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Acknowledgements. We thank M. Cavigelli, J. Easter, P. Groffman, D. Jenkinson, P. Matson and S. Snapp for comments on the manuscript; J. Duxbury for discussions of ^{13}C natural abundance methodology; and E. A. Paul for funding and analytical support of lysimeters and the NO_3^- leaching component. This work was funded in part by USDA-ARS.

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Motion integration in a thalamic visual nucleus

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Thalamic nuclei have long been regarded as passive relay stations for sensory information en route to higher level processing in the cerebral cortex. Recently, physiological and theoretical studies have reassessed the role of the thalamus and it has been proposed that thalamic nuclei may actively participate with cortical areas in processing specific information^{1–4}. In support of this idea, we now show that a subset of neurons in an extrageniculate visual nucleus, the lateral-posterior pulvinar complex, can signal the true direction of motion of a plaid pattern, indicating that thalamic cells can integrate different motion signals into a coherent moving percept^{5–8}. This is the first time that these computations have been found to occur outside the higher-order cortical areas^{5,6,9,10}. Our findings implicate extrageniculate cortico–thalamo–cortical loops in the dynamic processing of image motion, and, more generally, as basic computational modules involved in analysing specific features of complex visual scenes.

The integration of motion signals is usually considered to be a two-stage process^{5,11}. The first stage involves the analysis of object features as one-dimensional components, which are integrated at a second stage. It has been argued that the first stage is inherently limited in its coding of local motion signals (the aperture problem⁵), and that the second stage, combining the outputs from the first, is necessary to generate a global percept of an object in motion. This

second stage has been attributed to cortical networks, as have all forms of higher-order processing. However, models have been proposed in which thalamic nuclei participate in these processes, interacting closely with the neocortex^{1–4,12–14}. A common implication of these models is that cells on both sides of the cortico–thalamic loop have similar higher-order response properties, although there has been no clear demonstration of subcortical neurons responding to higher-order visual stimuli. In well-developed visual systems, the pulvinar region is a likely candidate for a subcortical counterpart to the cortex where a loop involved in the analysis of moving objects could be established. The pulvinar complex represents a higher-order nucleus because it receives its major input from layer V cortical neurons, rather than directly from retinal ganglion cells; it is also in reciprocal communication with virtually all visual and associative cortical areas^{15,16}. This region is often associated with visual attention^{17,18} and visually guided movement¹⁹, but theories of its function remain speculative¹⁵. In cats, the physiological response properties in the lateral-posterior pulvinar (LP-pulvinar) complex indicate that these cells code attributes of image motion such as direction, velocity, and the relative motion between an object and its background²⁰. On the basis of these response properties and connectivity patterns, we considered that the LP-pulvinar complex could participate in analysing the global motion of complex scenes. We therefore studied the sensitivity of cells in the cat's LP-pulvinar complex to moving plaid patterns. This stimulus comprises two superimposed drifting gratings differing only in orientation. A human observer perceives a single rigid pattern moving unambiguously with a direction and velocity uniquely consistent with the constraints imposed by the motion of the individual components^{5,7,8}. At the neuronal level, a cell that is selective for the global motion of the plaid pattern responds with a profile similar to that of a single grating moving in the integrated direction ('pattern' motion selectivity), rather than

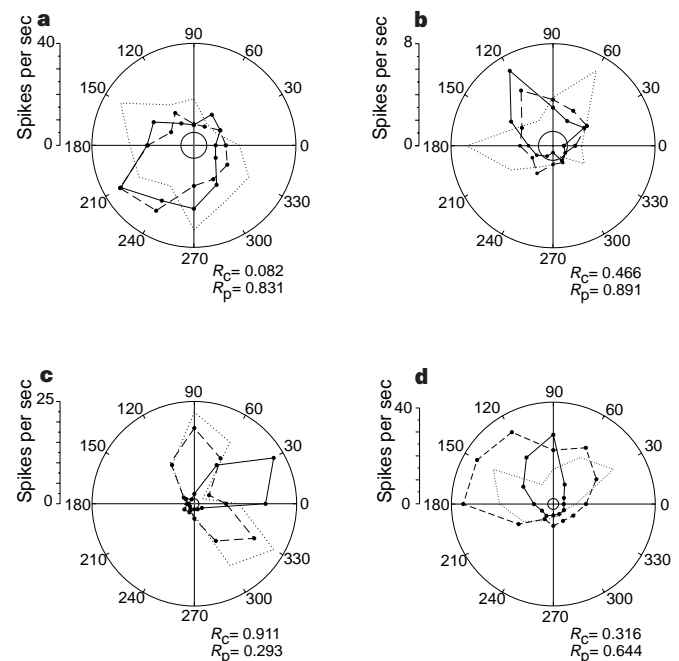


Figure 1 Polar graphs illustrating the responses of LP-pulvinar neurons to gratings (solid line) and plaid patterns (dashed line) drifting in 12 directions of motion. We considered the response to gratings alone as the predicted profile for a truly pattern-motion selective unit. The dotted line represents the predicted response to plaids for a component-motion selective unit. **a, b**, Pattern-motion selective neurons. **c**, The response of a component-motion selective cell. **d**, The discharges of an unclassified direction-selective cell. The small central circles represent spontaneous activity levels.

in the directions of the oriented components comprising the pattern ('component'-motion selectivity)^{5,6}.

We recorded from 67 direction-selective units in the LP-pulvinar complex, and found a subset of 21 cells that responded unequivocally to the pattern motion of plaids. For the two cells illustrated in Fig. 1a, b, there is a close correspondence between the directional tuning function computed from the responses to moving gratings and plaids, indicating that these neurons are able to signal the pattern's true direction of motion. Another subset of seven LP cells (10.5%) gave bilobed tuning curves, with peaks roughly symmetrical to the peak obtained in the single grating experiment (Fig. 1c). These responses closely match the tuning curve predicted for component responses, indicating that these neurons process the one-dimensional motion signals making up the plaid pattern. The remaining 39 units (58.2%) could not be grouped in either of the two categories (unclassified direction-selective cells; Fig. 1d).

We classified the cells' responses to plaids on the basis of the calculation of partial correlation coefficients, comparing the responses to plaids to the predictions of component and pattern motion⁸ (Fig. 2). These data show that a substantial proportion of neurons (~31%) in the LP-pulvinar complex lie in the region found to be selective to pattern motion. Component responses were also present, indicating that both local and global information is processed at the thalamic level. As a comparison, we measured the responses to moving plaid patterns from cells in the primary visual cortex (area 17) and in the posteromedial part of the lateral suprasylvian cortex (a region often referred to as the functional analogue of the primate middle temporal (MT) area²¹). We found that most neurons in these areas were component-motion selective and that there was no pattern-motion direction selective cells, consistent with previous reports^{6,22}.

Histological reconstruction of the electrode tracks indicated that most pattern-motion selective cells in the LP-pulvinar complex (80%) were located in the medial part of the lateral posterior nucleus (LPm) whereas the remaining units were found in the

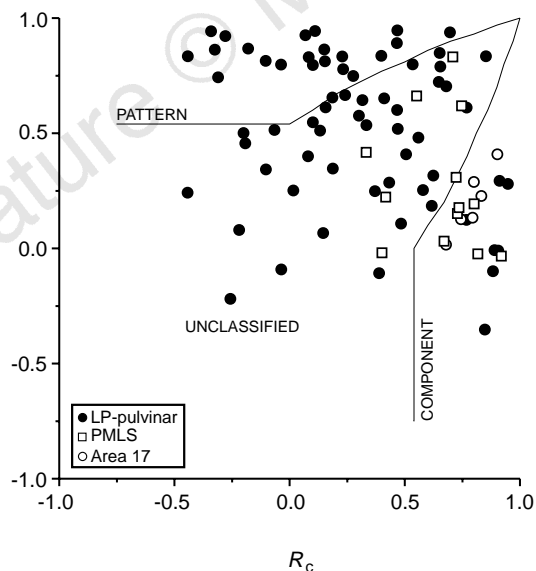


Figure 2 Scatter plot of partial correlations for pattern and component selectivity: filled symbols, neurons in the LP-pulvinar; open circles, area 17; and open squares, PMLS cortex. Each direction-selective unit was classified by quantifying the degree of correspondence between the response to plaid and the responses predicted from the pattern (responses to the grating alone) and the component models (that is, shifting the grating responses by 60° in both directions and summing the resulting curves around the clock). The data space is divided into three 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.

lateral section of this nucleus. The medial area corresponds to the tecto-recipient zone of the LP-pulvinar, which receives a major input from the superior colliculus and establishes reciprocal connections with the anterior ectosylvian visual (AEV) cortex^{15,23}. This extrastriate area is the only region of the cat visual cortex described as possessing a population (~55%) of pattern-motion-processing cells⁶ similar to those observed in primate area MT⁸⁻¹⁰. The presence of pattern-motion selective cells on both sides of the AEV-LPm loop raises the possibility that this cortico-thalamic network is a module specifically involved in the processing of motion information.

We performed two sets of experiments investigating the physiological link between these two regions. First, we measured the responses of 16 LP neurons to plaids before and after pharmacological deactivation of visuotopically corresponding regions of the AEV cortex. Eight LP cells were classified as pattern selective, of

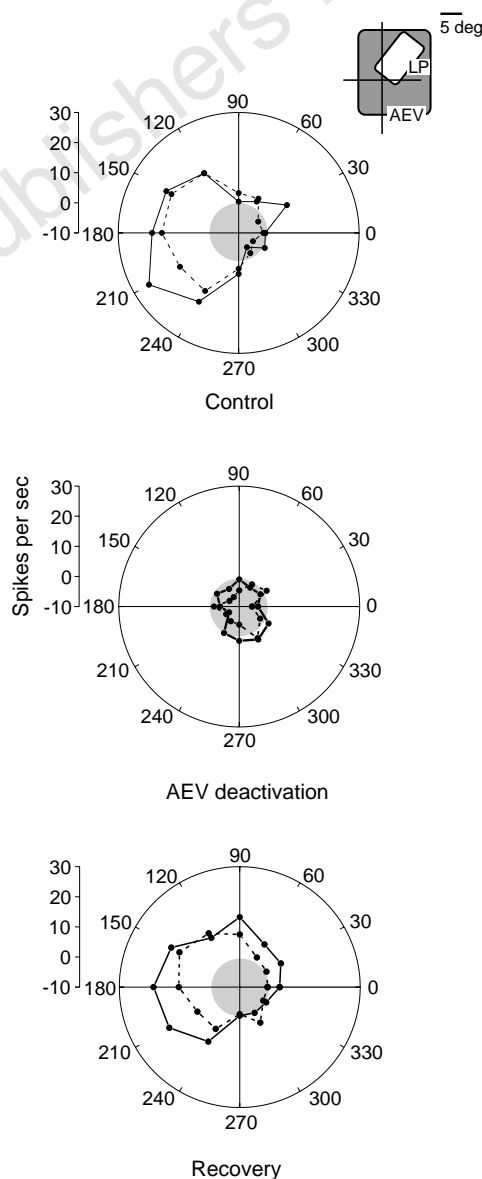


Figure 3 Effect of deactivating the AEV cortex on a pattern-motion selective neuron in the medial part of the lateral posterior nucleus. During cortical deactivation, a strong suppression of the cell's overall response and a concomitant loss of its ability to signal direction of the drifting grating (solid line) and plaids pattern (dashed line) was observed (blocking index of -0.25 and -0.4, respectively). In each polar graph, data points within the shaded region represent cell discharges below spontaneous activity levels. The inset shows the location of the receptive field of the thalamic neuron in reference to the AEV scotoma.

which half were affected by cortical deactivation: for three of these cells, the plaid responses were strongly reduced (Fig. 3); for the fourth they were enhanced (data not shown). These results demonstrate that the lateral posterior nucleus and AEV cortex are functionally linked and, furthermore, that this loop is likely to be involved in processing higher-order motion information. However, the finding that the responses of four pattern-motion selective units were not altered by the cortical deactivation suggests that pattern selectivity in LP-pulvinar does not depend solely on descending projections from the AEV (see below). Blocking the AEV cortex also reduced the responses to plaids for three out of five component cells and two out of three unclassified direction-selective units. That component cells were affected by cortical deactivation is surprising, given that almost no such cells were found in the AEV⁶. One explanation is that local velocity signals from the lateral posterior nucleus are used by the AEV for integrating or comparing local and global motion signals. Alternatively, deactivation of the AEV might affect lower-level motion areas, which in turn project to the LP nucleus. This finding may also indicate that simultaneous excitation of both regions is needed for information to be processed along the cortico-thalamic loop²⁴. In the present case, disrupting the feed-

back input short-circuits the loop and decreases the probability of thalamic firing.

To determine whether pattern motion responses in LP-pulvinar neurons depend solely on inputs arising from the AEV, we recorded in the extrageniculate thalamus of three cats with acute bilateral ablation of the anterior ectosylvian cortex (see Methods). In all animals, we could still record pattern-motion selective responses (Fig. 4). These data, together with the fact that cortical deactivation does not affect half of the pattern-motion cells, indicate that LP-pulvinar neurons can process pattern motion from inputs other than those provided by the AEV cortex. To test this, we studied pattern-motion sensitivity in the LP-pulvinar complex of cats with ablation of the AEV and the lateral suprasylvian cortex, generally considered to be the main motion area in cats²¹, although no pattern-selective cells have been found in the lateral suprasylvian subdivisions investigated²². Ablation of the two cortices yields a global reduction in the visual responsiveness of LP cells, and in the number of direction-selective neurons. Testing with drifting gratings showed only three of 16 units to prefer a specific direction of motion; responses to plaids of all cells were unclassified direction-selective. Thus, the persistence of pattern-motion selectivity in LP neurons after removal of the AEV cortex appears to depend on the integrity of the lateral suprasylvian cortex. These data support the proposition²⁵ that there is a subpopulation of lateral suprasylvian neurons that can code the true direction of moving objects. It is also possible that intrinsic computations are taking place within the thalamus (for example, integration of multiple-component signals). Moreover, the absence of pattern-motion cells indicates that subcortical inputs from the superior colliculus do not account for pattern selectivity in the LP-pulvinar complex. This observation agrees with previous reports showing that deactivation of the superior colliculus does not alter the responses in the medial part of the lateral posterior nucleus¹⁵, and that this region does not contain pattern-motion units⁸.

The finding that LP neurons can code the integrated motion of plaid patterns indicates that the LP-pulvinar complex is important in motion integration, and also supports the theoretical notion that clusters of thalamic cells, in conjunction with cortical assemblies, participate in the analysis of complex percepts^{1,3,4}. One possibility is that sensory maps in the AEV and lateral suprasylvian are used to establish a 'global' template in the LP-pulvinar complex. Through feedback loops, these maps could be used dynamically to compare the first and second stages of motion processing of an image encoded at cortical levels with the information stored at the thalamic level^{1,10}. In addition, successive iterations within the cortico-thalamic loops could help to refine the cortical image (for example, segmentation from motion).

Our findings may force a reconsideration of the computational steps involved in the analysis of moving scenes, which so far have been modelled only at the cortical level^{5,9,26}. Whereas the current 'two-stage processing' models have only been described in the primate visual system, there is evidence that they may also be present in the cat. Indeed, it has been shown that higher-order motion computations do occur in the cat extrastriate cortex⁶. Furthermore, computer-based analyses of connectivity patterns have indicated that intermediate cortical stages of motion analysis²⁶ are likely to be present in areas of the lateral suprasylvian cortex that have not yet been fully explored (for example, the posterolateral and anterolateral parts)^{6,25}. It remains to be determined whether the same pattern of responses described here also exists in the primate thalamic visual areas. The reciprocal connections between the pulvinar and middle temporal area²⁷ and the strong similarities in the organization of cat and primate extrageniculate pathways²⁸ support this view. This suggests that these cortico-thalamic loops represent a common module of computational organization in these species.

In conclusion, our demonstration that higher-order properties

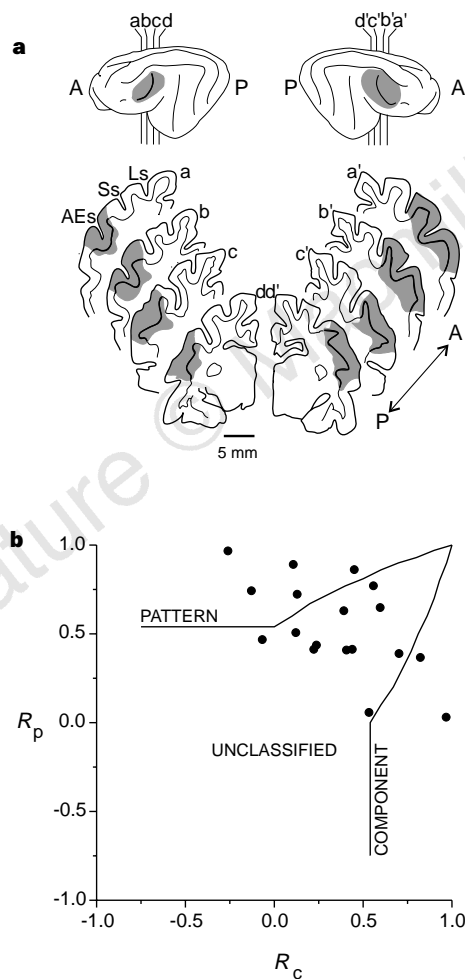


Figure 4 The effects of cortical ablations. **a**, Coronal sections showing the site and extent of the cortical ablations of one cat at various rostrocaudal H-C coordinates. Top, lateral view of the two hemispheres showing the location of the lesions a-d, a'-d'. **b**, Distribution of partial correlation coefficients of LP-pulvinar neurons of cats with bilateral ablation of the AEV cortex. Note the presence of all cell types and in particular, the pattern-motion selective units. Abbreviations: A, anterior; AEs, anterior ectosylvian sulcus; Ls, lateral sulcus; P, posterior; Ss, suprasylvian sulcus.

are analysed outside the neocortex is important for the reassessment of the role of the thalamus and cortico–thalamic loops^{1,3,4,8,9,13}. That neuronal responses to pattern motion can be found in the LP-pulvinar complex in anaesthetized preparations indicates that the function of thalamic nuclei goes beyond the mere relaying of sensory information in relation to the state of vigilance. We propose that the LP-pulvinar complex acts as a platform for processing and integrating specific aspects of an image in cooperation with the visual cortex. □

Methods

Cats were initially anaesthetized with acepromazine (1.0 mg per kg body weight) and atropine (0.2 mg per kg); general anaesthesia was carried out using a gaseous mixture of halothane (1–3%) and N₂O/O₂ (50/50%). The animal was paralysed by intravenous injection of gallamine triethiodide (10 mg per kg body weight per hour) and artificially ventilated (N₂O/O₂:70/30% and halothane 0.5%). Core temperature, electrocardiogram and electroencephalogram were continuously monitored. Pupils were dilated with atropine and nictitating membranes were retracted with phenylephrine hydrochloride (2.5%). The eyes were protected using contact lenses of appropriate refractive power. Animals were treated in accordance with the guidelines of the Canadian Council for the Protection of Animals. Varnished tungsten microelectrodes were used to record single-unit activity in LP-pulvinar cells. Neuronal activity was fed to a computer for peristimulus time histogram acquisition. Stimulation was carried out using drifting sinusoidal gratings and plaid patterns (Picasso image synthesizer; frame rate of 200 Hz) presented on a CRT (Data Check 5117; mean luminance of 14 cd m⁻², z axis gamma correction) placed 57 cm in front of the animal and subtending 28 × 28° of visual angle. Plaids were generated by a frame-interleaved method and composed of two superimposed sine-wave gratings differing in orientation (120°) and of identical spatial frequency, temporal frequency and contrast. Both plaids and gratings were presented for at least 4 complete trials consisting of 12 interleaved directions of motion in 30° increments. Responses to plaids were classified as pattern-selective or component-selective by calculating partial correlations using the following equation⁸: $R_p = (r_p - r_c r_{pc}) / [(1 - r_c^2)(1 - r_{pc}^2)]^{1/2}$. R_p represents the partial correlation coefficient for the pattern prediction, r_c is the correlation coefficient of the plaid response calculated from the component model, r_p is the correlation coefficient for the plaid response from the pattern model and r_{pc} is the correlation coefficient for the two models. Similarly, R_c is the partial correlation defined for the component-selective 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 zero⁸. Electrolytic lesions were made along recording tracks and cell localization was determined.

Deactivation experiments. In eight experiments, a glass microelectrode filled with γ -aminobutyric acid (GABA, 200 μ M, stained with 1% Chicago sky blue) was lowered into the AEV. It was inserted in the headstage of a nanopump (WPI) modified to allow simultaneous recording. Placement of the electrode in AEV was determined on the basis of stereotaxic coordinates and visual cues. The deactivation procedure was performed only if there was a visuotopic correspondence between the receptive fields in lateral posterior nucleus and AEV cortex. All LP receptive fields were located between +12 and -15° for elevation and -5 and +20° for azimuth. Cortical activity was continuously recorded before, during, and after the injection. The deactivation solution was injected and continuously delivered at a rate ranging between 80 and 90 nl min⁻¹ for the first 2 min and maintained at 20–30 nl min⁻¹ throughout the testing period. The mean (\pm s.d.) volume injected was 460 (\pm 140) nl, and the mean diameter of these injections inferred from Chicago sky blue staining²⁹ was 1.2 (\pm 0.2) mm. Tested LP cells were kept for further analysis only if the injection of GABA yielded a clear suppression of the AEV multi-unit activity and if the location and extent of the injection site could be determined. For each cell, a blocking index was calculated by dividing the mean response of the LP unit during deactivation by the mean control response recorded before blocking. Indices of zero and one would indicate, respectively, that cell discharges were either totally abolished or not affected. Details of the deactivation technique are given elsewhere²⁹.

Cortical ablations. In three experiments, we recorded from the LP-pulvinar complex in cats with acute bilateral lesioning of the AEV, that is, the anterior ectosylvian sulcus including the entire visual area. The dura was resected and

the cortex was removed by aspiration of the grey matter lying along the ventral bank of the anterior ectosylvian sulcus and overlying the claustrum²³. In two additional experiments, the lateral suprasylvian cortices were also removed in conjunction with the AEV. The cortex located in the medial and lateral banks of the suprasylvian sulcus (the six subregions defining the lateral suprasylvian cortex²⁰) was ablated by aspiration. The cavities were filled with sterile gelfoam and sealed with warm agar and wax. Recordings in the LP-pulvinar complex were made after a 12–16 hour period of recuperation following the surgical procedures. To determine whether the trauma associated with the destruction of both the AEV and the lateral suprasylvian cortices had caused a general depression of brain activity, we first recorded from a few neurons in the lateral geniculate nucleus, superior colliculus and primary visual cortex. In all of these regions, cell properties were similar to those observed in intact animals.

Received 2 September; accepted 2 October 1998.

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Acknowledgements. This work was funded in part by MRC and FCAR grants to C.C. We thank J. A. Movshon for providing the analysis software for the classification of neuronal responses and for commenting on the manuscript, and C. L. Baker Jr, A. M. Herbert, J. Faubert and M. von Grünau for discussions and suggestions. FRSQ provided most of the salary support for C.C., L.M. and A.D. were supported in part by FCAR-Centre and FRSQ-FCAR fellowships, respectively.

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