Temporal interactions in direction-selective complex cells of area 18 and the posteromedial lateral suprasylvian cortex (PMLS) of the cat

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Abstract
Temporal interactions in direction-sensitive complex cells in area 18 and the posteromedial lateral suprasylvian cortex (PMLS) were studied using a reverse correlation method. Reverse correlograms to combinations of two temporally separated motion directions were examined and compared in the two areas. A comparison to the first-order reverse correlograms allowed us to identify nonlinear suppression or facilitation due to pairwise combinations of motion directions. Results for area 18 and PMLS were very different. Area 18 showed a single type of nonlinear behavior: similar directions facilitated and opposite directions suppressed spike probability. This effect was most pronounced for motion steps that followed each other immediately and decreased with increasing delay between steps. In PMLS, the picture was much more diverse. Some cells exhibited nonlinear interactions, that were opposite to those in area 18 (facilitation for opposite directions and suppression for similar ones), while the majority did not show a systematic interaction profile. We conclude that nonlinear second-order reverse correlation characteristics reveal different functional properties, despite similarities in the first-order reverse correlation profiles. Directional interactions in time revealed optimal integration of similar directions in area 18, but motion opponency—at least in some cells—in PMLS.

Keywords: Cat extrastriate area, Motion vision, Random pixel array, Second-order reverse correlation, Motion opponency

Introduction
Direction selectivity for texture motion has been described for several different cortical areas in the cat including area 17, area 18, and the posteromedial lateral suprasylvian cortex (PMLS) (Hammond & MacKay, 1975, 1977; Hamada, 1987; Crook, 1990; Casanova et al., 1995; Merabet et al., 2000). Such cells, presumably complex cells, share the ability to solve the motion correspondence problem in moving random-dot patterns, and are thought to play a role in motion coherence detection. Complex cells form an inhomogeneous group and are further subdivided into "standard," "special," and "intermediate" complex cells. In areas 17 and 18, direction selectivity for moving (random) textures is common for special complex cells, displaying end-stopping behavior (Hammond & Ahmed, 1985; Hammond & Pomfrett, 1989, 1990). End-stopping refers to reduced sensitivity for stimuli extending beyond the receptive-field boundaries. Apart from the presence of end-stopping behavior, complex cell receptive fields in areas 17 and 18 (all subgroups) are relatively homogenous (Orban, 1984). Receptive fields of direction sensitive neurons in PMLS, which form the vast majority (Spear, 1991), are generally more complex. PMLS cells may be selective for, for example, expansion or contraction (Toyama et al., 1985). They may also exhibit center-surround organization with a silent, inhibitory surround (Spear & Baumann, 1975; Camarda & Rizzolatti, 1976), or double-opponent direction-selective center-surround organization (Von Grünau & Frost, 1983; Von Grünau et al., 1987). Based on more elaborate spatial interactions in PMLS receptive fields one might also expect more prominent temporal interactions. Surprisingly, however, our previous study, in which we characterized temporal response properties using a motion reverse correlation paradigm (Borghuis et al., 2003), showed that the majority of neurons in PMLS had temporal response characteristics very similar to those in area 18 (Vajda et al., 2004). Only a small subset of PMLS neurons displayed a more complex pattern, in the form of biphasic reverse correlation functions. For most PMLS cells, we
found monophasic dynamics that were quantitatively similar to those for area 18 (Vajda et al., 2004).

The present study is an extension of our previous study, in which we described the first-order temporal characteristics of directional selectivity in areas 18 and PMLS (Vajda et al., 2004). Here we specifically examined temporal interactions between different motion directions in both areas. The purpose of this study was twofold; first to study differences in temporal characteristics in areas 18 and PMLS in more detail. In our previous study, we found no clear differences in temporal profiles for area 18 and the majority of cells in area PMLS. The question thus arises whether the more complex interactions in PMLS receptive fields do show up as specific temporal interactions.

The second purpose was to examine whether biphasic profiles, found in area PMLS, arise from specific directional interactions. Biphasic profiles in PMLS are similar to those described in area MT (Borghuis et al., 2003; Perge et al., 2005) and consist of a second phase at longer latencies that opposes the short latency effect. Such biphasic cells are especially sensitive to a change in motion direction, from antiprefered to preferred. One possible explanation for biphasic behavior is delayed inhibition from motion in opposite directions, in which case one would expect large effects from preceding directions. Alternatively it might result from, for example, short term adaptation (Priebe et al., 2002), which is a rapid reduction of sensitivity at high excitation levels. Short-term adaptation varies excitation level, but would be independent of specific directional combinations. By studying temporal properties of directional interactions, we can find out to what extent biphasic behavior results from direction interactions.

To study temporal interactions between different motion directions, we adapted the MRC technique (Borghuis et al., 2003) and examined reverse correlation profiles to combinations of two temporally separated motion directions. A first-order analysis, as previously applied, averages directional interactions across all temporal combinations of directions. Here we use a second-order analysis in which spikes were correlated with pairs of motion impulses, one temporally shifted relative to the other. If direction-specific interactions do play a role, then this will show up as disproportionally large contributions from these combinations of directions to the first-order correlations. If, on the other hand, temporal interactions play no role, the second-order profiles should be predictable from the first-order profiles. Comparing the predictions to the measured profiles for different temporal combinations thus allows one to pinpoint nonlinear temporal interactions such as facilitation and suppression. Results reveal clearly different interactions in areas 18 and PMLS, and indicate different roles in feline motion detection.

Materials and methods

The physiological preparation, recording procedure, visual stimuli, measurement protocol, and general data collection were described more extensively in our previous paper (Vajda et al., 2004). In brief, nine adult cats were used in this study. The experiments were carried out according to the guidelines of the Law on Animal Research of the Netherlands and of the Utrecht University’s Animal Care and Use Committee. Anesthesia for the tracheotomy and craniotomy was induced by intramuscular injection of ketamine (15 mg/kg) and xylazine (0.5 mg/kg) (Aescoket-plus, Aesculaap, BV). During recordings, anesthesia was maintained by ventilating the animal with a mixture of 70% N₂O and 30% O₂, supplemented with 0.3–0.6% halothane (Sanofi Santé, BV, Maassluis, The Netherlands). Rectal temperature was monitored and maintained at 38°C. Lidocaine ointments (Xylocaine®, Astra Pharmaceutica BV, Zoetermeer, The Netherlands) were applied at pressure points. Heart rate, blood pressure, in- and expired N₂O, O₂, and halothane were monitored during the experiment (Ohmeda 5250, RGM). Muscle relaxation was maintained by intravenous infusion of pancuronium bromide (Pavulon, N.V. Organon, Oss, The Netherlands) at 0.11 mg/kg/h together with 1.94% glucose in a Ringer solution.

Pupils were dilated with 1% atropine sulphate (Pharmachemie, BV, The Netherlands) and the nictitating membranes were retracted with 2% phenylephrine hydrochloride (Veterinary dispensary of Utrecht University, The Netherlands). The retinæ were projected on a white screen at 57-cm distance from the eyes, and the positions of the foveæ were estimated from the positions of the optic disks and from the orientation of blood vessels. The eyes were focused at the appropriate viewing distance with gas-permeable, contact lenses. Focal correction was assessed by back-projection of the retinal blood vessels onto a white screen. The animal was placed in a stereotaxic apparatus (Molenaar & Van de Grind, 1980) with its head fixed by ear bars and tooth clamps. Extracellular single-cell recordings were obtained with tungsten microelectrodes (impedance 1.0–5.4 MΩ at 500 Hz), insulated with glass or parylene (World Precision Instruments, Inc., Sarasota, FL). A craniotomy of 0.5-cm diameter was performed above area 18, at Horsley-Clarke coordinates P 2-7 and ±(L1.5-L6.5). For PMLS a craniotomy of 0.8 cm was made at Horsley-Clarke coordinates A4–P4 and ±(L13–L21) (Reinoso-Suarez, 1961). For area 18, the electrode was advanced vertically, for PMLS at an angle of 30 deg, through an incision in the dura. Craniotomies were sealed with agar (3% in Ringer solution).

We will briefly summarize the measurement procedures and basic first-order analysis before we focus on the description of the second-order analysis, the main topic of the present paper.

Random pixel arrays (RPAs) consisting of 50% bright and 50% dark pixels (Julesz, 1971) were generated by a Macintosh G4 computer. The frame rate of the stimulus monitor (Sony, Multiscan 400 PS) was 100 Hz. The mean luminance and contrast of the RPAs were set to 50 cd/m² and 0.99, respectively. At the viewing distance of 57 cm and monitor resolution of 1024 × 768 pixels, the unit pixel size was 0.03 deg × 0.03 deg of visual angle. The default pixel size of the RPA was 0.24 deg × 0.24 deg. For cells with larger receptive fields, pixel size had to be increased to 0.48 deg × 0.48 deg for obtaining direction-selective response (Vajda et al., 2005). Unless stated otherwise, the stimulus window measured 24 deg × 21 deg, which was large enough to cover the full receptive field.

A detailed measurement protocol is given in the Methods section of our previous paper (Vajda et al., 2004). In short, complex cells, sensitive to the direction of moving RPAs, were selected and their preferred velocity was determined for motion in the preferred direction. For a subset of cells in both areas (28% in PMLS and 31% in area 18), the preferred step and delay values at the preferred velocity were determined by using the so-called single-step pattern lifetime (SSPL) stimulus, that contains motion information at a single combination of step size and delay of the moving RPA. For the remaining cells, the firing rate was too low to obtain reliable results from this type of experiment, due to the decreased motion energy content of SSPL stimuli. The selectivity for a single step/delay combination in a SSPL stimulus is achieved by replacing the RPA with a new, random pattern after each coherent step (for more stimulus detail see Vajda et al., 2005). In this way, responses were obtained for different combinations of
step size and delay, all corresponding to the cells’ preferred velocity. In cases where a clear optimum showed up in the step size/delay versus mean response plot, these optimal values were used in the MRC experiments. For the remaining cells, the smallest step and delay values were used. In PMLS, the smallest step and delay value was always the preferred combination. In area 18, we found 11 cells with clear optima at some intermediate step size and delay combination (Vajda et al., 2005). Although for the remaining cells optimal values could not be determined, and step and delay values were chosen arbitrarily, the results were found to be highly similar, for both the first-order and the second-order analysis. Once a texture direction-selective cell and its preferred velocity and step delay value as described above were determined, the reverse correlation experiment was started. In the MRC method (Borghuis et al., 2003) as we used it, a RPA makes a random walk, consisting of a random sequence of single steps in eight different directions (from 0 deg to 315 deg in steps of 45 deg). To obtain a balanced sequence in which all directions were presented equally often (several thousands of repetitions), a predefined array that contained equal numbers of all directions was randomly shuffled. At each step a new motion impulse (direction) was presented.

First-order and second-order reverse correlation analysis

In the first-order analysis, spikes were reverse correlated with the eight individual stimulus directions. This yielded a correlation function for the occurrence of a motion step, for each motion direction, and at each point in time preceding a spike. Because we were interested in direction selectivity, that is, a comparison across different directions, we normalized the resulting reverse correlation functions to obtain relative probabilities. The sum across all directions equals 1 and a value of 1/8 represents chance level (Fig. 1). From now on, relative probability of a stimulus or a stimulus combination preceding a spike will be interchangeably used with the term reverse correlation (RC) amplitude. In the second-order analysis, spikes were reverse correlated with all 64 possible combinations of stimulus direction pairs. The time interval (dt) between the members of each pair was always a multiple of the delay value between steps, and is therefore quantified as the number of steps separating the two directions. Successive motion steps, for example, correspond to a dt value of 1. The second-order analysis yielded relative probability functions for the occurrences of specific pairs of directions with various time intervals, at each point in time preceding a spike. For the second-order analysis, we used the latency of the second step relative to the spike as the time marker. Because both spikes (temporal resolution 0.5 ms) and motion steps were sparse, cross-correlations functions were somewhat noisy. The noise level was reduced by smoothing the probability functions using a sliding average with a Gaussian window with a standard deviation of 5 ms (see Fig. 2 in Borghuis et al., 2003). Although the rate of stimulus presentations was limited by the refresh rate of the monitor (100 Hz), each step was precisely timed and the temporal resolution for the correlations was therefore equal to that of the spike times.

Second-order MRC analysis

To develop a baseline for quantifying temporal interactions between different motion directions, we used the first-order results to obtain a “linear” prediction for combinations of motion steps. The “linear” prediction, which assumes no special directional interactions, is then compared to the measured correlation functions. To obtain a prediction based on independence of responses, we multiplied the probabilities for the two separate directions, separated in time by 1, 2, 3, or 4 motion steps. Multiplying the two separate probabilities provides the probability for their combination, if they are independent. By multiplying relative probabilities between correlation function shifted in time, we obtained 64 time functions expressing the relative probability of each possible direction combination to precede (cause) a spike. If motion directions act
independently, then the linear combination of separate probabilities with an appropriate time delay should accurately predict the relation between combinations and spikes. Fig. 2a illustrates eight out of 64 components of a second-order reverse correlation for successive ($dt = 1$) motion pairs. These are results for the area 18 neuron from Fig. 1. Fig. 2a shows measurements for eight direction combinations, for which the second motion step was in the cell’s preferred direction (PD), which was preceded by one of the eight different directions. In Fig. 2b, the predicted relative probabilities are shown for the same combination of directions as in panel a.

Fig. 2a shows that different direction combinations occur with different probabilities at different points in time preceding a spike. For example, the highest probability of firing occurred at around 40 ms after the second motion step, if a PD was preceded by a PD (curve with open circles in Fig. 2a). Such a result is not surprising, since the first-order probability curves have a certain width in time (Fig. 1). Thus the RC amplitude to the PD–PD stimulus combi-

![Fig. 2.](image-url)

(a) Second-order reverse correlation curves for eight direction combinations, where the second direction was always in the PD. Results are for the area 18 cell shown in Figure 1. Panel (b) gives the predicted second-order reverse correlation curves for the same cell and for the same direction combinations. Predictions were obtained by multiplying first-order correlations corresponding to the two directions, taking the time shift (in this case 1 frame) into account.
nation partly results from temporal integration of overlapping RC amplitudes to the PD at two subsequent time-steps. Such summation occurs for all combinations of directions and determines the time course of relative probabilities for combinations. The elevation of the relative probability for the PD–PD combination in Fig. 2a, however, cannot be entirely accounted for by combining RC amplitudes to the PD at two subsequent time-steps. This can easily be verified by comparing the measured RC amplitudes of Fig. 2a to the linear prediction in Fig. 2b. Fig. 2b shows that the predicted value for the PD–PD stimulus combination is less than what we measured. A similar effect was seen when the first direction differed 45 deg. and to a lesser extent for 90 deg difference relative to the PD. Suppressing effects were seen for successive (\(dt = 1\)) stimuli at angles of 180 deg or \(\pm 135\) deg relative to each other.

Fig. 2 shows clear differences between predicted and actually measured temporal interactions. To present similar results for all 64 combinations, rather than just the eight examples (as in Fig. 2), we plotted the full data set in a different format in Fig. 3. Different combinations are orderly arranged along the abscissa, whereas the time preceding spikes is presented on the ordinate. Darker shades correspond to high relative probabilities. Fig. 3a shows measured data and Fig. 3b the predicted values, based on a first-order analysis.

Fig. 3a shows a regular pattern of facilitation (black spots) and suppression (white spots), and Fig. 3b illustrates that this pattern follows the prediction based on linear temporal integration reasonably well, at least qualitatively. To quantify the differences, predicted RC amplitudes were subtracted from the measured ones with results as illustrated for one cell in Fig. 3c. The resulting differences, called relative prediction errors, were expressed as a percentage of the total RC-amplitude range for a cell (maximum–minimum of the measured probability values). Fig. 3c shows that the prediction errors vary by \(\pm 15\\%\). The errors suggest a regular pattern of directionally selective interactions. In the results, we will describe and quantify these interactions for complex cells in area 18 and in PMLS.

Results

Area 18

Data for 32 complex cells in area 18 were qualitatively highly similar. In all cases, the first-order analyses revealed a similar, monophasic reverse correlogram with a mean peak latency of about 56 ms. The pattern of nonlinear, directional interactions was also highly similar across the whole population of cells. Therefore, we summarized the results by averaging the relative prediction errors for all cells, which we will refer to as the mean relative prediction error. It is expressed as a percentage of the actual measurement (see last paragraph of Material and methods). To compare cells with different direction preferences, all directions were expressed relative to the cell’s preferred direction. Fig. 4a shows the results for different pairs of successive (\(dt = 1\)) stimulus directions. The pattern of nonlinearities (errors in the linear predictions due to interactions between members of a pair) is similar to that for the cell in Fig. 3. Mean prediction errors were between +8 and \(-12\\%\) (Fig. 4a). In order to capture the pattern of directional interactions, we plotted the important segment of Fig. 4a in another format in Fig. 4b. Fig. 4b shows a matrix of \(8 \times 8\) directions. These are the angles of the first (y-axis) and second (x-axis) direction relative to the cell’s PD and can be seen as a rearrangement of the results of Fig. 4a at a section around 47 ms. Around this point in time, where maximum deviations were observed, the mean percentage values were averaged over a time interval of 11 ms. Fig. 4b shows these averages for all 64 direction combinations. Enhancing effects were seen for successive (\(dt = 1\)) stimuli in the same direction (both in PD and both in non-referred (ND) direction), or in similar directions (\(\pm 45\) deg, and to a lesser extent also at \(\pm 90\) deg). Suppressing effects were present when directional differences were larger, either \(\pm 135\) deg or \(\pm 180\) deg (PD–ND or ND–PD).

To quantify the nonlinear interactions, and to reveal the time course, we determined the mean relative prediction error across the group of cells, for \(dt\) values ranging from 1 to 4. This yielded 64 time functions, one for each direction combination. The degree of nonlinearity was then quantified by the variance across the 64 directions, for each prespike time. This corresponds to calculating variances along the x-axis in Fig. 4a, for each point in time (y-axis). The resulting variance curves are shown in Fig. 5. They show the overall size and time course of nonlinear directional interactions.

For successive (\(dt=1\)) stimulus combinations, the largest variance occurred at about \(-50\) ms. The longer the time between stimuli, the lower the peak of the variance curves, corresponding to a reduction of nonlinear temporal interactions. The peak shifted towards shorter times with increasing \(dt\). This was however largely determined by the analysis method: predictions based on multiplying the first-order probability functions for larger \(dt\)’s, shifted the resulting peak(s) away from the reference spike-time (prespike times were measured from the second stimulus). Subtracting these curves from the measured, nonshifted ones, thus resulted in a shift of the peak towards the reference spike-time.

PMLS

Our previous first-order analysis revealed two basic types of reverse correlograms in PMLS: monophasic and biphasic ones (Vajda et al., 2004). Monophasic reverse correlograms, like in area 18, exhibited preferences for a single direction, or a small number of neighboring directions, at a mean peak latency about 60 ms. Biphasic cells, on the other hand, showed increased sensitivity for their nonpreferred direction (ND) at longer latencies. These cells thus show a preference for a direction reversal, from nonpreferred to preferred. Five out of 36 PMLS cells exhibited biphasic behavior. The majority of the PMLS cells thus showed monophasic response behavior. Because of their distinct first-order reverse correlation characteristics, we will first present results of the second-order analysis on monophasic PMLS cells and thereafter consider the biphasic cells.

Monophasic PMLS cells

An example of a monophasic cell’s first-order reverse correlogram is shown in Fig. 6a. For the same cell, the relative prediction errors for \(dt = 1\) are shown in Fig. 6b. In Fig. 6b, the majority of nonlinear interactions is visible between 30 ms and 60 ms. Positive effects were seen for the combination of first ND, second PD, but also first PD, second ND and first \(-135\), second \(+45\) were more effective than predicted. For all of these stimulus combinations, the first and second directions were opposite to each other. Suppressive effects were seen predominantly at combinations of first PD, second PD, and to a lesser extent at combinations, where the
first and second directions were either 0 deg or 45 deg apart. The directional interactions for this monophasic PMLS cell were opposite to those found for area 18. Five cells from the entire monophasic population in PMLS ($n = 31$) showed similar nonlinear temporal interactions. The majority of cells in PMLS however showed no obvious, systematic directional interactions. Fig. 7 shows the relative prediction errors averaged for all monophasic PMLS cells, for successive ($dt = 1$) motion steps.

**Fig. 3.** (a) Second-order reverse correlogram for the same cell as in Figs. 1 and 2. All 64 combinations of two successive ($dt = 1$) directions are plotted as a function of time, up to 300 ms. The major x-axis represents the angle of the second direction relative to the PD. Within each second direction category, the angles of the first directions are given, relative to the PD. (b) Predicted second-order RC amplitudes for the cell in (a). Ordering of the first and second directions are the same as in (a). (c) Differences between the measured second order RC amplitudes and predicted ones shown as percentages of the difference between maximum and minimum of the measured RC amplitudes. Stimulus categorization as in the previous subfigures.
Unlike our finding for the area 18 cell population, the mean relative prediction error plot did not show a systematic pattern of nonlinear interactions (Fig. 7). Although the range of relative prediction errors was similar to that in area 18 (compare shading values in Figs. 4a & 7), the nonlinear interactions were randomly spread throughout the different stimulus combinations and prespike times. These interactions therefore represent a higher noise level in the PMLS recordings, rather than systematic directional interactions. This is also reflected in the variances over time, as shown in Fig. 8 for four $dt$ values.

The variance curves in Fig. 8 do not show a systematic increase or decrease, except that the curves for $dt = 3$ and $dt = 4$ show a slight elevation near time zero. This is a small, and irrelevant effect which presumably results from spurious correlations at large time
intervals. For such large time-shifts peaks in the first correlogram aligns with noise in the other, making the predictions highly variable. This results in somewhat higher residual values, but does not influence our conclusions on the monophasic PMLS cells.

**Biphasic PMLS cells**

First-order reverse correlograms for a biphasic PMLS complex cell are depicted in Fig. 9a. The cell had a preferred delay of 80 ms, the value used in MRC measurements. The first peak in the first-order correlogram had a latency of about 60 ms. Previously, we have shown that different delay values did not significantly alter the first-order reverse correlogram shape and only a slight shift to longer latencies was observed with increasing delay values (Vajda et al., 2004). The time difference between the two peaks was 105 ms. The biphasic behavior could be due to several different phenomena. It could result from cell-specific, intrinsic response properties, such as short-term adaptation, or from network interactions, for example, a delayed negative feedback from similarly tuned cells. Although our data do not allow us to distinguish linear combinations from, for example, adaptation effects, we can differentiate between linear combinations, and nonlinear, direction-specific interactions. If the second peak is due to a specific combination of directions, say ND–PD, then we should expect large prediction errors around the time of the second peak, that is, at a delay of 150–160 ms.

Only for a single biphasic cell, the one shown in Fig. 9, did we find an increased prediction error at the expected time of around 150–160 ms. Fig. 9b shows a positive prediction error around this time for a combination of PD followed by the ND, that is, RC-amplitude increase larger than expected on the basis of first-order correlograms. Clearly, this effect is opposite to what causes the biphasic profile. To establish the noise level in interaction plots, we extended the nonlinear analysis to a time period of 1 s rather than the 300 ms used up to now. Then we plotted the variance curves for $dt = 1, 2, 3, 4$, for all five biphasic cells (not shown) and did not see any consistent increase or decrease that would have surpassed the noise level. The analysis thus excludes that nonlinear interactions due to specific combinations of directions play a major role in causing a biphasic reverse correlation profile.

**Summary of the main results**

The main finding of the present study is that area 18 complex cells show considerable nonlinear interactions between the members of a pair of temporally separated motion directions (Figs. 4 & 5) and that most of the PMLS complex cells do not show such nonlinear effects (Figs. 7 & 8). Reverse correlograms for area 18 neurons exhibited facilitatory nonlinear (second-order) temporal interactions for motion directions less than 90 deg apart (Figs. 4a & 4b). Suppressive effects were observed for directions separated by at least 135 deg (Figs. 4a & 4b). Successive ($dt = 1$) motion directions caused the strongest nonlinear behavior. The nonlinear interaction effects decreased with increasing temporal separation of the members of a direction pair (Fig. 5).
Results for PMLS cells were heterogeneous. Few monophasic neurons exhibited nonlinear behavior, and only one nonlinear biphasic cell was encountered (Fig. 9). The type of nonlinear interaction found in monophasic PMLS neurons was quite opposite to that found in area 18. Opposite motion directions caused facilitatory and similar directions inhibitory temporal interactions (Fig. 6). The entire monophasic cell population, however, did not show a systematic increase or decrease in magnitude of the interactions (Figs. 7 & 8).

Discussion

Studies that have analyzed higher order temporal and/or spatial interactions mostly used (ternary) white noise stimuli of optimally oriented, multiple, or single bars (Citron & Emerson, 1983; Emerson et al., 1987; Jacobson et al., 1993; Gaska et al., 1994; Baker, 2001). Studies on complex cells were focused on nonlinearities in processing of image luminance and possible direction selectivity that might arise from extra nonlinear behavior of primarily linear
(space-time oriented) luminance filters (Emerson et al., 1992; Baker, 2001; Touryan et al., 2002). Nonlinear direction-selective subunits in complex cells have been found (Emerson et al., 1987) and evidence is accumulating that their nonlinear behavior resembles a squaring operation (Emerson et al., 1992; Touryan et al., 2002) that might underlie the computation of motion energy (Adelson & Bergen, 1985). These studies concerned the generation of complex cell direction selectivity. In the present study, however,

Fig. 7. Mean temporal interactions for $dt = 1$ for the PMLS cell population (see Figs. 3(c) & 4 and text for further explanation). Stimulus categorization as in Fig. 3(a).

Fig. 8. Variance of mean prediction errors as a function of prespike time, for monophasic PMLS cells. Different curves are for different time intervals ($dt$ value as indicated in the inset) between the two members of a stimulus pair. The curves show the variance across stimulus combinations, averaged across the whole population of monophasic PMLS cells.
direction selectivity of complex cells was a prerequisite, a starting point. We did not study the emergence of direction selectivity. Taking the complex cells’ first-order directional-selective behavior (Vajda et al., 2004) for granted, we wanted to find out whether there are nonlinear temporal interactions in directionally selective responses of these neurons.

Our main finding is that area 18 and PMLS complex cells that were sensitive to the direction of texture motion, differed in their second-order temporal behavior: area 18 neurons formed a homogeneous group, exhibiting facilitatory nonlinear temporal interactions for similar motion directions, and suppressive interactions for opposite directions. These effects were strongest for directions that

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**Fig. 9.** (a) First-order reverse correlograms for a biphasic PMLS cell. (b) Differences between the measured second-order profiles ($dt = 1$) and the predicted values based on the first-order profiles from (a). Errors are given as in Figs. 3(c) and 6(b) (percentage of the RC amplitude). Stimulus categorization as in Fig. 3(a). This cell had a preferred delay of 80 ms.
had small temporal offsets \((dt = 1, dt = 2)\). PMLS, on the other hand, included a variety of cells. From the monophasic cell population, some cells exhibited a nonlinear second-order interaction effect, that was opposite to that found in area 18. For these cells, opposite directions were facilitatory and similar directions were inhibitory. From the cells with a biphasic first-order reverse correlation profile only one showed some nonlinear temporal interaction, while the rest of the biphasic cells had linear second-order temporal characteristics.

Area 18 neurons

In area 18, an RPA making multiple steps in the preferred or similar directions was more effective in eliciting spikes, than would be predicted from the first order reverse correlograms. This effect was largest for successive \((dt = 1)\) stimuli. Motion steps in opposite directions were less effective than predicted. These results clearly showed that the cell’s response to a motion pulse depended strongly on the recent history of stimulus directions. Reverse correlograms to stimulus pairs differed from the linear combination of the separate RC amplitudes. For complex cells in area 18 the effects increase responsiveness to stimulus pairs of similar directions, and thus enhance coherence detection. Temporal integration of briefly presented motion stimuli is therefore highly effective in these cells.

Fig. 5 showed that the nonlinear effects rapidly vanished as the time between members of pairs of motion steps increased. The question arises to what extent the observed nonlinear effect directly correlates with the cells’ response level. Do the effects depend on temporal overlap of first-order RC amplitudes, or do they remain, even after the overlap has completely disappeared? To answer this question, we calculated the population variance curve for the first-order RC amplitudes of all area 18 complex cells. Such a curve gives an estimate of the overall amplitude and width of the first-order RC amplitudes. Next we determined the temporal overlap in this curve and the variance curve, shifted by the mean time interval for the different \(dt\) values. On average, a \(dt\) value of 4 corresponded to a time delay of 80 ms (a single step delay was on average 20 ms). We found that the decline in nonlinear effects corresponded nicely with the decline in temporal overlap: for a time-shift of 80 ms the variance curves still showed a small overlap. This raises the question to what extent the described nonlinear interactions may be due to a direction-independent static nonlinearity. Static nonlinearities have been described for a wide range of cortical neurons and mostly consist of an acceleration at low response amplitudes, and saturation at higher amplitudes. The main effect that we observed in area 18 was enhancement, which would correspond to an accelerating response curve. The idea is that a single motion step is relatively ineffective due to the initial, shallow slope of the stimulus–response curve, whereas a second stimulus can push the response into the steeper part. Similarly, an inhibition due to a nonpreferred direction would pull the response level down into the shallower part and hence cause suppression. We were not able to determine to what extent such a static nonlinear compression explains the observed nonlinearities. Plots of relative prediction errors as a function of the measured RC amplitude for direction combinations clearly showed direction-specific effects. But it was impossible to quantify these differences. Moreover, the proper way of extracting a static nonlinearity would be to plot prediction errors against the instantaneous response level, which is not available in our data structure. Thus, we cannot exclude a contribution from a static, response level dependent, nonlinearity to the observed directional interactions.

PMLS neurons

For monophasic PMLS neurons, that showed nonlinear second-order behavior, the opposite of the area 18 directional interactions was observed: opposite stimulus directions (or nearly opposite) caused an increase of responsiveness, while similar directions decreased spike probability. Such a behavior makes a cell more sensitive to sudden changes in directions (temporal motion contrast). Sensitivity for temporal motion contrast was found for monophasic PMLS cells, and obviously does not imply a biphasic first-order profile. Biphasic reverse correlation profiles, seen in five PMLS cells were, in fact, found not to result from specific combinations of stimulus directions. The first-order profile shows a preference for ND followed by the PD. The nonlinear interaction analysis however did not reveal any such preferences. For the one cell showing an effect it was in fact reversed. The biphasic profile in these PMLS cells therefore results from another mechanism, that is, a mechanism intrinsic to the cell’s responsivity to single directions.

Concluding remarks

Area 18 neurons form a homogenous population in terms of nonlinear second-order behavior in the temporal domain. This area seems to play a straightforward role in local motion coherence detection where optimal integration is required. PMLS cells on the other hand form a heterogeneous population, where motion opponency rather than optimal integration seems to play a more important role. A minority of the cells, those with a biphasic profile, seem to be tuned to reversals of directions. These temporal characteristics reflect yet additional roles of PMLS neurons (detecting motion contrast and reversals of motion), besides the variety of functions already mapped out: speed discrimination (Pasternak et al., 1989), three-dimensional motion (Akase et al., 1998; Rauschecker et al., 1987; Brenner & Rauschecker, 1990; Li et al., 2000; Brossseau-Lachaine et al., 2001), depth perception (Krüger et al., 1993b; Bacon et al., 2001) or other motion-related tasks such as ocular near response (Bando et al., 1992; Takagi et al., 1992; Takada et al., 2000; Toda et al., 2001), saccade-related responses (Yin & Greenwood, 1992; Li et al., 2000, 2001), ocular following reflex (Zernicki & Stasiak, 1994) or visual attention, direction discrimination, and learning (Lomber, 2001; Lomber et al., 1996a,b).

The biphasic profile that we found in a minority of the PMLS cells remains somewhat of a puzzle. It shows that these cells are especially sensitive to direction reversals. However, specific temporal interactions related to opponency were only found in monophasic cells, indicating that biphasic behavior has a different origin. The time difference between the first and second peak was, on average, about 60 ms. This seems too long for lateral interactions to play a major role. The time difference was much longer than would be expected for local interactions, and also much longer than the delayed cortical response in macaque V1 and MT areas for a change of nonpreferred to preferred motion directions (Bair et al., 2002). It should be noted though that the difference in peak latencies does not directly correspond to the latency between opponent mechanisms, but depends on the time course of responses as well. A small latency combined with broad profiles may
result in a much larger separation of the two peaks. Yet, the most likely explanation at present seems to be an intrinsic, short-term adaptation mechanism (Priebe et al., 2002). Adaptation would reduce sensitivity below its normal resting value, after an instantaneous increase in the level of excitation. The time course of biphasic behavior corresponds fairly well to that for short-term adaptation in macaque area MT neurons. Since the reverse correlation functions plot relative probabilities, this shows up as a negative second phase. Simulations of the reverse correlation paradigm showed that short-term adaptation may indeed induce biphasic behavior such as we observed (unpublished results). If this hypothesis is correct, then our data suggest that (short-term) motion adaptation first starts to play a role at the level of PMLS in cat extrastriate visual cortex.

References


