for review, see Rauschecker, 1988).

1.2.2.2. The retino-colliculo-extrastriate system

In addition to its connections with the LGN, the retina projects to a number of diencephalic and mesencephalic structures among which, the colliculus is the most important for visual perception. Projections from the superior colliculus reach the extrastriate cortex through the lateral posterior nucleus of the thalamus (LP). The presence of an extrageniculate system was proposed for the first time in the cat by Sprague et., al (1977), who reported that destruction of areas 17 and 18 did not prevent, and only marginally but slowed down the learning of certain visual patterns. However, when lateral suprasylvian area was destroyed and areas 17 and 18 were left intact, the ability to learn the pattern was severely impaired. Thus they established the existence of extrastriate parallel pathways playing an active role in visual processing.

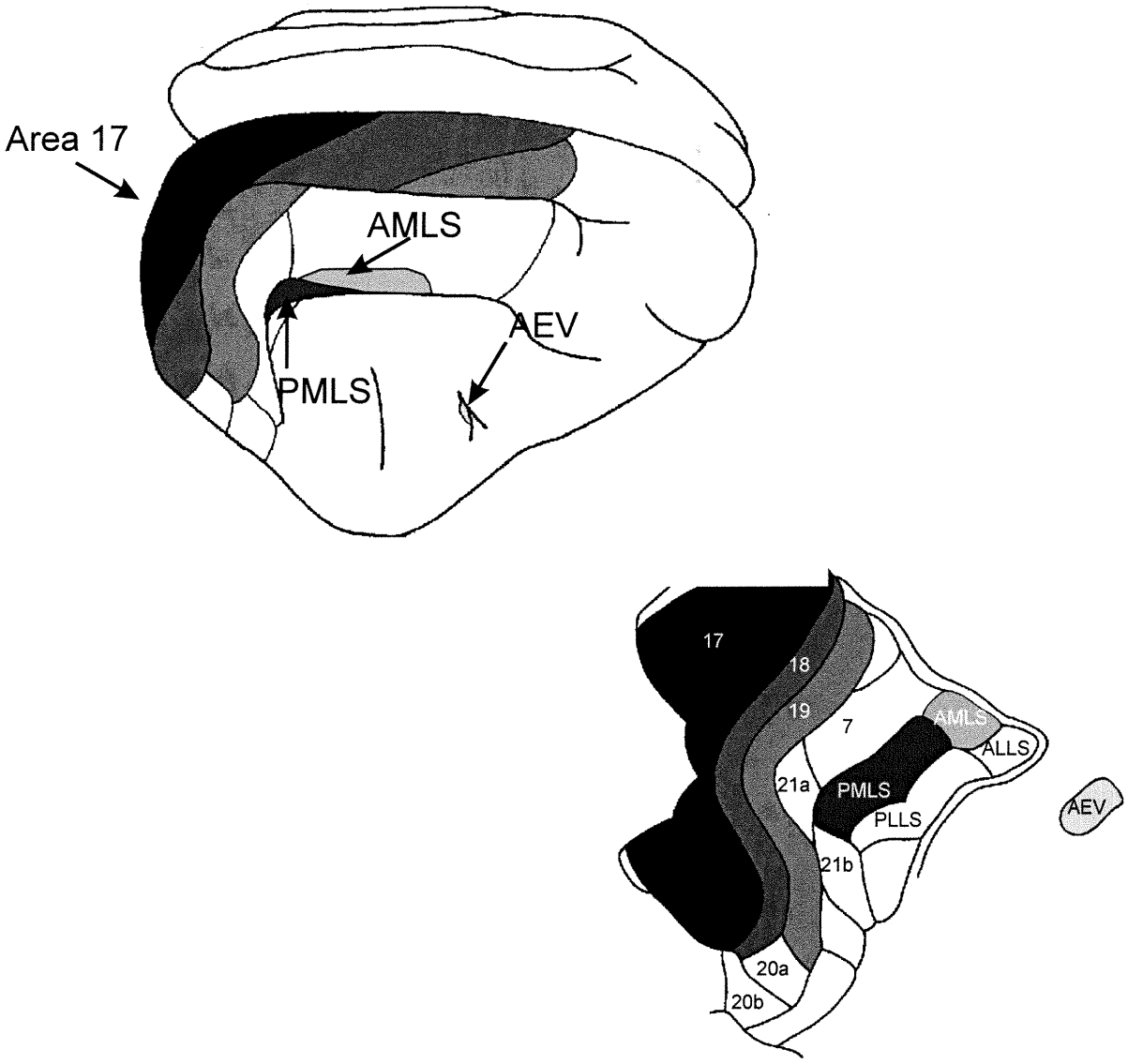

Figure 2. Location of visual cortical areas in the cat brain. The top figure shows a dorsolateral view. Arrows identify the location of the cortical areas discussed in this study The bottom figure represents a flat-mounted view showing the relations and relative size of each cortical area. Abbreviations: AEV: anterior ectosylvian , AMLS: anteromedial lateral suprasylvian , PMLS: posteromedial lateral suprasylvian, PLLS: posterolateral suprasylvian, ALLS: anterolateral suprasylvian. Adapted from Sereno and Allman (1991) and Spear (1991).

In support of this idea, Berson and Graybiel (1978) showed that the lateral suprasylvian area (LS) receives visual afferents from the superior colliculus via the lateral posterior-pulvinar complex (LP-pulvinar) of the thalamus. Neurons in the LS cortex still respond to some visual stimuli after striate cortex ablation (Doty, 1971; Spear and Bauman, 1979; for reviews see Creutzfeldt, 1988; Lomber et al., 1996). Therefore, in the cat, the lateral posterior-pulvinar (LP-pulvinar) complex has been identified as the thalamic relay of the second visual pathway, transferring visual input from the superior colliculus to the cortex, and related to "ambient vision".

1.3. Two stage of motion processing

When we watch a movie, we see a sequence of images in which objects appear in a sequence of positions. Although each frame represents a frozen instant of time, the movie gives us a convincing impression of motion. Somehow the visual system interprets the succession of still images so as to arrive at a perception of a continuously moving scene. This phenomenon represents one form of apparent motion. How is it that we see apparent motion? One possibility is that our visual system matches up corresponding points in succeeding frames and calculates an inferred velocity based on the distance traveled over the frame interval.

There have been many algorithms and models developed to compute motion. Most of them are variations and different implementations of a few basic types of methods, based on gradient, correlation, or spatio-temporal energy models. In the following we will briefly review these basic methods.

When an image moves across the retina, it stimulates a series of receptors, one after the other. Reichardt (1961), Barlow and Levick (1965) proposed that a directionally selective neuron works like a detector that compares the luminance distributions seen at position A and time t1 with that seen at position B and time t2 (see figure 3 panel A). This detector is based on linear spatio-temporal filters, combining signals over time and space weighted by a function simply represented by the positive and negative zones in the receptive field. Thus, the comparator model, which physiologists have found in retina, is perfectly adequate as a model for the detection of a simple motion of a single spot.

In a typical global matching model, the visual system would perform a match over some large region of the image, in essence performing a template match by sliding the image from one frame to match the image optimally in the next frame (e.g., movie). Most cross-correlation models (see figure 3 panel B) are examples of the global matching approach (Adelson and Bergen, 1985).

Not all stimuli fall naturally into such a description. In the scene in which there is an ambiguity in the velocity field, the motion is more complex and matching models may not suffice to compute motion perception. The most easily understood example of this general problem is the motion of an extended edge, or "aperture problem" (Adelson and Movshon, 1982). To illustrate this problem, consider the rightward-moving diamond. The aperture problem stems from the directional ambiguity of motion whenever the portion of the image is visible within a restricted region. Consider for example an edge of the diamond moving behind a circular aperture as shown in figure 4 panel A. An observer viewing such a display can know the direction of motion only if the correspondence points along the edge are known. In the absence of unique points of correspondence, the observer perceives motion perpendicular to the moving line (see figure 4 panel B). Therefore, we can conclude that local motion analyzers are limited by their small receptive fields and may not provide the best interpretation of the object's motion as a whole. Somehow, this cue by cue analysis must be integrated into a coherent perception of a unitary object moving rightward. How might this be accomplished computationally?

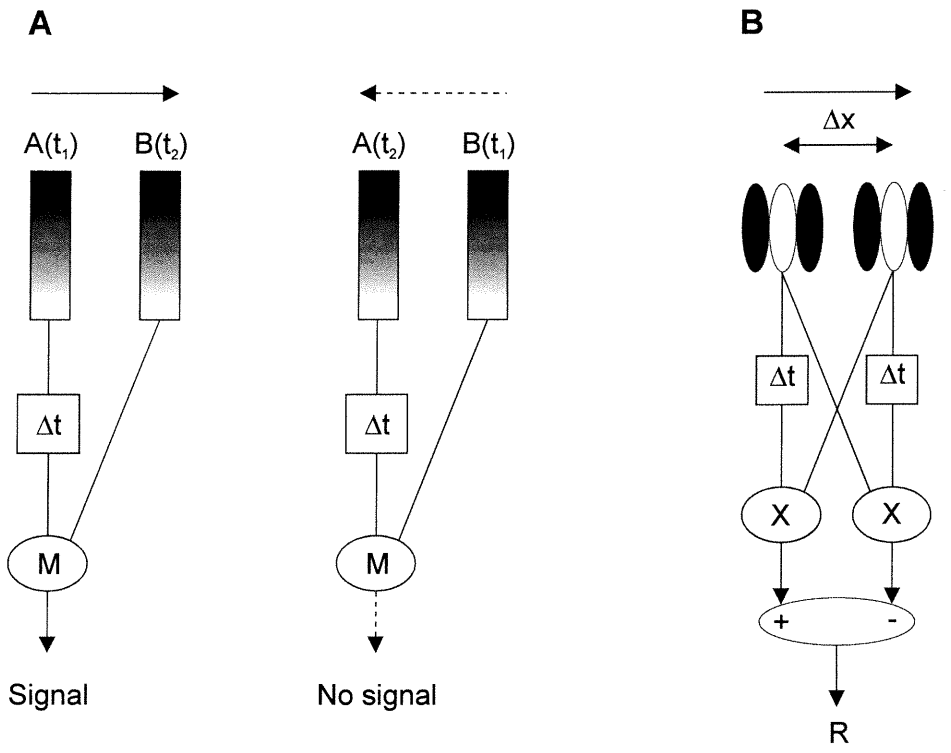

Figure 3. Models of motion perception (**A**) Scheme of a comparator model. This detector consists of two photoreceptors separated by distance x (A-B). Its input is given by the light intensities as measured by these photoreceptors. One of the inputs has been delayed by a time interval t. The unit M adds the signal from these photoreceptors. When the pattern moves in the detector "preferred direction" the temporal separation of the signals in both input channels may be compensated for by the delay. In this way both signals may coincide at the multiplication stage, giving rise to a large output signal. When the stimulus is in the null direction, the temporal sequence of the signals in both channels is reversed. The delay increases their separation in time of arrival at the multiplication stage, which results in two small responses peaks (for review, see Borst and Egelhaaf, 1989). (**B**) Scheme of a cross-correlation model. The correlator employs responses of two oriented receptive fields. The X units add the excitatory signal from one correlator to the inhibitory signal from the other to determine the overall response of the detector. In this example, a positive response represents motion to the right; a negative response represents motion to the left. In summary, this correlation unit combines signals by multiplying them together (for review see Wilson, 1994).

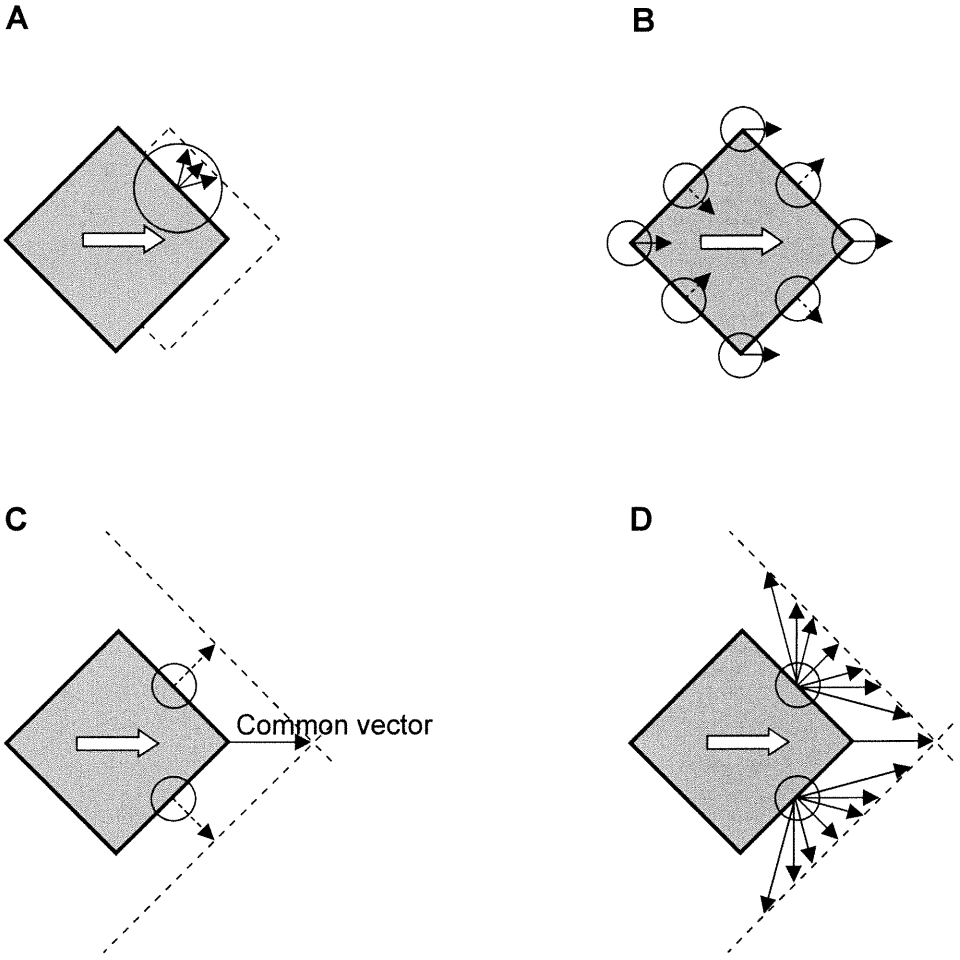

Figure 4. The "aperture problem". (**A**) The motion of a moving edge behind an aperture. (**B**) Local estimates of motion. Because of the aperture problem, a diamond moving rightward will produce local estimates of motion in different directions at different positions along its perimeter. Only the corners yield accurate information. (**C**) *Intersection of constraints* (IOC) is a simple method proposed by Adelson and Movshon, 1982. This 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 an object. (**D**). Another solution of the aperture problem proposed by Hildreth and Koch (1987). This method uses the IOC from the two edges of the object associated with the top of its vertex.

One simple and elegant theory specifies how to combine the constraints provided by all local motion analyses into a best estimate of the global motion (see panel C and D). The formal solution can be extracted by the intersection of constraints[1], i.e. vectorial sum, imposed by the moving edges in order to signal the true direction of the object's motion (Adelson and Movshon, 1982; Movshon et al., 1985; Movshon, 1990; Stoner and Albright, 1992).

The aperture problem appears in a slightly different appearance as the "correspondence problem" in successive time samples of a moving image (Julesz, 1971; Ullman, 1979); if there is a white spot A in the first sample, and similar spots at B and C in the second sample, this gives two alternative possible motions for A. How does our visual system resolve these problems?

On the basis of this theoretical hypothesis it has been suggested that motion integration occurs in at least two stages (Adelson and Movshon, 1982; Williams and Sekuler, 1994; Watamaniuk, 1989; Stoner and Albright, 1992; Nowlan and Sejnowski, 1995). The first stage

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[1] Movshon (1990) suggests that the neurophysiological realization of this function requires the existence of cells that integrate signals of local motions detectors and code the veridical direction of motion of an object. He speculates that these cells compute the motion of the whole object rather than the oriented contours comprising that object. Using plaid patterns (Movshon et al., 1985) that were created by superposing two grating stimuli, it was observed that some neurons respond to components of movement (*component-motion selective cells*) and others respond to the overall pattern of movement (*pattern-motion selective cells*)

(see figure 5) would extract the local motion characteristics of an image. These local signals are combined at a second stage to form a globally coherent motion percept. In agreement with this model of motion integration, Braddick (1974) provided evidence for two distinct motion processes in apparent motion. He called them short-range and long-range process. The short-range process is supposed to correspond to low-level motion detectors, while the long-range process is supposed to correspond to a more interpretative and cognitive mechanism.

1.4. Motion processing - implicated structures

1.4.1. Motion processing in primates visual system

We usually move through the world we perceive. Appropriate behavior therefore requires that we receive accurate information about the motion of objects. How does motion processing operate at the cellular level?

The foundation for our understanding of the neuronal mechanisms underlying motion processing was set with the discovery of an explicit neural representation of motion in the form of cells that exhibit selectivity for the direction in which an image moves across the retina. In primates, this property of directional selectivity is first seen at the level of the primary visual cortex. Therefore, motion is initially processed in V1, then continues through several successive cortical visual areas including, most notably, the middle temporal area (MT), an extrastriate visual area selectively involved in cortical analysis of visual motion (Zeki, 1974). MT receives ascending visual inputs via a rich set of cortical (V1, V2, and V3) and subcortical afferents and in turn projects to higher-order cortical areas that provide visual inputs to the posterior parietal cortex (Maunsell and Van Essen, 1983; Weller et al., 1984). One correlate of the hierarchy in the motion pathway is progressively increasing receptive field (RF) size.

Thus the RFs of MT cells are larger than those of their inputs by as a much as a factor of 10 and smaller than those of its targets by a similar ratio (Maunsell and Van Essen, 1983; Movshon and Newsome, 1996). Most cells in MT are sensitive to motion (Dubner and Zeki, 1971; Zeki, 1978) and appear to be specifically tuned to direction and speed of motion (Albright, 1984; Maunsell and Van Essen, 1983; Rodman and Albright, 1987). A number of studies have more precisely established the role of MT in motion analysis, with a major function appearing to be integration and comparison of the output signals from local motion detectors (Movshon et al., 1985; Rodman and Albright, 1989). Behavioral experiments have revealed that MT neurons carry directional signals of sufficient precision to account for the psychophysical sensitivity of behaving monkeys (Britten et al., 1992), and that electrical microstimulation of MT can influence the direction discrimination task in a specific manner (Salzman et al., 1992). Additional experiments showed that lesions of MT impaired performance on the psychophysical direction sensitivity while leaving contrast thresholds unchanged (Newsome and Pare, 1988). Taken together, these findings strongly support the idea that directional signals in the motion pathway, and specifically in area MT, contribute directly to the perception of motion (Britten et al., 1993).

MT provides the major inputs to the middle superior temporal area (MST) (Maunsell and Van Essen, 1983; Boussaoud et al, 1990). The

MST contains a preponderance of directionally selective neurons (Desimone and Ungerleider, 1986; Van Essen and al., 1981), including many that respond selectively to complex optic flow (Andersen et al., 1990; Duffy and Wurtz, 1991). Ascending projections from MST are then distributed to several regions of the parietal, frontal, and temporal lobes (Baussaoud et al., 1990). Thus MST occupies an advanced level within the motion pathway and is well situated to distribute motion information broadly to several higher cortical centers. Furthermore, physiological studies show that the sensitivity of MST neurons to visual motion is similar to that measured psychophysically (Celebrini and Newsome, 1994), and that microstimulation of MST neurons alters the visual choice of a monkey towards the direction to which the stimulated neurons are more sensitive (Celebrini and Newsome, 1995).

On the basis of "two-stage" model of motion processing, it has been suggested that the first stage take place in the primary visual cortex while, the second stage of motion analysis is believed to take place in higher order visual cortical areas such as MT and MST. Figure 5 illustrate the "two-stage" model of motion processing in the primate visual cortex adapted from Sereno (1993) and Nowlan and Sejnowski (1995).

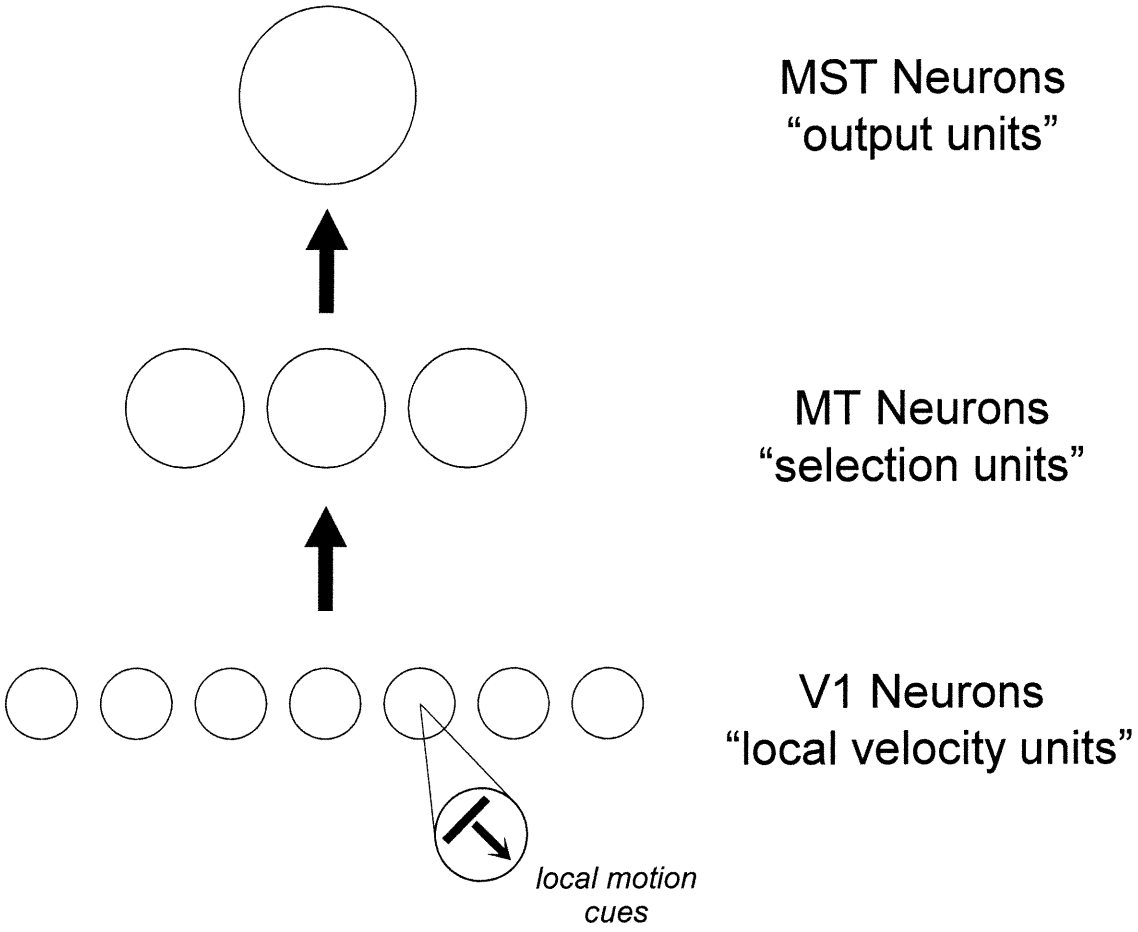


Figure 5. The selection model of motion processing. Schematic representation of the stage of motion analysis in primate visual cortex. The model suggest that local units (i.e. V1) signal local motion displacements. These signals converge onto selection units (area MT) that integrate local motion cues into a coherent direction. The final output stage (purposed to be MST) would combine the activity of selection units for subsequent processing of a more complex scene. Adapted from Sereno (1993), Nowlan and Sejnowski (1995); (Merabet, 1999)

1.4.2. Motion processing in cat visual system

The receptive field properties of direction-selective neurons in cat striate cortex, i.e; areas 17 and 18 (Hubel and Wiesel, 1962; Movshon, 1975; 1978) suggest that striate cortex constitutes a part of the motion detection system. Behavioral studies (Pasternak et al., 1992; 1995) support this hypothesis. The cat's motion system continues through extrastriate cortical areas. Three extrastriate areas of interest in this study are anteromedial lateral suprasylvian (AMLS), posteromedial lateral suprasylvian (PMLS) and anterior ectosylvian visual (AEV) cortex (figure 2)

Six subdivisions of LS cortex have been identified (Palmer et al., (1978) on the basis of separate topographic maps (AMLS, ALLS, PMLS, PLLS, DLS and VLS); of these areas, PMLS has received the most attention. Indeed, this area contains neurons with relatively large receptive fields, a high proportion of neurons selective for the direction of target motion, general preference for low spatial and high temporal frequencies and binocularity. Other characteristics include strong and selective responses to relative motion between an object and its background (von Grunau and Frost, 1983) and bias in preferred directions away from the area *centralis* (Rauschecker et al., 1987). Pasternak et al., (1989) and Rudolph and Pasternak (1996) showed that while lesions of LS cortex did

not affect sensitivity to the direction of simple motion, the permanent deficits were observed in the ability to process complex motion information. Its position on the cortical sheet, connectivity, and physiological properties have led to the suggestion that it is both an important motion processing area and an area homologue to MT (Payne, 1993). However, it appears, that PMLS does not contain neurons pattern-motion selective for plaids (Gizzi et al., 1990), a property found in many neurons of the monkey MT area (Movshon et al., 1985). Other areas within LS cortex are not very well studied. Recently, Li and his co-workers (2000) reported that neurons in postero-lateral lateral suprasylvian area (PLLS) are selective to radial motion, suggesting that this area may play a role in optic flow information processing. It has also been shown in our laboratory (Ouellette, 2001) that a majority of neurons in AMLS cortex were direction selective, and a subset can code for the direction of complex motion (plaid and global motion).

The LS cortex provides inputs to the anterior ectosylvian visual area (AEV) located in the fundus of the anterior ectosylvian sulcus (Scannell et al., 1995). Besides its favorable connectional relationship, the AEV contains many neurons that respond selectively to the direction of stimulus motion (Benedek et al., 1988; Mucke et al., 1982; Olson and Graybiel, 1983, 1987). Also, Scannell et al., (1996) showed that AEV

neurons contribute directly to the integration of local motion signals predicting that AEV might be a high-level motion processing area.

The fact that visual motion can be processed in the extrageniculate pathway had been postulated 30 years ago, based on behavioral studies showing that in a cat without striate and peristriate cortex (17, 18 and 19 area) some visually guided responses and avoidance of obstacles is conserved (Doty, 1971). Recent research reassessed (Rauschecker, 1988; Chalupa, et al., 1983; Casanova et al., 1989; Casanova and Savard, 1996; Merabet et al., 1998) the role of visual structures included in the retino-colliculo-extrastriate system in motion analysis, a pathway where the LP-pulvinar complex seems to be strategically placed. The role of the LP-pulvinar complex in visual motion processing will be described below (pages 27-31).

1.5. The pulvinar – a likely candidate as a higher-order visual region

The thalamus is an egg-shaped mass of diencephalic neurons arranged into nuclei. It develops on each side as the second and by far the largest of the four longitudinal nuclear zones of the diencephalic wall. Each thalamus is medial to the posterior limb of the internal capsule. Despite the assumption by le Gros Clark (1962), that the thalamus could be involved in higher integrative functions, thalamic nuclei have long been

regarded as passive relay stations for information *en route* to higher level processing in the cerebral cortex. However, in last decade physiological and theoretical studies have proposed that thalamic nuclei participate in higher order processing by interacting closely with the neocortex (Mumford, 1991; Sherman & Guillery, 1996; Miller, 1996; Singer, 1994).

In all mammals studied, a region of the posterior dorsal thalamus, located medial and caudal to the dorsal lateral geniculate nucleus, has been found to contain a variable number of nuclei that are associated with the visual pathway. These nuclei, generally retinotopically organized, are collectively termed the "lateral posterior-pulvinar complex" in cats, and "pulvinar complex" in primates (Mason, 1978; Bender, 1981; Raczkowski and Rosenquist, 1981; for review, see Garey et al., 1991).

1.5.1. Historical perspectives

In the human brain the pulvinar is the largest nucleus in the thalamus. The size and the differentiation of the pulvinar increase markedly as one ascends the phylogenetic scale, as similar expansion occurred in associative areas. Early anatomical studies (Le Gros Clark and Northfield, 1937) revealed reciprocal connections between pulvinar and what were then considered cortical association areas. Most ideas about pulvinar functions have been based on the functions of those

structures with which it is connected. Thus, this anatomical evidence led to the idea that the pulvinar plays a role in higher integrative functions, as suggested for the first time by Le Gros Clark (1962).

More than, 40 years ago it was reported that visual evoked potentials could be recorded from the cat LP-pulvinar complex (Buser, 1959). In addition, single-unit recordings demonstrated the presence of visually responsive cells in the cat's LP-pulvinar complex (Godfraind et al., 1969, 1972; Mathers and Rapisardi, 1973). Furthermore, studies of the functional relationship between LP and cortical areas have shown that functional blockade of the LP-pulvinar complex produced substantially modified visual responses in the cat's visual cortex (Chalupa et al., 1973). In the monkey, behavioral studies reported that learning of visual pattern discrimination was markedly impaired after pulvinar lesions (Chalupa et al., 1976). These early studies suggested that the pulvinar nucleus in primate and the LP-pulvinar complex of the cat is involved in visual functions in relation with cortical areas.

What appeared to be, for many years, unawareness on the part of visual physiologists for the LP-pulvinar complex, was mainly the results of insufficient information on the physiology of LP-pulvinar cells. This lack of detail was due, in large part, to the very real difficulty to record from cells in this part of the thalamus. This problem has been overcome and

our knowledge of the functional organization of the LP-pulvinar complex has progressed considerably.

1.5.2. Neuroanatomy of the LP-pulvinar complex

One of the major obstacles in elucidating the functional organization of the LP-pulvinar complex has been the absence of pertinent anatomical knowledge. The first clear indication that the LP-pulvinar of the cat is comprised of multiple, relatively well-defined subfields formed on the basis of anatomical connectivity was reported in 1972 by Graybiel (see also Berson and Graybiel, 1978; Updyke, 1983). The LP-pulvinar complex was differentiated into three zones: 1) the pulvinar proper, that receive its main source of ascending visual inputs from the pretectum (Niimi and Kawahara, 1973); 2) the lateral portion of LP, considered the striate recipient zone because it is the only subdivision innervated by projections from areas 17 and 18 (Kawamura et al., 1974; Updyke, 1977); and 3) the medial LP, the principal tectorecipient zone, innervated by afferents issued from neurons in the superficial layers of the superior colliculus (Graybiel, 1972). Subsequently, these regions were better identified by differential

staining[1], to contain acethylcholinesterase (AChE) by Graybiel and Berson (1980). Each of these zones is reciprocally connected with extrastriate visual areas (Berson and Graybiel, 1983; Raczkowski and Rosenquist, 1983). For example, Mucke and colleagues (1982) found that the LPm is reciprocally connected with the lateral bank of the suprasylvian visual areas and with the anterior ectosylvian visual area (AEV). On the other hand, Abramson and Chalupa (1985) have shown that the LPl exhibits reciprocal connections with areas 18, 19 and the medial bank of the suprasylvian cortex. Figure 6 illustrates the subdivisions of the LP-pulvinar and its connectivity with cortical and subcortical areas. The laminar distribution of reciprocal connections between cortical areas and LP-pulvinar complex indicates that the thalamic zone receives its major input from pyramidal cells in layer V. In turn, only layer I of the striate areas receives inputs from the lateral posterior nucleus, while all extrastriate areas receive majority of projections from layer IV (Abramson and Chalupa, 1985; for review, see Chalupa, 1991). Therefore, on the basis of these results and using Rockland's rules of hierarchy[2] we may suggest

---

[1] It has been shown (Graybiel and Berson, 1980) that the LPm as well as the pulvinar can be identified by their high content of AChE. In contrast, the LPl appears pale compared with neighboring subdivisions and can be easily demarcated.

[2] Rockland and Pandya (1979) suggested that a connection between two cortical areas is considered as ascending in the hierarchy if it terminates mainly in cortical layer IV. It is considered descending in the hierarchy if it avoids layer IV, and terminates strongly in layer I and possibly in layer VI as well.

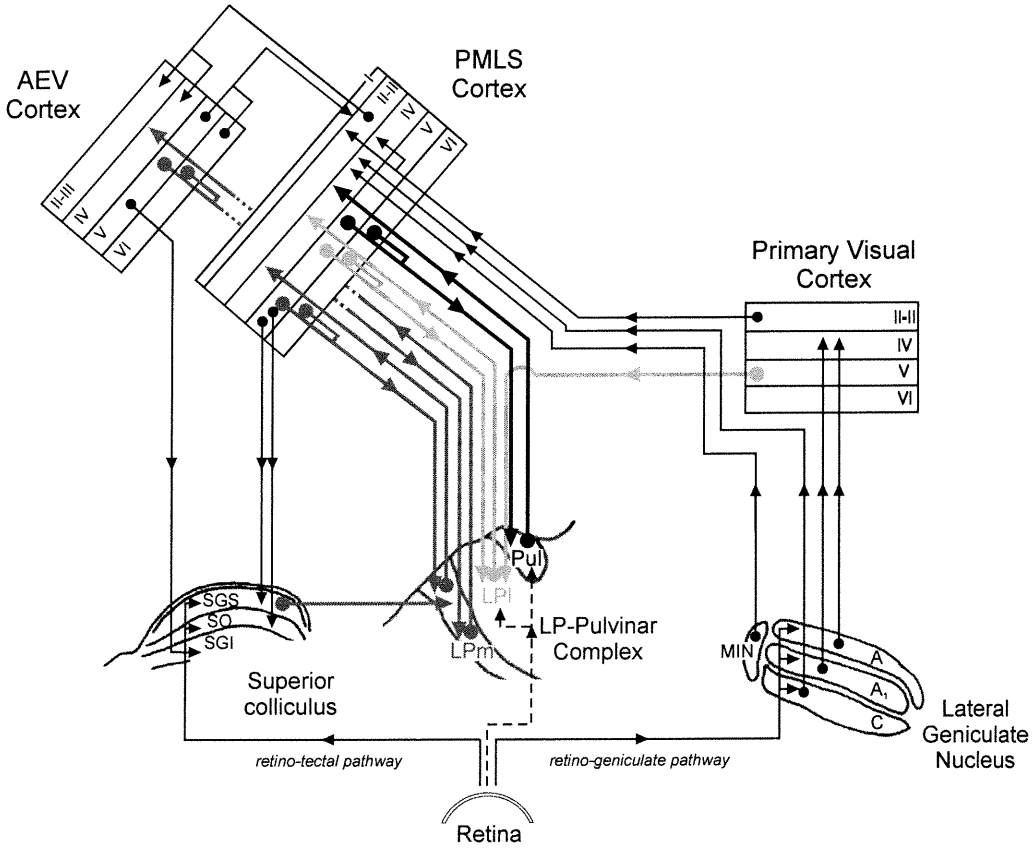


Figure 6. Subdivisions of the LP-pulvinar complex and the major visual pathways implicating subcortical-cortical connectivity in the cat. The connections involving LP-pulvinar complex are represented by tick lines of different gray levels (note that some projections are not shown in order to clarify the diagram). (Casanova et al, 2001).

that LP-pulvinar complex is a visual region positioned between striate and extrastriate areas.

Based on its reciprocal connectivity patterns, the LP-pulvinar complex appears to be placed at the center of several cortico-thalamo-cortical loops, playing a crucial role in *re-routing* information to a new visual area (Creutzfeldt, 1988; van Essen et al., 1992). Moreover, being in relationship with extrastriate areas known to be involved in motion analyses, it was proposed that LP-pulvinar complex is in a strategic position to play an active role in visual motion processing in relation to cortical areas placed on the other side of the loop (Rauschecker, 1988).

1.5.3. Neurophysiological response properties

Mason (1978) reported that cells in the cat LP-pulvinar complex were more responsive and easier to drive with moving stimuli than with flashing stimuli. Unlike cells in the LGN, physiological response properties of cells in the cat LP-pulvinar complex indicate that they code attributes of image motion such as direction, velocity and relative motion between an object and its background (Casanova & Savard, 1995). 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, 1997). In addition, neurons in the LP-pulvinar complex are mostly

binocular (Casanova et al., 1989) and their receptive fields are quite large (more than 400 deg^2), (Chalupa & Abramson, 1988), suggesting that this area may play a role in visual integration. Behavioral studies indicate that the cat LP nucleus is involved in the control of visually guided movement (Fabre-Thorpe et al., 1986).

In primate, the pulvinar has often been associated with visual attention. For example, Robinson and Peterson (1992) described visual responses of neurons in the dorsomedial portion of the lateral pulvinar (termed Pdm) that are selectively modified by attentional variables. Another group of neurons, found throughout the pulvinar, discharge in relation to saccadic eye movements (Perryman et al., 1980; Acuna et al., 1990). Many neurons in the pulvinar that respond to real motion do not discharge when eye movements cause similar motion of a stimulus across the retina (Robinson and Peterson, 1985). Such neurons were encountered in the retinotopically organized regions of the inferior and lateral pulvinar. As suggested by the authors, neurons that discriminate between real and self-induced movement could play a role in the suppression of perception during eye movement activity.

Based on its connectivity pattern and its neurophysiological properties, the LP-pulvinar complex, strategically placed between the geniculo-cortical and retino-tectal systems, seems to participate in the processing of visual information (Creutzfeldt, 1988).

1.5.4. Higher integrative functions

The fact that the pulvinar was found to be reciprocally connected with associative areas (le Gros Clark, 1937), suggests that it could play an important role in higher integrative functions. On the basis of reciprocal connectivity with the cat extrastriate areas, the LP-pulvinar complex has been considered an integral part of the extrastriate visual system (Hutchins and Updyke, 1988), and proposed to play a functional role in dynamic processing of complex visual scenes (Sherman and Guillery, 1996; Crick and Koch, 1998).

In agreement with this hypothesis, our laboratory has recently demonstrated that a subset of neurons in the cat LP-pulvinar complex can integrate different motion signals of a plaid pattern into a coherent direction (Merabet et al, 1998), indicating that thalamic cells could compute the motion of the whole (Adelson & Movshon, 1982), likely through cortico-thalamo-cortical loops. The fact that pattern-selective responses exist at the thalamic level demonstrates for the first time that higher-order properties exist outside extrastriate cortical areas, and indicates that LP-pulvinar complex plays an important role in motion integration. Also, these findings lend credence to the theoretical models proposing that specific thalamic nuclei participate in more complex

aspects of sensory processing (e.g. Mumford, 1991; Miller, 1996). The most pattern-motion selective neurons in LP-pulvinar complex were located in LPm, which is reciprocally linked to the AEV cortex (Mucke et al., 1982). The presence of pattern-motion selective cells on the both sides of the AEV-LPm (Scanell et al., 1996; Merabet et al., 1998) raises the possibility that there may be a cortico-thalamo-cortical loop involved in pattern-motion selectivity. Deactivation of different visual motion areas which are reciprocally connected to LP-pulvinar complex suggest that these cortical regions and LP nucleus are functionally linked by multiple cortico-thalamo-cortical loops and that functional integrity of both components of the loop is necessary to carry out certain aspects of motion analysis (Rauschecker, 1988).

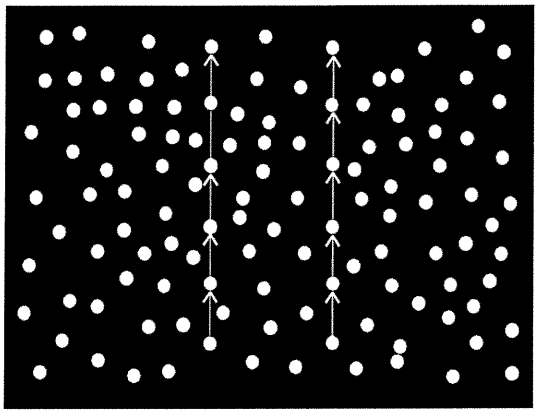
2. Hypothesis and Purpose

The visual system is often confronted with scenes that contain many objects moving in various directions. These object motions must be combined to give a coherent and global motion direction. This kind of integration was defined as global motion processing, and was believed to take place in higher-order visual cortical areas. In contrast, our laboratory showed that LP-pulvinar neurons could perform higher-order neuronal operations indicating the presence of pattern-motion selective cells in the cat's LP-pulvinar cells.

The purpose of this neurophysiological study is to investigate whether or not the cat's LP-pulvinar neurons can signal the global displacement of a random dot kinematograms (RDKs) (see figure 7) wherein the individual elements do not provide any coherent local motion cues. Also, we wished to determine whether there is a relationship between RDK-defined and plaid-defined motion selectivity at the cellular level.

On the basis of cellular response in LP-pulvinar complex to plaid patterns, the receptive field properties of the cells, and its reciprocal connectivity with extrastriate areas involved in complex motion perception, we raise two main hypotheses regarding the participation of this nucleus in global motion processing. 1) the LP-pulvinar cells should perform the

A. Simple RDKs motion



B. Comples RDKs motion

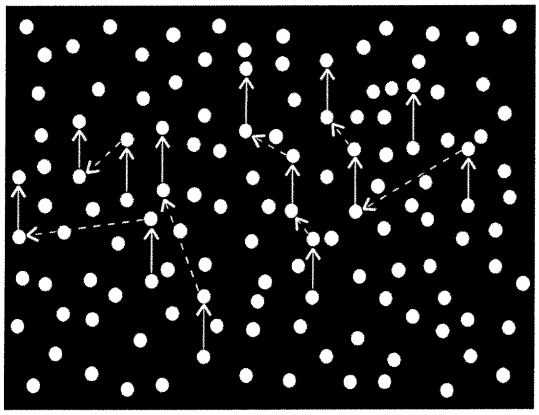


Figure 7. Visual stimuli used in this study. (A) Simple random dot kinematograms (simple RDKs): each dot follows a straight and continuous path. (B) Complex RDKs: the dots had a lifetime of two-frames,that is they moved only once before being randomly repositioned. Consequently, there must be spatial and temporal integration of the dots displacement over an extended area in order to signal the veridical direction of the pattern.

higher-level spatio-temporal integration necessary to process the complex visual scene. In addition, this kind of integration should be comparable to that found in extrastriate cortical areas with which it exhibits reciprocal relations (i.e. PMLS) and 2) there may be specialized mechanisms for processing different types of complex motion (plaid and global motion) within the LP-pulvinar complex.

The coding of the direction of motion of such pattern by LP-pulvinar neurons would indicate that their large receptive fields could process the visual integration over the space and time required to detect the global displacements of multiple objects in visual scene.

The results of this investigation are presented in the form of one article accepted for publication in the *European Journal of Neuroscience* (in press; see annex). In the conclusion of this study will attempt to address the role of the thalamus involved in different aspects of motion processing.

3. Article: "Global Motion Integration in the Cat's Lateral Posterior-Pulvinar Complex"

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Accepted by: *European Journal of Neuroscience*

EJN

European Journal of Neuroscience

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Published by Blackwell Science, Paris, Oxford, London, Edinburgh, Berlin, Vienna, Melbourne, Tokyo

March, 2001. Revised manuscript. European Journal of Neuroscience

Receiving Editor: Tamas F. Freund

Global Motion Integration in the Cat's Lateral Posterior-Pulvinar Complex

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Word count:

Abstract:	201
Introduction:	424
Methods:	1,244
Results:	1,857
Discussion:	1,107
Fig. legends:	651
References:	647
Total:	6,131

Total pages: 25

Number of figures: 9

Key words: complex motion, cortico-thalamo-cortical loops, higher-order processing, spatio-temporal integration, extrageniculate thalamus.

Running head: Motion integration in pulvinar

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ABSTRACT

Our laboratory previously showed that thalamic neurons in an extrageniculate nucleus, the lateral posterior-pulvinar complex (LP-pulvinar) could perform higher-order neuronal operations that had until then only been attributed to higher-level cortical areas. To further assess the role of the thalamus in the analysis of complex percepts, we have investigated whether neurons in the LP-pulvinar complex can signal the direction of motion of random dot kinematograms wherein the individual elements of the pattern do not provide coherent motion cues. Our results indicate that a subset of LP-pulvinar cells can integrate the displacement of individual elements into a global motion percept and that their large receptive fields permit the integration of motion for elements separated by large spatial intervals. We also found that almost all of the global motion sensitive neurons were not systematically pattern-motion selective when tested with plaid patterns. The results indicate that LP-pulvinar cells can perform the higher-level spatio-temporal integration required to detect the global displacement of objects in a complex visual scene, further supporting the notion that extrageniculate thalamic cells are involved in higher-order motion processing. Furthermore, these results provide some evidence that there may be specialized mechanisms for processing different types of complex motion within the LP-pulvinar complex.

INTRODUCTION

Visual scenes often contain many elements moving in various directions that need to be combined to yield a global and coherent motion percept. On the basis of psychophysical and electrophysiological evidence, it has been suggested that motion integration occurs in at least two stages (Adelson & Movshon, 1982; Stoner & Albright, 1992, Watamaniuk *et al.*, 1989). The first stage, likely to take place in the primary visual cortex, would extract the local motion characteristics of an image. However, the individual local motion signals encoded at this first stage are often inherently ambiguous because of the restricted spatial extent of the receptive fields of first-order neurons (the aperture problem; see Adelson & Movshon, 1982.). This problem can be resolved at a second stage that combines the locally measured signals over space and time to form a globally coherent motion percept. This second level of analysis is believed to take place in higher-order visual cortical areas such as the middle temporal (MT) area in primates (Movshon *et al.*, 1985; Rodman & Albright, 1989) and the anterior ectosylvian visual (AEV) cortex in cats (Scannell *et al.*, 1996).

Our laboratory has recently reported that neurons in the main extrageniculate structure of the visual thalamus, the lateral posterior-pulvinar (LP-pulvinar) complex, can signal the veridical direction of motion of a plaid pattern (Merabet *et al.*, 1998), thereby indicating that these

neurons can integrate two ambiguous local motion signals into a coherent moving percept. In addition, we demonstrated that these cells are functionally linked to the AEV cortex, which is the only cortical area in cats known to carry out such integrative neuronal operations (Scannell *et al.*, 1996). These findings support the hypothesis that the thalamus is involved in higher order functions that were, until recently, only associated with cortical areas beyond the primary visual cortex. The finding that LP-pulvinar cells can perform higher-order motion integration is thus of fundamental importance in the renewed efforts of several laboratories to assess the contribution of the thalamus to higher level functions using theoretical and experimental means, (Mumford, 1991; Miller, 1996; Sherman & Guillery, 1996). To further examine the role of thalamic nuclei in complex sensory processing, we have investigated whether or not LP-pulvinar neurons can signal the global displacement of a random dot kinematogram wherein comprising elements that do not provide any local coherent motion cues. The coding of the direction of motion of such pattern by LP-pulvinar neurons would indicate that their receptive fields could perform the higher-level spatio-temporal integration necessary to detect the global displacement of objects in a visual scene.

METHODS

General procedures. Cats were pre-anaesthetized with acepromazine (1 mg/kg body weight) and atropine (0.1 mg/kg). General anesthesia was carried out using a gaseous mixture of halothane (1-3%) and N_2O/O_2 (50/50%). Animals were treated in accordance with the guidelines of the Canadian Council for the Protection of Animals. All surgical wounds and pressure points were infused by a local anaesthetic (Lidocaine hydrochloride 2%). Heart rate and O_2 blood saturation were constantly monitored with an oxymeter (Nonin). A cannulation of the right cephalic vein and a tracheotomy were performed. Deep tendon reflexes were checked to ensure a satisfactory level of anesthesia during the surgery. The cat was then placed in a stereotaxic frame and was paralyzed by intravenous injection of gallamine triethiode (10 mg/kg/hr) and artificially ventilated (N_2O/O_2: 70/30% plus halothane 0.5-1%). Core temperature, electrocardiogram, and electroencephalogram were continuously monitored. Pupils were dilated with atropine and nictitating membranes were retracted with local application of phenylephrine hydrochloride (2.5%). The eyes were protected using contact lenses of appropriate refractive power. A craniotomy was done over the LP-pulvinar complex and the dura was retracted. The exposed cortex was covered with warm agar on which melted wax was applied to create a sealed chamber.

Recordings and visual stimulation. Varnished tungsten microelectrodes were used to record single-unit activity in LP-pulvinar cells. The electrodes were placed after the mapping of the visual field represented in the lateral geniculate nucleus (at two or three distinct coordinates) to verify the precision of stereotaxic adjustments. Neuronal activity was amplified, displayed on an oscilloscope, and played through an audio monitor. A window discriminator was used to isolate single units from the overall signal and waveforms of the action potentials were routinely examined. Digital signals were then fed to an acquisition software (spike2, CED, Cambridge UK) via an analogue digital interface (CED 1401 plus). The response for each stimulus condition was recorded as peristimulus time (PSTH) and interspike intervals (ISIs) histograms (binwidth of 10 ms and 1 ms, respectively) and was saved for further statistical analysis.

Visual stimuli were generated by a Macintosh G3 computer and were back-projected by a LCD projector (InFocus Systems, frame rate of 67 Hz) on a screen subtending 80° x 107° of visual angle placed 57 cm in front of the animal. The screen (Da-Lite) is made of a precise optical coating applied to an acrylic substrate (Da-Plex) permitting a display of high optical quality and a uniform diffusion of the light projected onto it. Receptive fields were first characterized by presenting drifting sinusoidal gratings. Then, random dot kinematograms (RDKs) consisting of white

Fig. 1 near here

dots (100% contrast) on a black background were used to study global motion processing. Two stimuli were used to differentially emphasize global motion mechanisms. For convenience, these will be referred to as simple and complex RDKs (Figure 1). The simple RDK (panel A) was essentially a sequence of *phi* motions that include motion energy and only required minimal simultaneous motion integration over an area of the visual field. In that configuration, each dot follows a straight and continuous path. The dot lifetime was equal to that of presentation time (no repositioning), and the display was a rigidly translating random dot field with no noise. For complex RDKs (panel B), the dots had a lifetime of two-frames, that is, they moved only once before being randomly repositioned, i.e., being displaced in another spatial location. Over a temporal sequence of a given set of displacements, 100% of the dots contributed to the global motion sequence. Each dot had an equal random probability of beginning at the first or second frame of their motion sequence. In that stimulus, half of the dots were displaced in the motion direction while the remaining half were repositioned randomly at a time (Figure 1). In other words, the signal and noise frames have been segmented by half on any given frame presentation so that when half of the dots give the motion signals the remaining ones repositioned themselves (the reverse being observed in the next sequence). This configuration is similar to the "*Combined* condition" described by Williams

& Sekuler (1984). In the complex RDK, there is never more than a single *phi* motion jump before repositioning. Consequently, there must be spatial and temporal integration of the dots displacement over an extended area of the visual field in order to signal the veridical direction of the pattern. Computing the following index compares response strength to both stimuli: mean response to complex RDKs at optimal direction (MRC)/mean response to simple RDKs at optimal direction (MRS). A MRC/MRS value below 1 would indicate that responses to simple RDKs are more robust than those to complex RDKs.

Varying the spatial (D) and temporal (T) intervals at which the dots were plotted allowed for the control of the perceived velocity of the motion stimulus. The maximum displacement within which a cell still preferred a direction of motion of the pattern (D_{max}) was also determined for a subset of neurons. The dots diameter was varied between 0.1 and 1° of visual angle, and in most cases, given the large size of LP-pulvinar receptive fields, the optimal responses were obtained for 1° dots. The presentation time was 4 seconds for both types of motion. The interframe interval was always equal to the frame duration. Stimuli were presented for at least 4 complete trials consisting of 12 interleaved directions of motion in 30° increments. For a subset of cells, responses to drifting plaids were studied. Plaids were generated by a frame-interleaved method and were composed of two superimposed sine-wave gratings differing in orientation

(120°) but of identical spatial frequency, temporal frequency and contrast. Responses to plaids were classified as pattern motion (PM) or component motion (CM) selective by calculating partial correlations using the following formula: $R_p=(r_p-r_cr_{pc})/[(1-r_c^2)(1-r_{pc}^2)]^{½}$ (Movshon *et al.* 1985, corrected). 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.

For each cell, a direction selectivity (DI) index was calculated using the formula DI= 1- N/P, where N is the mean response in the non-preferred direction minus spontaneous activity, and P is the mean response in the preferred direction minus spontaneous activity. Cells with a DI greater than 0.5 were considered as selective to the direction of the stimulus motion.

Electrolytic lesions were made along each recording track. At the end of each experiment, the animal was killed by an overdose of sodium pentobarbital (Euthanil, 120mg/Kg). The brain was removed from the skull and fixed in a solution of buffered formalin (10%). After five days, 40-100

μm serial sections of the brain were cut in the frontal plane. Every third section was stained to reveal acethylcholinesterase (AChE) activity (Koelle & Fridenwald, 1949) in order to distinguish the three major zones in the LP-pulvinar, i.e., the medial and lateral zones of the LP (LPm and LPl), and the pulvinar (Graybiel & Berson, 1980). The remaining sections were stained with cresyl violet and were matched with the AChE sections to locate the lesions and determine the position of the cells recorded in the LP-pulvinar.

RESULTS

General observations.

A total of 134 visual cells were recorded in the LP-pulvinar complex. The general properties of the cells were typical of those previously reported (Chalupa et al., 1983, 1989; Casanova et al., 1989). The majority of cells (89.5%) was orientation selective (mean bandwidth ± SD: 36.8 ± 2.32°) and preferred a given direction of motion of drifting gratings (67.9%). The mean optimal spatial frequency was 0.14 ± 0.01 c/deg and the majority of cells (76%) exhibited band pass tuning functions (mean ± SD: 2.19 ± 0.12 octaves), and the remaining cells were low pass.

Global versus local motion sensitivity.

Direction tuning functions. Out of the 134 neurons, 89 were tested for their sensitivity to simple and complex RDKs. The remaining 45 units were lost before the completion of the tests or their visual discharges were too variable to be analyzed with confidence.

Eighty-eight percent (79 out of 89) of the LP-pulvinar cells responded to the motion of simple RDKs, and a subset of those (54 of 79, 68%) was selective to the direction of motion. Almost two-third of these direction selective units (33 out of 54) were also direction selective for complex RDKs. Figure 2 shows the response profiles of a cell to both stimuli. The unit was relatively finely tuned for the simple RDK direction (bandwidth of 41.1°) but responded to a broader range of directions (bandwidth of 96.3°) when stimulated with the complex RDK. In addition, the responses evoked by the simple RDK were more robust and sustained than those observed with the complex RDK (see below). Additional examples of direction tuning curves are shown in figure 3. Panel A exemplifies the fact that, for most units, responses to simple RDKs were more robust than those computed from complex RDKs. In panels B and C, for both stimuli, the cells responded optimally with comparable strength when the pattern was drifted at directions between 60° and 90°. Panel D illustrates the few cases in which the responses to the complex RDK were more robust than those computed from the simple RDK. In all these

Figs. 2 & 3 near here

examples, direction selectivity was preserved whether simple or complex RDKs were presented. For comparison purposes, we studied the responses of a subset of 14 neurons in area 17. All 8 of the simple RDK direction-selective neurons either did not respond to complex RDKs or, as shown in panel F, responded to all directions of motion.

Overall, the mean bandwidth (expressed as the half-width of the tuning curve at half-height) for direction computed from complex RDKs was 75.5 ± 6.9°, a value that is significantly greater than that computed from simple RDKs (57.44 ± 4.7°; t-test, t = 2.14, P = 0.035) for these cells. The direction bandwidth distribution of cells responding to both stimuli is shown in figure 4.

Fig. 4 near here

The 18 remaining units only signaled the direction of simple RDK defined patterns (see panel D). Their mean direction tuning was 47.4 ± 5.3°, a value not significantly different from that computed from simple RDKs for neurons responding to both stimuli (t-test, t = 1.31, P = 0.19).

Response profile and strength. In general, mean optimal firing rates were greater for simple RDKs than those for complex RDKs (see Figure 2A-C and Figure 3A). The distribution of the strength index (see Methods) is shown in panel C of Figure 2. Clearly most MRC/MRS values are distributed below 1, indicating that LP-pulvinar cells were generally less responsive to complex RDKs (mean MRC/MRS of 0.65 ± 0.06).

Examination of the PSTHs seemed to reveal that, in general, discharges to simple RDKs were more sustained than those evoked by complex RDKs. In the latter case, it was not unusual to observe the presence of burst discharges separated by silent periods. To verify these qualitative observations, we examined the distribution of ISIs computed from optimal responses to both stimuli (see insets in Figure 5). In order to confirm the above postulate, one should expect to find longer ISIs in the responses to complex RDKs than in the discharges evoked by simple RDKs (Casanova et al, 1995; Merabet et al., 2000). Figure 5 shows the ratio distribution of the number of ISIs between 100 and 400 ms divided by the number of ISIs between 1 and 400 ms. For cells that responded to both stimuli (panels A and B), the distribution of the ratios is significantly different. The mean ratios are 0.09 ± 0.01 and 0.19 ± 0.02 for simple and complex RDKs (t-test, $t = -3.45$; $P < 0.001$) confirming the observation that, when compared to simple RDKs, responses to complex RDKs are less sustained. We also found that response profiles of neurons coding only the motion of simple RDKs tended to differ from the discharges of complex RDK-sensitive units to simple RDKs (compare panels A and C; means of 0.09 ± 0.01 and 0.16 ± 0.03, respectively, t-test, $t = 2.26$; $P = 0.027$).

Fig. 5 near here

Therefore, the LP-pulvinar complex appears to contain two populations of direction-selective neurons. The first one can signal the

direction of simple and complex motion-defined RDKs, and the second can only signal the direction of simple RDKs. We investigated whether the two subsets of cells differ with respect to their general receptive field organization. We found that the mean receptive field size of complex RDKs selective cells (mean 721 ± 61 deg²) was significantly larger ($t = 3.07$, $p = 0.003$) than the mean of units that only responded to the simple condition (mean: 431 ± 47 deg²). The distribution of receptive field sizes of the two cell groups is shown in Figure 6A. We also observed differences ($t = 2.52$, $P = 0.015$) for the receptive field location of the two types of cells (panel B of Figure 6, mean eccentricity of 23.4° ± 3.1 and 18.5° ± 2.3 for global and local motion selective cells, respectively). For both groups, we did not find any relationship between receptive field size and eccentricity. This may be related to the fact that most receptive fields studied were large and were located more centrally than peripherally. Finally, these two groups of neurons could not be distinguished on the basis of their preference and selectivity for orientation, nor for spatial and temporal frequencies. Of note is the fact that cells responding to complex RDKs tended to exhibit lower preferred spatial frequencies than neurons that only responded to simple RDKs ($t = -1.75$, $P = 0.08$).

Fig. 6 near here

Influence of stimulus size. We investigated whether LP-pulvinar cells can discriminate the direction of complex RDKs when the latter was restricted within the boundaries of their receptive fields. It was noted that units with large receptive fields (9 cells, mean area of 779 ± 151 deg²) retained their ability to discriminate the global motion direction. A representative example is shown in Figure 7. Panel A illustrates the responses of a LP-pulvinar neuron when most of the cat's visual field (full screen stimulus) was stimulated with simple and complex RDKs. For both stimuli, the unit exhibited a clear preference for a specific range of motion (DIs), but the response to complex RDKs was more robust than that of simple RDKs. Panel B shows the response of the same cell while the patterns were confined to its receptive field. Despite a small difference in the preferred direction (30°, which correspond to the increment used to study direction selectivity), the response strength and selectivity (DI) was comparable to the full-screen condition. The other 5 neurons had smaller receptive fields (mean: 424 ± 88 deg²) and when the pattern was restricted to the receptive field, these units could still be driven by a complex RDK but the response profile was altered because their direction selectivity was reduced. Direction selectivity for simple RDKs was unaffected.

Fig. 7 near here

Influence of spatial and temporal intervals. The spatial interval between partner dots (D) yielding the optimal cell responses for complex RDKs was

determined for 20 cells. Preferred spatial intervals were mainly distributed between 0.7° and 6.51° of visual angle and the mean value was 2.82° ± 0.33°. The optimal spatial interval increased with receptive field size ($r = 0.53$, $P = 0.014$). The largest spatial interval (D_{max}) for which LP-pulvinar cells could code the direction of complex RDKs (the temporal interval being constant) ranged between 2.18 and 10.66° (mean D_{max} of 6.63° ± 1.04°). Examples of the responses of two neurons as a function of D are presented in Figure 8. These two units differed in their receptive field size (see insets). Panel A shows a cell that exhibited maximal directional preference for a D of 3°. For D values greater than 3°, direction selectivity was greatly reduced, and overall, responses became less robust for the largest D value tested. Panel B depicts the responses of another LP-pulvinar cell with a smaller receptive field than in Panel A. Direction selectivity was roughly constant for low D values but was almost abolished for a D of 2.8°. There appears to be a close relationship between receptive field size and optimal D values (panel C), such that large LP-pulvinar receptive fields can code the direction of motion of global RDKs whose elements are separated by large distances.

Fig. 8 near here

We also examined the responses of 11 cells when varying the temporal interval (T) between the appearances of given partner dots, i.e. the duration of the single *phi* motion jump (computed between the extinction of the dot at its initial spatial position and the appearance of the

dot at its new spatial location). For all units, optimal responses were obtained for short temporal intervals (around 16 ms). A representative example is shown in panel D of Figure 8, where the response of a cell to both directions of motion is presented as a function of increasing T values. Direction selectivity and response strength were markedly reduced at T values greater than 32 ms.

Relationship with pattern-motion selective units. Given that some neurons in the LP-pulvinar complex can signal the veridical direction of drifting plaid patterns, we have investigated for a subset of 21 cells, whether global and pattern-motion selectivity were coupled. Results are presented in Figure 9. Most complex RDKs selective units (8 out of 14) were "unclassified direction selective" cells for plaids, i.e. they could not be categorized, on the basis of the calculation of partial correlation coefficients (see Methods), in either the pattern- or component motion categories. Five units were component motion selective and one was found to be pattern motion selective. Similarly, the 7 simple RDKs sensitive units tested were either component motion selective, unclassified direction selective, and, in one case, pattern motion selective. These data suggest that there is no strong relationship between RDK-defined global and plaid-defined pattern-motion selectivity.

Fig. 9 near here

Cell localization. The position of 28 of 33 complex RDK sensitive cells and 15 of 18 simple RDK units was assessed. In both cases, most of the units were located in the LPl or striate-recipient zone. Twenty-one complex RDK sensitive units were located in the LPl and the remaining 7 cells were located in the LPm. We found in each subdivision a pattern motion selective neuron. Eleven simple RDK selective cells were located in the LPl, and 4 were found in the LPm.

DISCUSSION

The results of this study indicate that a subpopulation of direction selective cells in the cat's LP-pulvinar complex can signal the true direction of a complex stimulus that requires the integration of local motion signals over space and time. These neurons differ from those only responding to simple RDKs by their receptive field size and eccentricity, and by their response profile. This finding represents the first evidence that global motion processing takes place in subcortical structures, and provides further support for the notion that LP-pulvinar neurons are involved in higher-order visual processing (Merabet et al., 1998) which had only been attributed to cortical areas beyond the primary visual cortex in previous conceptualizations of motion processing (Movshon et al.,

1985; Newsome & Paré, 1988; Nowlan & Sejnowski, 1995; Scannell et al., 1996).

In agreement with the notion that a large visual area of integration is necessary for global motion processing (Downing & Movshon, 1989), it was observed that the spatial extent of the receptive field of complex RDKs selective cells was significantly greater than that of simple RDKs selective units. In addition, our data revealed that the area of the large LP-pulvinar receptive fields is sufficient to integrate local motion cues in a coherent and global direction of motion. This capacity to adequately signal the global motion direction within the receptive field was less pronounced for receptive fields of a smaller size. Nonetheless, these same neurons were able to code the global motion direction of a full-screen pattern. It is therefore likely that, for small LP-pulvinar receptive fields, the analysis of global motion requires the recruitment of neighboring cells to integrate motion information over an area larger than that of the classical receptive field. Of fundamental importance is the fact that LP-pulvinar neurons can code the displacement of elements in complex RDKs for large distances. Indeed, the D_{max} was as high as 8°. This long-range spatial process occurred for short temporal intervals between the appearance of the two elements, and further, was positively correlated with receptive field size. These findings are comparable to those obtained in area MT of primates. By systematically varying the distance and time interval between

successive stimuli in apparent motion displays, Mikami et al. (1986) found that MT neurons can detect directional differences over spatial intervals that were roughly three times larger than those perceived by neurons in the primary visual cortex, while the temporal limits were similar for both areas. They reported, as we did, that the maximum spatial interval was correlated with receptive field size. The finding that MT lesions reduced the monkey's ability to discriminate global motion direction for large spatial intervals (Newsome & Paré, 1988) further supported the Mikami et al. data.

Our data suggest that there is no strong correspondence between PM and complex RDK selectivity nor between CM and simple RDK selectivity. Figure 9 shows indeed that complex and simple RDK selective cells were found in the three statistically defined areas. In other words, neurons sensitive to complex RDKs were not systematically pattern-selective when tested with drifting plaids[1]. A similar observation can be made for simple RDK selective neurons and CM selectivity. Since most successful recordings were made in the LPI despite many attempts to reach the LPm, where lie the majority of PM selective neurons (Merabet et al., 1998), it precludes us from making definite conclusions regarding the sensitivity of a given cell to plaids and RDKs, particularly with regards to

PM selectivity. Nevertheless, the above observations suggests that the nature of the integration underlying responses to the two kinds of patterns may differ, despite the fact that non-linear mechanisms are involved in both cases (Adelson & Movshon, 1982; Adelson & Bergen, 1985; Baker & Hess, 1998). The simple RDKs condition requires that contiguous receptive fields correlate their activation in respect to one another, which can be represented by simple motion mechanisms such as Reichardt detectors or similar units (Adelson & Bergen, 1985). On the other hand, simultaneous integration of single event *phi* motion over an area of the visual field (as was the case for complex RDKs), requires integration of higher order directional motion (Williams & Sekuler, 1984; Watamaniuk *et al.* 1989). This inevitably involves another stage of analysis that integrates activation of receptive fields that are distant from one another (long range processes). It is not surprising, therefore, that the receptive field sizes of cells that responded to complex motion were larger than the receptive field sizes of cells that responded primarily to simple motion cues. Although plaid motion also involves a non-linear process like the complex motion task used here, it does not necessarily require long-range interactions. Rather, the process can be a second, non-Fourier (or rectification) stage,

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[1] One has to be cautious here since this classification is based on statistical evaluation of plaid responses and cells considered as unclassified may well be sensitive, to some extent, to pattern motion.

the likes of which have been proposed by Wilson et al., (1992). Thus, we propose that different cells are responsive to plaids than those sensitive to complex RDKs.

Functional considerations. This study provides additional evidence that the LP-pulvinar complex is part of neural networks involved in higher-order motion processing. Others and we previously suggested that cortico-thalamo-cortical loops involving the LP-pulvinar may be used, in part, to refine computations at cortical levels (Mumford, 1991; Miller, 1996; Merabet *et al.*, 1998). While little is known about the neural basis subtending global motion processing in the cat, there is some indication that the lateral suprasylvian (LS) cortex contributes to the latter. Rudolph & Pasternak (1996) reported that the destruction of the LS cortex impair the capacity of the cat to discriminate the direction of global RDKs. In support of that, we recently found that a subset of direction-selective neurons in the posteromedial part of the LS (PMLS) cortex, but not in the striate cortex (see Figure 3F), can code the direction of complex RDKs identical to that used in the present study (preliminary data, not shown). Therefore, the LP-pulvinar neurons are likely to process global motion in close relationship with PMLS cortex. Interestingly this putative loop would be distinct from that described on the basis on plaid pattern selectivity. Pattern selective cells were mainly located in the LPm (Merabet *et al.*, 1998), which is reciprocally linked to the AEV cortex (Mucke *et al.*, 1982),

which is the only known cortical area in cats that contains such neurons. Complex RDKs sensitive units were found in the LPl that establish connections with the PMLS cortex (Abramson & Chalupa, 1985). The fact that complex RDKs motion sensitive units are not systematically clearly pattern motion selective may indicate that the LP-pulvinar is not part of a circuit processing complex motion in general, but is rather directly involved in specific calculations carried out by different cortical modules subsuming different aspects of motion processing.

Acknowledgments. This work was supported by a CIHR grant (# MT-14825) to C.C. We thank A. Herbert and I. Ohzawa for commenting on a draft of the manuscript and F. Huppé-Gourgues and M. Villeneuve for providing help in some experiments. We also thank J.A. Movshon for providing the analysis software for the classification of plaid responses. FRSQ provided most of C.C.'s salary. (Chercheur boursier program), CIHR provided J.F.'s salary (investigator program), D.D. was supported in part by an FCAR fellowship. Part of the visual software development (complex RDKs) was financially supported by a grant from the Réseau FRSQ de recherche en santé de la vision to C.C. and J.F.

Figure legends.

Figure 1. Schematic of the simple and complex RDKs. Filled lines represent motion signals while broken arrows illustrate the random repositioning the corresponding dot. Each rectangle equals one stimulus frame.

Figure 2. Responses of an LP-pulvinar neuron to simple (trace a) and complex (trace b) RDKs shown as PSTHs (panel A) and corresponding tuning curves (panels B and C, respectively. S.E.M bars are too small to be visible). Note that the response to the complex RDK is less robust and less sustained than that of the simple RDK. Panel D shows the distribution of the strength index for all complex RDK selective cells. In panel B, data points within the shaded region represent cell discharges below spontaneous activity levels. Vertical and horizontal scales in panel A are 2 spikes/bin and 1 sec, respectively. SA: spontaneous activity.

Figure 3. Polar graphs illustrating the responses of LP-pulvinar neurons (panels A-E) and of an area 17 cell (panel F) to simple (empty symbols) and complex (filled symbols) RDKs drifted in 12 directions of motion. Panels A–D are examples of complex RDKs sensitive neurons. Panel E presents a cell that only responded to simple RDKs. Panel F shows the

RDK responses of a complex cell in area 17. Data points within the shaded regions represent cell discharges below spontaneous activity levels. Elements size was 1° except in panel B and panel F where it was 0.3°. The bar in each data points represents S.E.M.

Figure 4. Distribution of RDK direction bandwidths computed from tuning curves of complex RDK selective cells.

Figure 5. Response profile to RDKs illustrated by the distribution of the ISIs $_{100\text{-}400}/_{1\text{-}400}$. Complex RDK selective neurons : Panels A and B show the ratios computed from responses to complex and simple RDKs, respectively. Simple RDK selective neurons (panel C): Ratios were calculated from responses to simple RDKs. Insets depict the mean number of spikes (and S.E.M.) for each ISI up to 400 ms (1 ms resolution). Two-way sample Kolmogorov-Smirnov indicates that the distributions of ISIs in panels A-B are significantly different. This observation stands when comparing distributions in panels A-C.

Figure 6. Distribution of receptive field size (panel A) and eccentricity (panel B) for simple and complex RDK selective units.

Figure 7. Effects of restricting the patterns' dimension to receptive field size. Panel A shows the responses to full-screen simple and complex RDKs and panel B illustrates the discharges of the same cell when both stimuli only covered the receptive field. One may note that the LP-pulvinar neuron can signaled the true direction of motion of complex RDKs in both conditions. Conventions are as in figure 3.

Figure 8. Panels A and B : Influence of spatial interval between partner dots on response strength and direction selectivity. The large LP-pulvinar receptive field in panel A could signal the motion of complex RDKs whose comprising elements were separated by large spatial distances. The smaller receptive field shown in panel B coded much shorter displacements. Insets illustrate receptive field location and size (765 and 195 deg^2 in panels A and B, respectively). Panel C: Correlation between receptive field size and preferred spatial interval of all LP-pulvinar cells ($r = 0.53$, $p = 0.014$). Panel D : Influence of temporal interval between partner dots. The direction selectivity and discharge rate of the LP-pulvinar neuron to the complex RDK were strongly reduced for intervals greater than 16 ms. In panels A-C, the dashed lines represents spontaneous activity levels. Numbers on top of bar graphs represent direction index values. Error bars represent S.E.M.

Figure 9. Scatter plot in which the partial correlation for pattern and component selectivity of simple (open circles) and complex (filled circles) RDK selective neurons are plotted against each other. 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.

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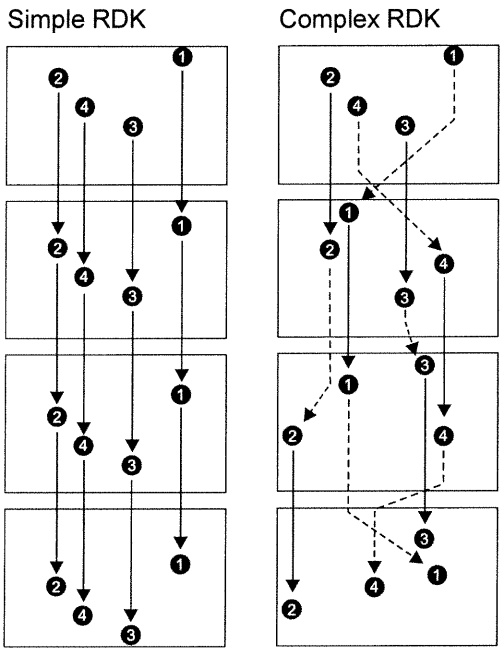

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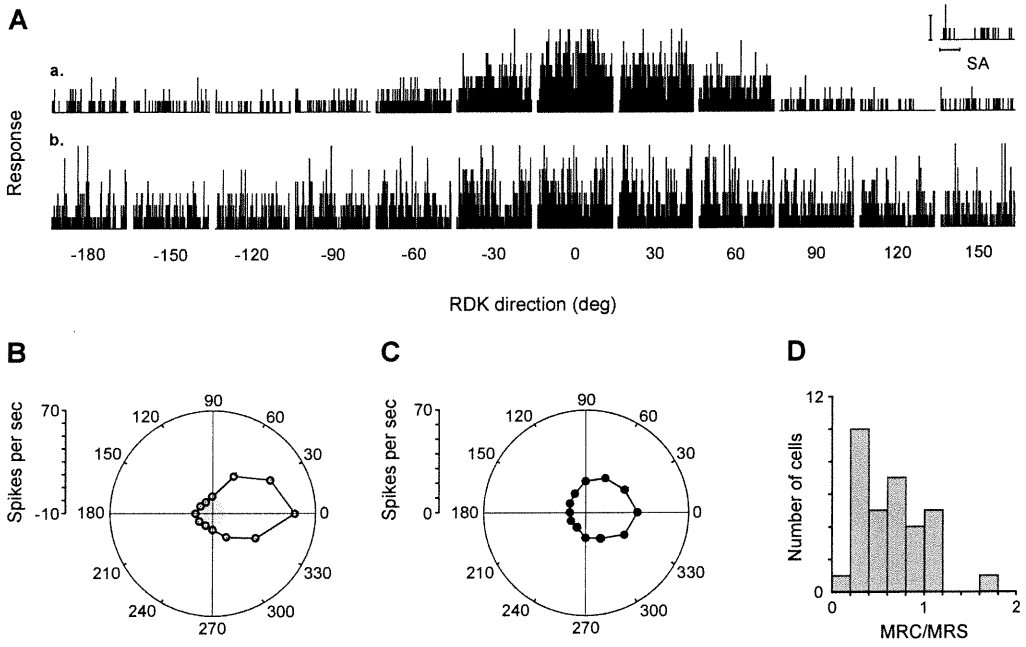

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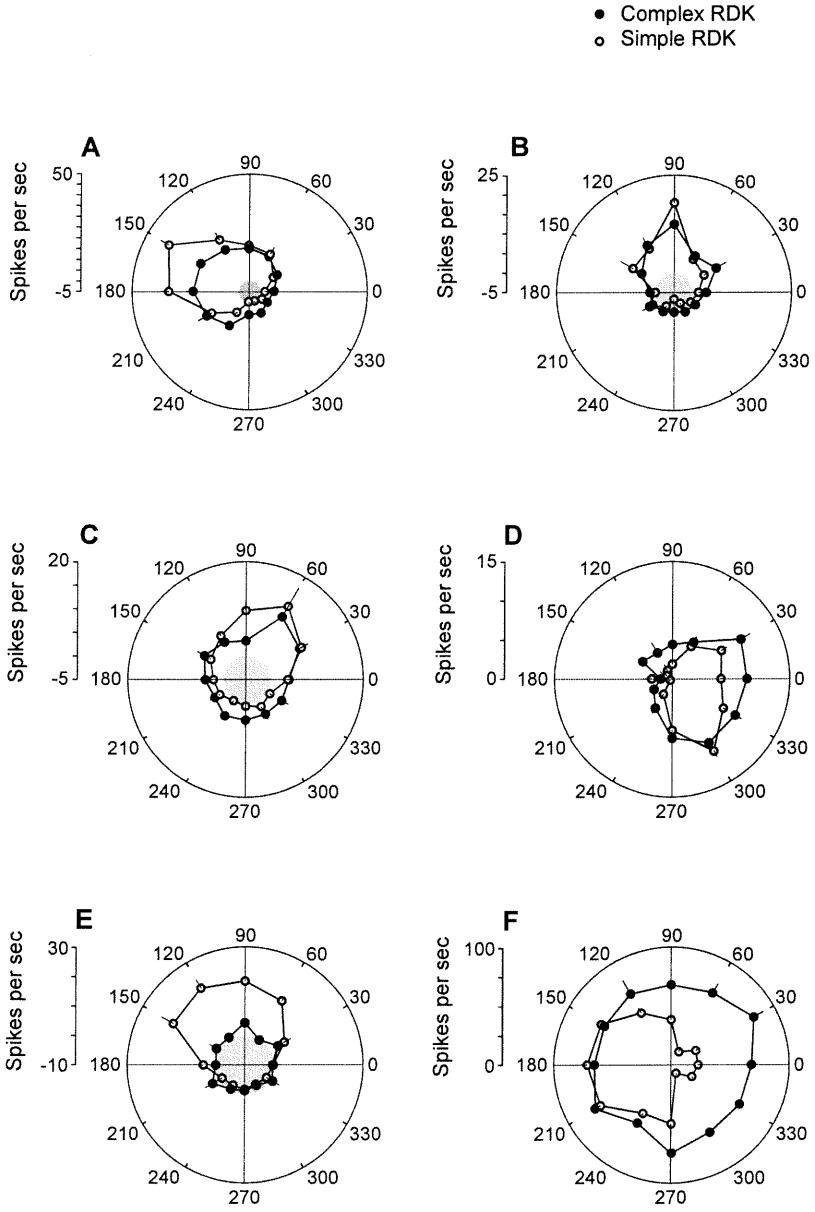

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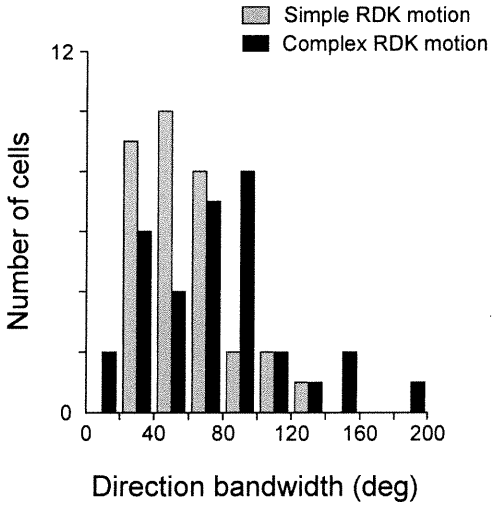

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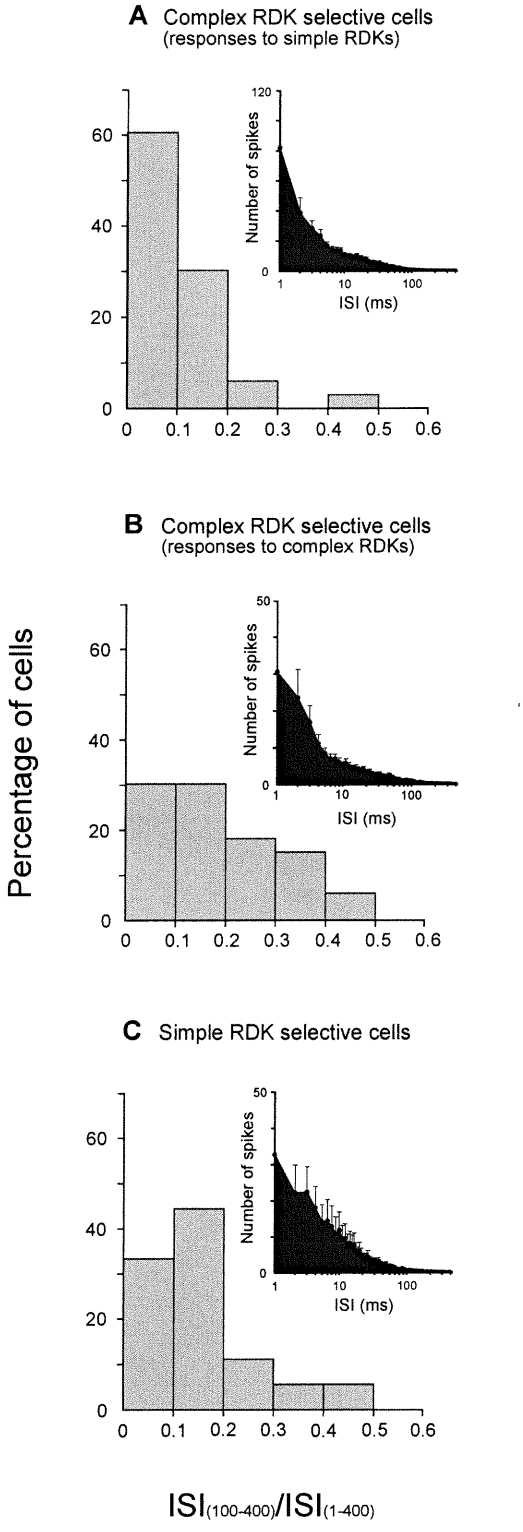

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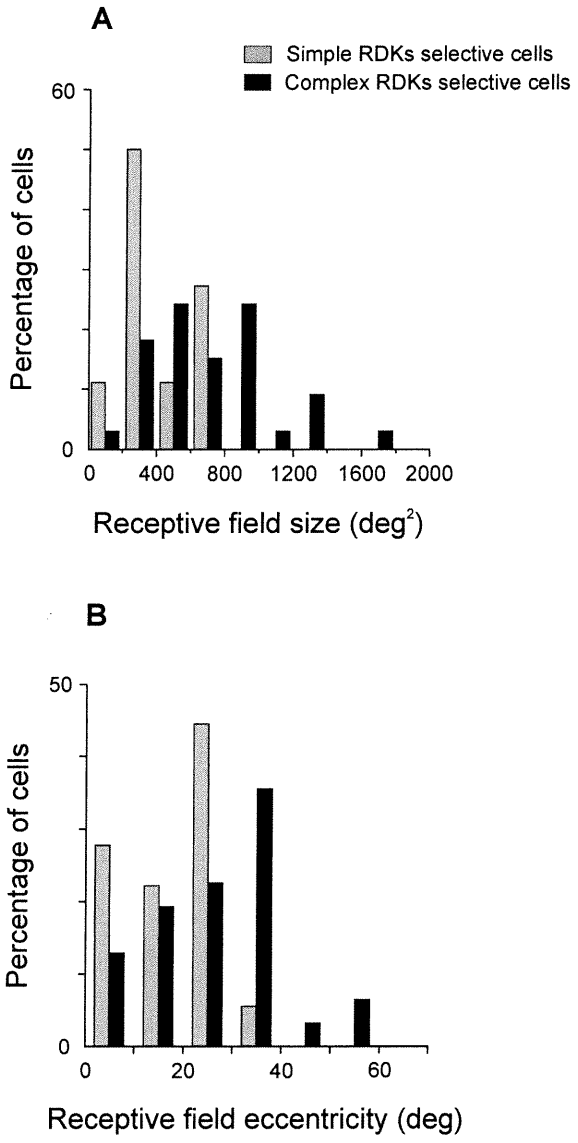

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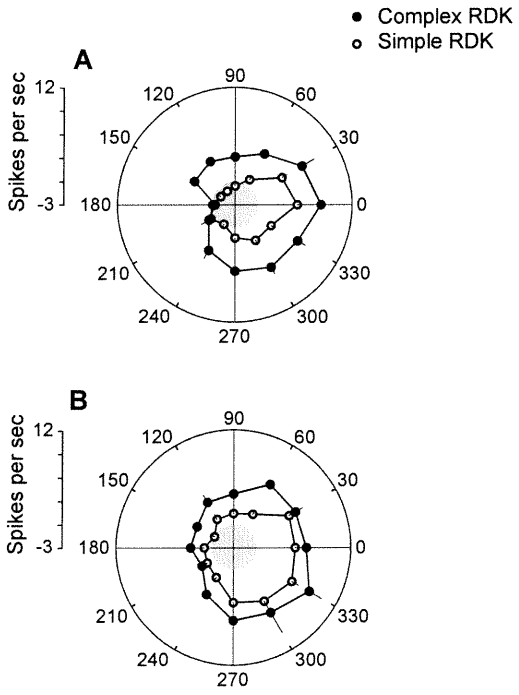

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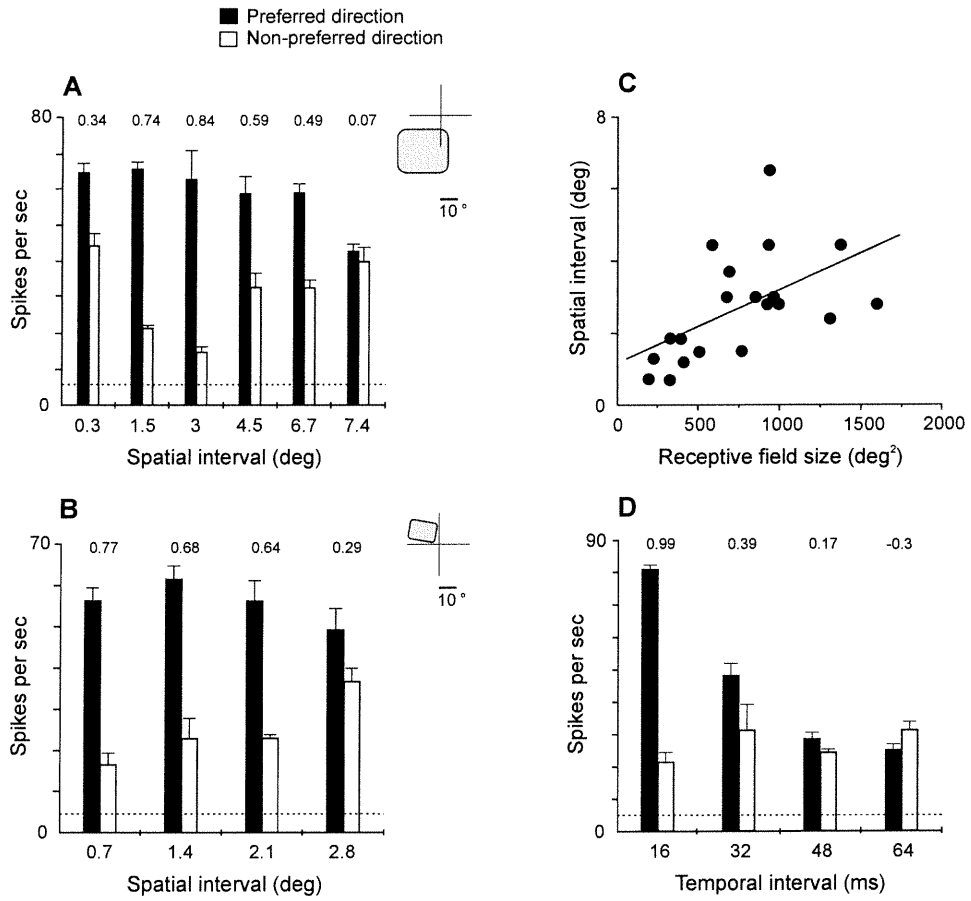

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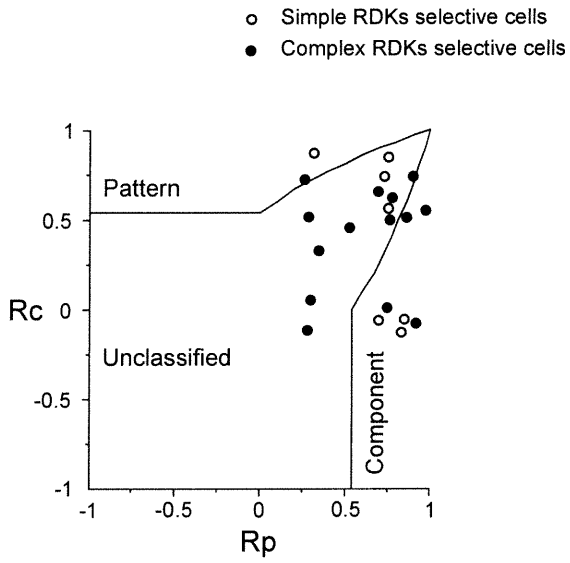

Figure 9. Dumbrava *et al.*

4. Discussion

4.1. Summary of findings

4.1.1. Motion integration in extrageniculate thalamus: Response to global motion pattern.

4.1.1.1. Global versus local motion sensitivity

In the first part of this study, we investigated the role of LP-pulvinar neurons in global motion detection of dynamic random dot stimuli. Simple and complex random dot kinematograms (simple-RDKs and complex-RDKs) were used to study global motion processing. The results from this study have shown that a subset of visual cells can signal the true direction of complex-RDKs, suggesting that global information are processed in LP-pulvinar complex. Thus, this thalamic region can integrate different motion signals moving in various directions, giving a coherent and global motion direction. Another subset of cells were selective only to the direction of simple-RDKs. Therefore, the LP-pulvinar complex appears to contain two populations of direction selective cells. The first one can signal the direction of simple and complex motion-defined RDKs, and the second one can only signal the direction of simple

random dots motion. These two populations of cells differ with respect to their response strength and profile. Examination of the PSTHs seemed to reveal a distinction between random dots motion sensitivity of simple and complex-RDK selective cells i.e., response profiles were less sustained for simple RDK-selective neurons than those for complex-RDK selective cells, suggesting that simple-RDK selective cells fire in phase relationship with dot patterns (Gulyas et al., 1987; Snowden et al., 1991). Previous hypotheses had proposed that in primary visual cortex averaging of many phase invariant simple cells could produce the phase invariant complex cell (Holub and Morton-Gibson, 1981; De Valois et al., 1982). On the basis of this suggestion we raise the hypothesis that inputs from simple RDKs-selective cells converge to complex RDKs-selective cells. Such a hierarchical process from phase-dependent to phase-invariant responses argued to be of great importance in motion processing (Borst and Egelhaaf, 1989) and is consistent (Snowden et al., 1991) with several recent models of human motion processing (Adelson and Bergen, 1985). Discharges to simple RDKs stimulus were also found take more sustained than those evoked by complex RDKs, suggesting different visual computation of these two kind of random dots stimuli.

In primates, neurophysiological, psychophysical and behavioral studies associate this type of complex motion integration with cortical areas beyond the primary visual cortex like MT and MST (Newsome and

Paré, 1988; Celebrini and Newsome, 1994; Rudolph and Pasternak, 1999; Britten et al., 1993).

In agreement with the notion that a large visual area of integration is necessary for global motion processing (Downing and Movshon, 1989) it was observed that the spatial extent of the receptive field of complex RDKs selective cells was significantly greater than that of simple RDKs selective units.

The fact that simple- and complex-RDKs selective cells exist at the thalamic level, suggests that structures from extrageniculate pathway are implicated in local and global information processing. While little is known about the neural basis of subtending global motion processing in the cat, there is some indication that the LS cortex contributes to the later. In agreement with previous studies (Rudolph and Pasternak, 1996) and with our hypothesis, we found complex RDKs selective units only in PMLS cortex and not in primary visual areas (Villeneuve et al., 2001).

These findings represent the first evidence that global motion processing can take place in subcortical structures, and provides further support for the notion that LP-pulvinar complex could be involved in higher-order visual processing (Merabet et al., 1998) which had previously only been attributed to cortical areas beyond the primary visual cortex in previous models of motion processing (Movshon et al., 1985; Newsome and Paré, 1988; Nowlan and Sejnovski, 1995; Scannell et al., 1996).

4.1.1.2. Influence of stimulus size

We investigated whether LP-pulvinar cells can discriminate the direction of complex RDKs when the latter was restricted within boundaries of their receptive fields. The results revealed that the area of the large LP-pulvinar receptive fields is sufficient to integrate local motion cues in a coherent global direction of motion. This capacity to adequately signal the global motion direction within the receptive field was less pronounced for receptive fields of a smaller size. Nonetheless, these same neurons were able to code the global motion direction of a full-screen pattern. It is therefore likely that, for small LP-pulvinar receptive fields, the analysis of global motion requires the recruitment of neighboring cells to integrate motion information over an area larger than that of the classical receptive field.

4.1.1.3. Influence of spatial and temporal intervals

In general, these results show that LP-pulvinar neurons can code the displacement of elements in complex RDKs for large distances. Indeed, Dmax was as high as 8 ^{o}. This long-range process occurred for

short temporal intervals between the appearances of the two elements, and further, was positively correlated with receptive field size. These findings support the suggestion that maximum distance over which a unit can be directionally selective will depend on the size of their receptive field, with larger receptive fields having the ability to encode larger displacements (Baker and Braddick, 1982; Nakayama and Silverman, 1984). Furthermore, the present results are comparable to those obtained in area MT of primates (Mikami et al., 1986; Newsome and Paré, 1988), showing that cortical cells with large receptive fields are still direction selective over a large spatial displacement, indicating that mechanisms mediating directional sensitivity can be very fast, especially for systems having large receptive fields.

4.1.2. Two specialized mechanisms for complex motion processing in LP-pulvinar complex

Our data suggest that there is no strong correspondence between pattern-motion and complex RDK selectivity, nor between component-motion and simple RDK selectivity. The above observation suggests that the nature of the direction integration underlying processing of two kinds of patterns may differ.

Adelson and Movshon (1982) first suggested that the motion of plaids was computed by a sequential two-stage process (non-linear computation). Simultaneous integration of single *phi* motion over an area of visual field, as was the case for complex RDKs, also requires integration of higher order directional motion (Williams and Sekuler, 1984; Watamaniuk et al., 1989). This condition probably excites distant receptive fields ("long range process") that involve another stage of analysis. Therefore, non-linear mechanisms are implicated in both cases. Despite this computational observation, we have found two kinds of responses; This leads to a key question: are these two motion patterns processed by the same or by different mechanisms. Wilson et al., (1992) developed a model that incorporates parallel pathways that extract Fourier and non-Fourier[2] motion signals. These are then brought together in a final processing stage that computes the vector sum of Fourier and non-Fourier component motions (Figure 8). In the plaid stimulus the moving component gratings generate the pattern of Fourier component motion energy that is accomplished by Fourier pathway (Wilson, 1994). These signals are ultimately combined. Although plaid motion involves a non-

[2]Several mechanisms have demonstrated the existence of complex motion that is invisible to local motion detectors, and this has been termed non-Fourier (Badcock, 1989; Chubb and Sperling, 1989).

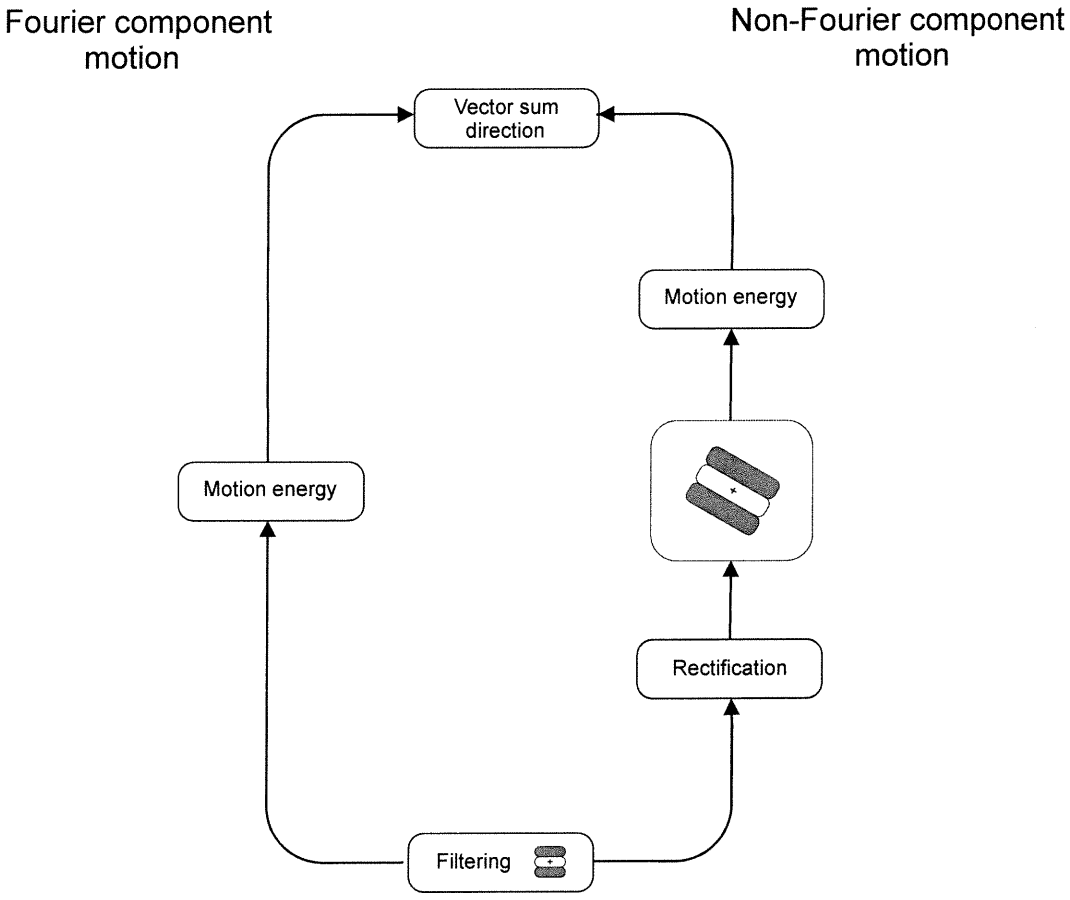

Figure 8. A neural model for two-dimensional perception (Wilson et al., 1992). Following initial oriented filtering, two parallel motion processing patways emerge. The one extract the motion energy of Fourier components (left), while the second, incorporates additional rectification and filtering stages for the extraction of non-Fourier component motion (right) (Wilson, 1994)

linear process like the complex-RDK motion, it does not necessarily require long-range interaction. Rather, the random dots motion integration can require additional rectification and second stage filtering process, the likes of which have been proposed by Wilson et al., (1992). Thus, we propose that different cells are responsive to plaids than those sensitive to complex RDKs.

4.2. Thalamo-cortical subsystems involved in visual motion processing

The concept that thalamus may be the *key to understanding the cortex* has stated at the beginning of the last century (see Creutzfeldt, 1983, Rauschecker, 1988).

This study provides evidence that LP-pulvinar complex is part of the neural networks involved in higher-order motion processing. But this concept is not a novel one. On the basis of very similar global and local organization of receptive field properties and functional connectivity, Rauschecker (1988) suggested the possible visual function of LS cortex and LP nucleus as a *LP/LS subsystem*. The hypothesis was raised about the possible implication of LP/LS subsystem in motion perception, thus refining visual information from occipital cortex to parietal areas. Thalamic neurons in LP-pulvinar complex have been shown that they could perform

visual neuronal operations, in relation with PMLS and AEV cortex (Merabet, 1998; Merabet et al., 2000). The results of this study represent an extension of this hypothesis. Furthermore, by using the same stimuli as those used in the present study, our laboratory found neurons in LS cortex (PMLS and AMLS) that show similar response to complex RDKs (Villeneuve et al., 2001; Ouellette et al., 2001). The fact that LS cortex and LP show comparable mechanisms of global motion integration suggests that these areas may be functionally linked. These findings reinforce the Rauschecker's hypothesis that the existence of cortico-thalamic subsystems goes beyond the LS cortex and LP. The fact that deactivation of AEV cortex alters pattern-selective responses in LP suggests that other subsystems (LP/AEV) could also exist (Merabet, 1998), perhaps computing the motions of the whole object. Moreover, pattern-motion selective cells were mainly located in the LPm (Merabet, 1988), which is reciprocally linked to AEV cortex (Mucke et al., 1982), a cortical area in cats that contains such neurons. Complex RDKs selective units were found in the LPl, that establish connections with LS cortex (Abramson and Chalupa, 1985). Ouellette et al., (2001) have found pattern-motion selective neurons in AMLS cortex. On the basis of these anatomical and physiological results we can now propose the hypothesis that in cat visual system, the LP-pulvinar complex may serve to process multiple aspects of visual motion that are carried out along multiple cortico-thalamic loops.

The data are sparse at present, but a speculative scheme may be suggested. The LP-pulvinar complex appears to be placed between one computational loop implicating the PMLS cortex that signals global motion and another implicating AMLS and AEV cortex that signals plaid pattern motion.

To clearly establish the role of these two subsystems, further experiments must be carried out. These investigations should explore the cortical areas such as AEV in order to confirm whether or not complex RDKs motion integration exist there. Furthermore, the effect of lesion of LS cortex on random dots motion integration in the LP-pulvinar complex should also be investigated.

4.3. The role of cortico-thalamo-cortical loops in visual motion processing

The visual system has many areas that can be distinguished on the basis of their connectivity, architectonics and receptive field organization. In a review article, Felleman and Van Essen (1991) arranged these areas in a rough hierarchy, with primary visual areas at the bottom. Van Essen (1992) suggested that the visual system must employ strategies for efficient information processing within the anatomical constraints imposed by its circuitry. What is the function of the thalamus in

these anatomo-functional circuitries? Mumford (1991) suggested that *the cortex contains multiple independent "experts" which analyze different aspects of visual scenes and that results are merely integrated in the thalamus.* On the basis of this theoretical hypothesis it was proposed that visual processing implicates a continual exchange between "bottom-up" and "top-down" processes (Mumford, 1994) and cortico-thalamic feedback may represent the neurophysiological substrate to co-ordinate computation within this system (Van Eseen, 1992). In support of this idea it was suggested that cortico-thalamo-cortical loops involving the thalamus may be used in part, to refine computations at cortical levels (Mumford, 1991; Miller, 1996; Merabet et al., 1998).

Given its anatomical disposition and its physiological response properties (particularly to complex visual stimuli), the LP-pulvinar complex is well positioned to modulate ongoing computational analyses throughout multiple levels of visual hierarchy (Merabet, 1999). Figure 9 (panel A) proposes a selection model of visual motion processing in cat incorporating the LP-pulvinar complex. In this scheme, the LP-pulvinar complex is in immediate relation with computations carried out at each cortical level. By possessing neurophysiological properties common to all

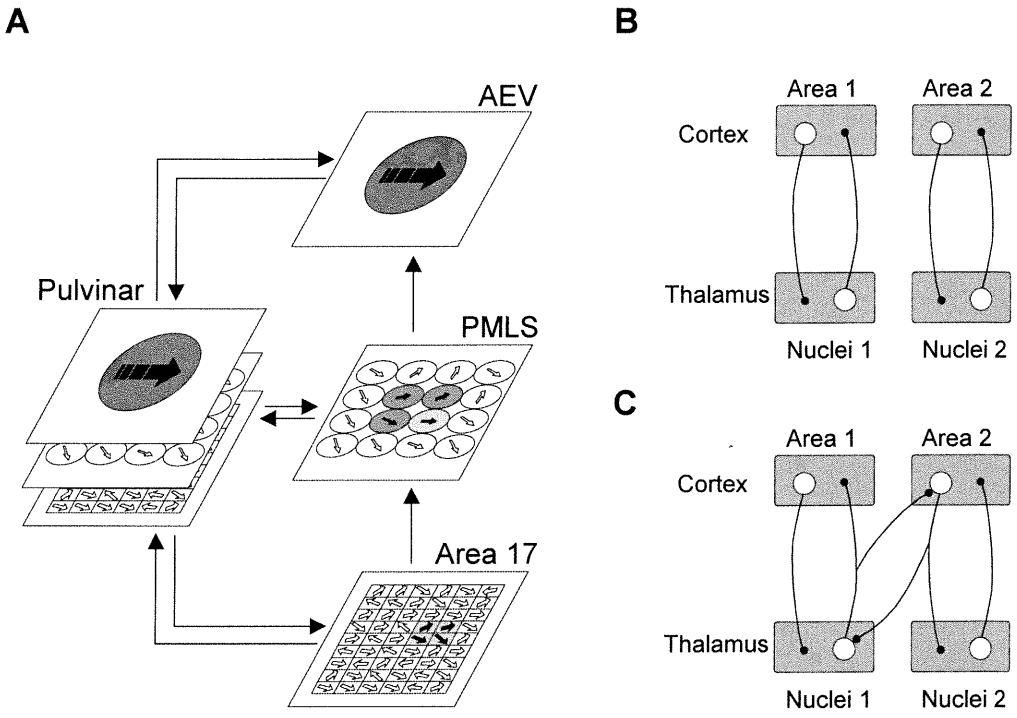

Figure 9. (A) Hypothetical schematic for integration of motion signals in primates based on two-stage model proposed (e.g., Nowlan and sejnowski, 1995), taking into consideration the LP-pulvinar complex. Local signals are processed in area 17, and then integrated at the second stage (that may be the PMLS), and third cortical level. (B) Direct cortico-thalamo-cortical loops. (C) Indirect cortico-thalamo-cortical loops. A given LP-pulvinar neuron projects to multiple areas via axon collaterals. (Casanova et al., 2001)

stages of the motion processing, this thalamic area can contribute through cortico-thalamo-cortical loops, to each step of motion integration process. For example, the LP-pulvinar complex may group appropriate neural assemblies in primary visual cortex (area 17) carrying out local motion analyses (e.g. simple RDKs selective cells). By integrating these local cues in parallel with LS cortex and AEV, the LP-pulvinar complex may provide for an enhanced computational pathway (Miller, 1996). This theoretical model of visual motion processing allows multiple analyses to occur in parallel (Merabet, 1999). Moreover, we suggest that LP-pulvinar complex is actively involved in specialized mechanisms carried out by different cortical areas subsuming different aspects of motion processing.

While there is overwhelming evidence that the thalamus is dynamically involved in cortico-thalamo-cortical loops, two anatomical descriptions proposing the organization of cortico-thalamic projections can be found. The first hypothesis suggest that information descending to the pulvinar from the various cortical areas can be kept separate, if each nucleus within the thalamus projects back to only the same region of cerebral cortex from which it receives inputs (Diamond et al., 1969). Thus, each thalamic nucleus would signal salience to its cortical field (Figure 9 panel B). Alternatively, the existence of both reciprocal and nonreciprocal patterns of cortico-thalamic connectivity was confirmed (for a review see Deschênes et al., 1998) (Figure 9 panel C). On the basis of the latter

hypothesis, the information can be passed from lower to higher areas of complexity by *mixing* at the thalamic level. The present results support the later hypothesis. For example, the majority of pattern-motion selective units (neurophysiological response assembly in AEV) were located in the medial part of the LP nucleus (LPm); however, the remaining units were in the lateral part. On the other hand, the majority of complex-RDKs selective cells (response assembly in PMLS) were found in the LPl. Thus, the lateral portion of LP nucleus may participate in different aspects of motion processing carried out by different cortical areas. In this context, we suggest that not only direct loops, but also indirect, non-reciprocal, cortico-thalamo-cortical loops, perhaps involving intrinsic connections between the subdivisions within the LP-pulvinar complex, may be involved in visual processing. This connectional model greatly reduces the number of representation units required to analyze a complex and dynamic visual scene (Singer, 1994).

To date, support for the notion that cat LP-pulvinar complex and primate pulvinar carry out comparable functions stems more from anatomical evidence (Creutzfeldt, 1988) rather than neurophysiological support. For example, it is not known if primate pulvinar is implicated in higher order visual functions (pattern selective cells, complex RDKs selective cells), or if the disruption of cortico-thalamo-cortical loops influences visual perception in any way in primates.

It is hoped that novel experimental approaches coupled with fresh points of view will see an amalgamation occurring when at very least, work on colliculus and cortex will together provide an insight into the true function of the enigmatic "pulvinar" (Grieve et al., 2000).

5. Conclusions

In an ongoing series of studies, anatomical and physiological techniques were employed to investigate the role of cat's LP-pulvinar complex and cortico-thalamo-cortical loops in visual motion processing. The demonstration of global motion integration in the cat's extrageniculate thalamus provides further support for the notion that LP-pulvinar neurons may be involved in higher-order visual processing. Furthermore, these results constitute evidence that the thalamus is not merely a state-dependent gateway, but that it takes an active part in central processing of sensory signals. The cortico-thalamic connectivity and higher-order functions of neuronal properties in the LP-pulvinar complex is in line with theoretical notions supporting the proposal that certain thalamic nuclei participate in the analysis of complex visual scenes (Rauschecker, 1988; Mumford, 1991). We propose that the LP-pulvinar complex in cat is implicated in cortico-thalamo-cortical ensembles that could signal coherent features of visual stimuli. Physiological and behavioral studies have gone much further, and they indicate other higher-order properties that could very well exist at the thalamic level, i.e: visual attention (Peterson et al., 1985) and saccadic eye movement (Robinson et al., 1986).

Evidence of cortico-thalamo-cortical loops involved in neuronal processing at other sensory pathways has also been reported.

Ergenzinger et al., (1998) have shown that acute and chronic administration of an NMDA receptor antagonist directly into the area 3b cortical hand representation results in suppression of activity in area 3b and an enormous enlargement of tactile receptive fields in the VP (ventral posterior nucleus of the thalamus) hand representation. In addition, Zhang et al., (1997) have shown that inactivation of cortical auditory neurons determines a reduction of auditory response in medial geniculate nucleus (MGN) neurons, suggesting that corticofugal system could mediate a positive feed-back that adjusts the tuning of neurons at earlier stages in the auditory pathway.

The results of these investigations force a re-evaluation of traditional "bottom-up" models of sensory processing, that view the thalamus as a simple relay nucleus to the cortex. Furthermore, we adhere to the suggestion that *the thalamus provides a dynamic relay that affects the nature and format of information that reaches the cortex* (Sherman, 2001).

In conclusion, cortico-thalamo-cortical loops may be described as computational model for the perception of the world around us, and in the preparation of action without further delay (Creutzfeldt, 1988). Almost all cortical area have relationship with thalamic nuclei; therefore, the organization of the cortico-thalamo-cortical loops can not be regarded as an organization restricted to sensory processing alone, and a similar

cortico-thalamo-cortical organization in motor processing could be present.

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