Pergamon

0042-6989(95)00324-X

Vision Res., Vol. 36, No. 18, pp. 2805–2813, 1996

Printed in Great Britain
0042-6989/96 $15.00 + 0.00

Responses of Complex Cells in Area 17 of the Cat to Bi-vectorial Transparent Motion

RICHARD J. A. van WEZEL,*† MARTIN J. M. LANKHEET, FRANS A. J. VERSTRATEN,*
ATHANASIUS F. M. MARÉE,* WIM A. van de GRIND*

Received 24 June 1994; in revised form 4 November 1994; in final form 9 October 1995

We examined the responses to transparent motion of complex cells in cat area 17 which show directional selectivity to moving random pixel arrays (RPAs). The response to an RPA moving in the cell's preferred direction is inhibited when a second RPA is transparently moving in another direction. The inhibition by the second pattern is quantified as a function of its direction. The response to a pattern moving in the preferred direction is never completely suppressed, not even when a second pattern is moving transparently in the opposite direction.

To the extent that supra-spontaneous firing rates signal the presence of the optimal velocity vector, these cells therefore still signal the presence of this line-label stimulus despite additional opposing, or otherwise directed, motion components. The results confirm previous suggestions that, for the computation of motion energy in cat area 17 complex cells, a full opponent stage is not plausible. Furthermore, we show that the response to a combination of two motion vectors can be predicted by the average of the responses to the individual components. Copyright © 1996 Elsevier Science Ltd.

Transparent motion Area 17 Complex cell Visual cortex Cat

INTRODUCTION

Looking at the branches of a tree moving in the wind, it is possible to visually segregate leaves on one branch from those on another branch at a different distance in the same visual region. Motion of different patterns in the same spatial region, if they can be segregated perceptually, is called "transparent motion" (e.g. Clarke, 1977; van Doorn & Koenderink, 1982). Transparent motion of oppositely directed patterns is experienced in daily life during ego-motion. Furthermore, the ability of organisms to see transparent motion helps them to avoid interference between the motion of shadows and that of surface patterns, and therefore to discriminate objects from shadows (Noest & van den Berg, 1993).

Transparent motion presents a challenge to the development of motion detection models. Such models have to include mechanisms to compute in parallel more than one motion vector in any local region of the image. The usual opponent-type motion detectors incorporate a subtraction stage where signals from two motion detectors tuned to opposite directions are subtracted (Reichardt, 1961; van Santen & Sperling, 1984, 1985; Adelson & Bergen, 1985). If the mechanism which provides the directional selectivity of cortical cells contains such a subtraction stage, then oppositely directed transparent motion would not elicit a directionally selective response.

Modelling studies combined with electrophysiological data, suggested that the computation of motion energy in cat complex cells does not include a full opponent subtraction stage (Emerson *et al.*, 1992). In this paper, we study the opponent interactions involved in motion processing in complex cells of cat area 17 with transparently moving random pixel arrays (RPAs). The RPAs consist of 50% bright and 50% dark pixels and are configured in such a way that two patterns can be moved transparently and independently. Transparency is obtained by spatially interleaving the pixels from the two patterns in a checkerboard pattern. In this way pure motion transparency can be created, without confounding luminance modulations. The direction of movement for the two patterns was varied over a wide range to allow for a complete description of the directional interactions involved in motion sensitivity at this early level in the motion system. We were especially interested to find out whether the cell's response could be cancelled by the presence of an opposite motion vector, and more generally, how the response to a combination of motion vectors can be predicted from the response to the individual vectors.

We find that the activity of all complex cells in area 17

*Helmholtz Institute and Department of Comparative Physiology, Utrecht University, Padualaan 8, NL-3584 CH Utrecht, The Netherlands.

†To whom all correspondence should be addressed at current address: Center for Neuroscience, 1544 Newton Court, Davis, CA 95616, U.S.A. [*Email* rjvanwezel@ucdavis.edu].

of the cat which are directionally selective to moving RPAs is suppressed by a second pattern moving transparently in a direction greater than about 45 deg from their preferred direction. However, a cell's response under these conditions always stays above its spontaneous activity. Further, the activity in response to an arbitrary combination of motion vectors can be predicted by the average response to the individual components. These results suggest that the mechanism which provides the directional selectivity for complex cells does not include a full opponent stage. Rather, the combination of responses to different motion vectors results in the average of the response to the individual vectors.

METHODS

Preparation

Twelve adult cats (2.5–4.5 kg) of either sex were prepared for acute recording sessions of up to 3 days duration. Surgical anaesthesia was induced by an intramuscular injection of ketamine (15 mg/kg), xylazine (0.5 mg/kg) and atropine (0.1 mg/kg). Anaesthesia was continued throughout the recording period with a 70%:30% N_2O/O_2 mixture, supplemented with 0.1–0.3% halothane. Animals were artificially ventilated at about 25 strokes/min, and the end-tidal CO_2 concentration was maintained within the range of 3.8–4.0%. Local anaesthetic (Xylocain) was applied to all wound margins and pressure points. At the initiation of artificial respiration, muscle relaxant (gallamine triethiodide, Flaxedil) was given with an initial dose of 25 mg/kg i.v., followed by a steady intravenous infusion at 10 mg/kg/hr in a glucose (1.25%) and Ringer solution. Heart rate, end-tidal CO_2, rectal temperature (about 38.0 deg) and blood pressure were continuously monitored.

Eye preparation

The corneae were protected with neutral contact lenses with an artificial elliptical pupil of 1.5 × 6 mm. The pupils were dilated with 1% atropine sulphate, and the nictitating membrane and eyelids were retracted with 10% phenylephrine hydrochloride. Focal correction was assessed retinoscopically and the eyes were focused with supplementary trial lenses for the appropriate viewing distance. The locations of both optic discs were determined by back-projecting an image of the retina on a screen in front of the cat. The positions of the areae centrales were then estimated from the positions of the optic discs and orientation of major vessels.

Recording

The cat was positioned in a stereotaxic apparatus (Molenaar & van de Grind, 1980); its head was fixed by means of ear bars and an upper jaw support with tooth clamps. Extracellular recordings were obtained from single cells in area 17 with tungsten microelectrodes isolated with parylene (World Precision Instruments, Inc). They had a tip of 1–2 μm and an impedance at 500 Hz of 1–2 MΩ. The electrodes were vertically advanced through the intact dura between Horsley–Clarke coordinates P1–P4 and L0.5–L3.0. Craniotomies were sealed with 2% agar in 0.9% saline, precooled to about 39°C. The agar was coated with a low melting point wax to prevent dehydration and to stabilize the preparation.

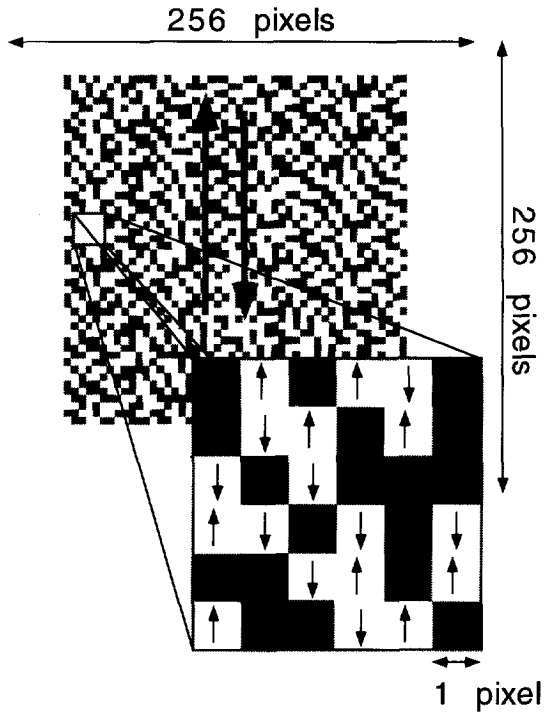

FIGURE 1. Schematic diagram of the stimulus design. A RPA of 256 × 256 random black and white pixels is divided up like a checkerboard with a check size of 1 pixel. One half of the pixels could be moved independently of the other half (in the figure, to the left and downwards, respectively). This setting gives a vivid impression of two, transparently moving patterns. The interleaving method prevents luminance-transparency cues. The speed of the moving RPAs was manipulated for lower speeds by dividing the frame rate (with a base frame rate of 90 Hz), for higher speeds by increasing the step size (in pixels per frame). The average luminance was set to 50 cd/m^2, and the average r.m.s. contrast level to 70%. At the viewing distance of 57 cm, the pixel size was 3.3 × 3.3 min arc.

Only cells with a directionally selective response to moving RPAs have been included in the analysis. As the criterion for directional selectivity we used a factor of two between the response in the preferred and that in the non-preferred direction. In addition, the response of the cell in the preferred direction had to exceed the average spontaneous activity plus twice the standard deviation.

As a search stimulus we used either moving RPAs or moving light and dark bars. Finding cells that were strongly sensitive to moving RPAs was most successful with low impedance electrodes (<2 MΩ at 500 Hz). To classify cells found with either stimulus we used moving bars (Hubel & Wiesel, 1962). Cells with relatively large receptive fields and overlapping "on" and "off" regions were classified as complex cells. In general, these cells were found deeper than about 1 mm in the cortex, and had a relatively high spontaneous activity [on average 12 ± 8 spikes/sec ($n = 38$)]. They sometimes showed

inhibition in the non-preferred direction, were mostly binocular, responded to both light and dark bars in a similar way and were broadly tuned for orientation, speed and direction. The receptive fields of the cells in this sample were located in the lower contralateral quadrant of the visual field, slightly below and lateral to the projections of the area centralis, but within 10 deg of either area centralis. The width of their receptive fields was on average 4.0 ± 1.8 deg. In this group of cells we did not encounter clearly end-stopped cells. Cells were not divided into distinct length summating groups. All results that will be described were obtained from stimulation of the dominant eye only.

Hammond and MacKay (1975, 1977) inferred from a wealth of circumstantial evidence that strongly texture-sensitive cells lie in two bands, one in layer III, and a deeper band in layer V. Evidence in support of this has been presented by Wagner *et al.* (1981), who labelled neurones responsive to texture motion with 2-deoxyglucose, and by Edelsteyn and Hammond (1988) who used extracellular recording and dye-marking techniques. The cells in our sample had all the properties these authors attribute to complex cells in layer V of area 17. We did not identify the complex cells we recorded from histologically.

Stimulus and data collection

The stimulus (see Fig. 1) was generated by custom image generation hardware driven by a Macintosh IIfx computer. On-line data acquisition and processing were performed with the same computer. The base frame rate of the monitor was 90 Hz. All motion frame exposure durations were integer multiples of the base frame exposure duration. The interstimulus interval was negligible. The display window was 14×14 cm and contained 256×256 pixels. The stimulus size was not adjusted to the size of the receptive field of the cell. The square pixels were 3.3×3.3 min arc. The distance between the screen and the eye of the cat was 57 cm. The average luminance of the RPA was set to 50 cd/m^2, with an average r.m.s. contrast of 70%. Further details of the stimulus have been published elsewhere (Fredericksen *et al.*, 1993). To generate two transparently moving patterns we spatially interleaved the 256×256 pixels display in a "checkerboard" pattern (see Fig. 1). In this way 50% of the pixels could be moved independently of the other 50%. When one half of the pixels move in a direction, or at a speed, different from the other half, the display gives a vivid impression of two, transparently moving patterns. We emphasize that the two patterns contain independently generated, random, black and white pixels but are statistically identical, and that they are not superimposed but spatially interleaved. Thus there is no confounding of luminance-transparency.

The experiments were performed in such a way that one RPA, to be called pattern 1, moved in a fixed direction at the cell's preferred speed (or was stationary), while the other RPA, to be called pattern 2, was varied pseudo-randomly in eight different directions to obtain a direction-tuning curve. Coarse sampling at 45 deg intervals suffices because the cells are broadly tuned for both direction and speed. In other experiments we used another paradigm in which we presented pseudo-randomly the following conditions: transparent motion, motion of both patterns in the same direction and motion of one pattern and the other either stationary or dynamically refreshed at 90 Hz. In this test only the preferred and non-preferred direction were measured. Five to eight presentations of 3 sec duration were usually obtained for each condition. For three cells in earlier experiments we used a stimulus presentation duration of 2 sec.

RESULTS

Figure 2(A) shows representative results for the average firing rate of a complex cell in response to two transparently moving RPAs. The peri stimulus time histograms (PSTHs) corresponding to the data points in the curves are shown above the diagram. In the top row of the PSTHs, pattern 1 is moving in the preferred direction, and in the bottom row, pattern 1 is stationary. In general, the cell response remained approximately constant during the presentation interval. We could not detect any significant changes in the response delay or motion-onset transient for the different conditions we will discuss further on. For this reason we quantified the response by the average firing rate for the whole interval of stimulus presentation.

The open triangles in Fig. 2(A) show the average firing rate obtained when pattern 1 is stationary and pattern 2 moves in the different directions indicated on the abscissa. This condition corresponds to a standard, direction-tuning curve for a moving textured pattern, except that only 50% of the pixels move. The preferred direction of motion, i.e. the direction yielding the largest response, is designated 0 deg. The non-preferred direction is defined as 180 deg from the preferred direction. Responses were recorded for motion in eight different directions of pattern 2. For the cell shown in Fig. 2(A), the average response in the non-preferred direction was equal to the spontaneous activity. About half of the other cells showed an inhibition for motion in the non-preferred direction; they responded with an average firing rate that was somewhat lower than their spontaneous activity. Occasionally, we encountered cells that responded equally well to opposite directions. We did not include these cells in the analysis for this paper. The directional tunings we obtained are relatively broad compared to the directional tuning for complex cells measured with gratings or bars. This phenomenon has been repeatedly reported by other authors (Hammond, 1978; Bishop *et al.*, 1980; Crook, 1990; Skottun *et al.*, 1994) and is probably due to the broad band of spatial and temporal frequencies in an RPA (Skottun *et al.*, 1994).

The circles in Fig. 2(A) represent the response of the same cell to a transparent stimulus in which pattern 1 moves in the preferred direction and pattern 2 moves in the different directions indicated on the abscissa. Both

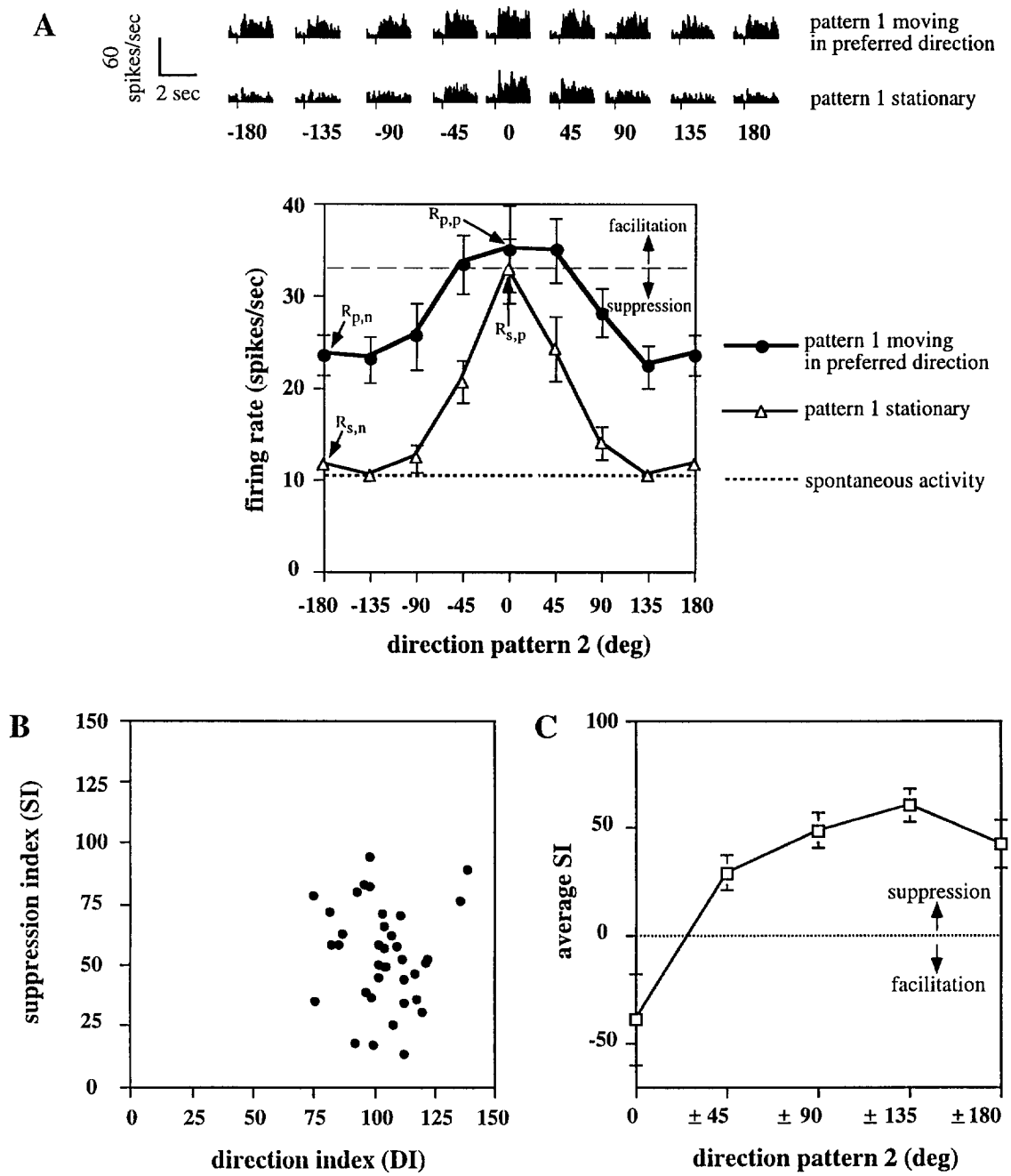

FIGURE 2. (A) PSTHs and average responses of a complex cell in area 17 of the cat to transparently moving RPAs at the preferred speed. Each motion interval lasted 2 sec and was preceded by a stationary phase of 1 sec. The tick marks under the PSTHs indicate the start of the stimulus motion. Stimuli were repeated 10 times for eight different directions in a pseudo-random order. During the stationary phase, the spontaneous activity in an 800 msec interval was measured. The open triangles show the average response of the cell when pattern 1 was stationary, with pattern 2 moving in the different directions indicated on the abscissa. The circles represent the response to different directions of pattern 2, with pattern 1 constantly moving in the preferred direction. The error bars represent ± 1 SEM. The spontaneous activity of the cell is indicated by the dashed line. The top thin horizontal dashed line indicates the response of the cell to one pattern moving in the preferred direction (equal to point $R_{s,p}$). Data points that fall below this thin line indicate suppression in the transparent condition. For calculations of the direction index (*DI*) and suppression index (*SI*) some points in the graph are indicated as follows: $R_{s,n}$, response to pattern 1 stationary, pattern 2 moving in the non-preferred direction; $R_{s,p}$, response to pattern 1 stationary, pattern 2 moving in the preferred direction; $R_{p,n}$: response to pattern 1 moving in the preferred direction, pattern 2 moving in the non-preferred direction; $R_{p,p}$: response to pattern 1 moving in the preferred direction, pattern 2 also moving in the preferred direction. Cell 931002, ipsilateral, receptive-field size 2.0 deg, eccentricity 1.0 deg, preferred speed 2.92 deg/sec. (B) Scatterplot of the direction index (*DI*) against the suppression index (*SI*) for 38 complex cells in area 17. See the Results for a definition of both indices. (C) The average suppression index (*SI*) of 14 complex cells as a function of the direction of pattern 2, with pattern 1 moving in the preferred direction. A negative SI means that the response to motion in the preferred direction (pattern 1) is increased by pattern 2, and a positive value means a suppressive effect of pattern 2. The average *SI* was calculated for both angle deviations from the preferred direction. The error bars represent ± 1 SEM.

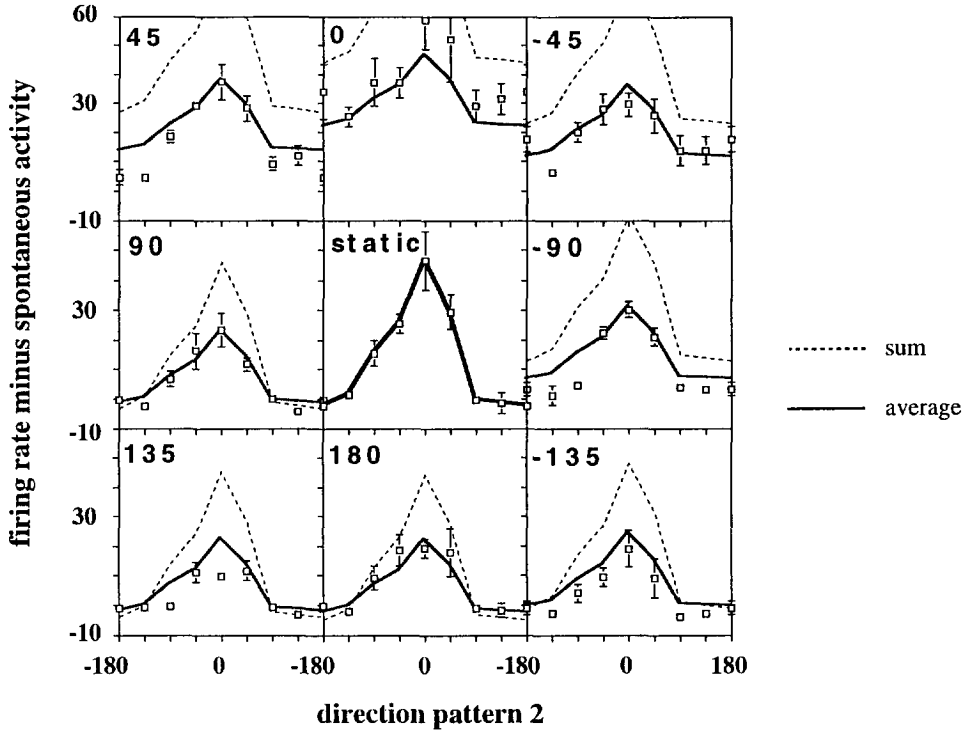

FIGURE 3. The average firing rate (in spikes/sec) minus spontaneous activity of a complex cell responding to pattern 1 moving in the direction as indicated in the top left corner of the diagrams, with pattern 2 moving in the directions as indicated on the abscissa. Both patterns were moving at the preferred speed. The middle diagram shows the directional tuning curve of the average firing rate when only pattern 2 moves in different directions and pattern 1 is stationary. The curves drawn in the other diagrams are based on the sum (dashed line) or the average (solid line) of the responses to one moving pattern (the middle diagram). Cell 931302, ipsilateral, receptive-field size 4.0 deg, eccentricity 8.0 deg, preferred speed 5.27 deg/sec.

patterns move at the preferred speed. The top dashed horizontal line represents the response when pattern 1 is stationary and pattern 2 is moving in the preferred direction ($R_{s,p}$). If data points for transparent motion fall below this line, the responses to the preferred direction of pattern 1 are suppressed by the transparent motion of pattern 2. The figure shows that motion of both patterns in the same direction ($R_{p,p}$), elicits slightly more activity than motion of only one half of the pixels ($R_{s,p}$). So for this cell the response depends slightly on the number of pixels that are moving in the preferred direction.

Over a range of about −45 to 45 deg relative to the optimal direction, pattern 2 causes an increase in response. For larger differences, pattern 2 clearly suppresses the response. Even a pattern which by itself causes an excitatory response (for example 90 deg, open triangles) can suppress the response to a pattern moving in the preferred direction under transparent conditions (90 deg, circles). Nevertheless, when the suppression is maximal, i.e. when the two patterns are moving oppositely ($R_{p,n}$), the cell still responds vigorously; the net activity is well above the spontaneous activity. Obviously, the presence of motion in the non-preferred direction cannot cancel the response to motion of a similar pattern in the preferred direction. If the firing rate is an indication of the cell's confidence that there is movement in a certain direction, then the cell still signals that direction, even in the condition where the two moving RPAs are opposed.

Quantitative differences between cells were noted in speed tuning, degree of suppression by motion in the non-preferred direction, sensitivity to pixel-density, spontaneous activity, etc. Nevertheless, the general response characteristics seen in Fig. 2(A) were typical for almost all complex cells we studied. To quantify the suppression, and to compare the suppressive interactions for different cells, we calculate a suppression index (*SI*). We also calculate a direction index (*DI*) according to the method introduced by Baker *et al.* (1981) and Orban *et al.* (1981). The *DI* is defined as 1 minus the ratio of the response when pattern 2 moves in the non-preferred direction [$R_{s,n}$ in Fig. 2(A)], to the response when pattern 2 moves in the preferred direction ($R_{s,p}$). Pattern 1 is stationary in both cases. Thus:

$$DI = (1 - (R_{s,n} - R_{spon})/(R_{s,p} - R_{spon})) \times 100 \quad (1)$$

where R_{spon} is the average spontaneous activity. In a similar way, the *SI* is defined as 1 minus the ratio of the response when pattern 1 moves in the preferred direction, while pattern 2 moves in the non-preferred direction ($R_{p,n}$) to the response when pattern 1 is stationary, while pattern 2 moves in the preferred direction ($R_{s,p}$). Thus:

$$SI = (1 - (R_{p,n} - R_{spon})/(R_{s,p} - R_{spon})) \times 100 \quad (2)$$

An index-value of 0 indicates no difference in response between $R_{s,n}$ (or $R_{p,n}$) and $R_{s,p}$, and values near 100 indicate large differences. Because the spontaneous activity has been subtracted from the driven activity, *DI*

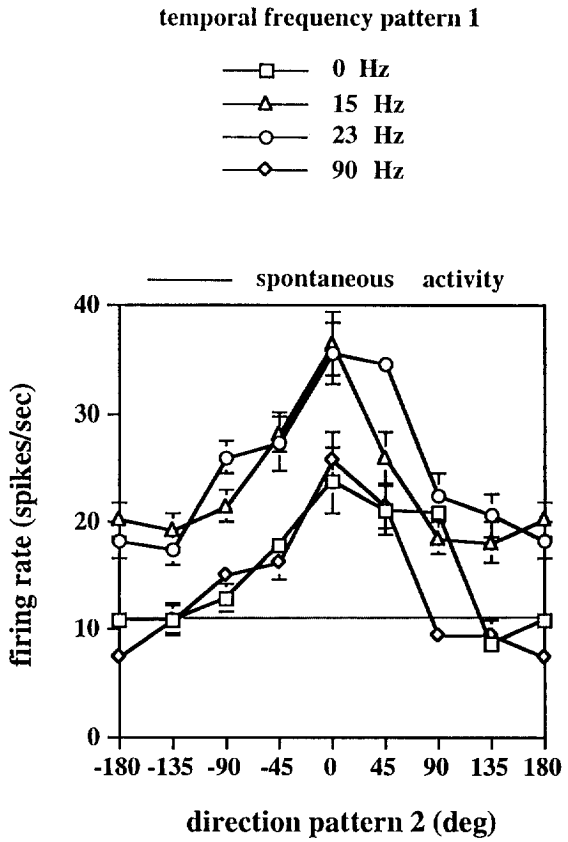

FIGURE 4. A comparison of the direction-tuning curves of a complex cell when pattern 1 is either stationary or dynamic noise. Pattern 2 is moving at the preferred speed in the different directions indicated on the abscissa. Pattern 1 is completely refreshed at different temporal frequencies (see inset). At a frequency of 90 Hz, there is no difference in response between stimulation with stationary (open squares) or dynamic noise (open diamonds). However, for dynamic noise at lower frequencies (open triangles and circles), the direction-tuning curves are uniformly shifted upwards. The error bars represent ± 1 SEM. Cell 931002, ipsilateral, receptive field size 2.0 deg, eccentricity 1.0 deg, preferred speed 2.92 deg/sec.

can exceed 100 when motion in the non-preferred direction ($R_{s,n}$) gives a response below the cell's spontaneous activity. In Fig. 2(B), the *DI* is plotted against the *SI* for 31 complex cells. The figure shows that the *SI* value of all recorded cells is more than 0, which indicates that the activity induced by motion in the preferred direction is always partly inhibited by a second pattern moving in the non-preferred direction. The average *SI* is 52 ± 23 ($n = 38$). There is no obvious correlation between the *SI* and the *DI*. In other words, there is no clear tendency for cells with strong directional selectivity to show either a larger or a smaller suppression. Even cells that show no inhibition of spontaneous activity in a standard direction-tuning curve [cells with a $DI < 0$, for example the cell in Fig. 2(A)], are suppressed when two patterns move transparently in opposite directions.

Figure 2(C) shows the average *SI*-value for 14 complex cells as a function of the direction of pattern 2. For negative *SI*-values, the response to motion in the preferred direction (pattern 1) is increased by pattern 2, and, at positive *SI*-values, there is a suppressive effect of pattern 2. The negative *SI*-value for a direction of 0 deg indicates that the response to two patterns moving in the preferred direction is higher than the response to one moving pattern and one stationary pattern. This dependency on pixel-density varies between cells and the ratio $R_{p,p}/R_{s,p}$ [see Fig. 2(A)] is, on average, 1.52 ± 0.50 ($n = 38$). Figure 2(C) shows that when pattern 2 deviates more than 45 deg from the cell's preferred direction, the response to motion in the preferred direction is suppressed. The average *SI*-value is an increasing function of the deviation of pattern 2 from the preferred direction. For this subset of 14 cells, the average *SI*-value for opposite directions is somewhat lower than for a deviation of 135 deg from the preferred direction.

The results discussed so far were obtained when pattern 1 moved in the preferred direction, thus providing a partial description of the possible interactions. To further explore the integrative and suppressive interactions for transparently moving RPAs, we measured the responses to all possible combinations of directions, when both RPAs moved at the preferred speed. The results for one cell, which is representative of the eight cells on which we performed completely this extensive test, are shown in Fig. 3. The open squares in the diagrams show the average response for each combination of different directions of pattern 1 (upper left corner) and pattern 2 (abscissa). The middle diagram is the response of the same cell when pattern 1 is stationary. The data in each diagram were recorded separately, which accounts for small differences in average response to stimulation with the same combination of directions. These differences can be a result of slow variations in response or possible adaptation effects.

In Fig. 3 we also show the two simplest predictions for the combined response based on the response to the separate RPAs. The dashed curve shows the prediction for summation of the individual responses (summation hypothesis). The solid curves represent the prediction based on the average of the individual responses. The calculations are based on the results shown in the middle diagram, where only pattern 2 is moving in different directions, and pattern 1 is stationary. The results clearly show that for all combinations of directions, the average of the response to the two components provides a fairly good prediction for the combined responses. The summation predicts responses that are much higher than the actual response to two transparently moving patterns. This is also the case for relatively small responses, for which response saturation or compression plays no role. The χ^2 values for the curves based on summation are about nine times higher than those based on averaging.

It is possible that the inhibitory effect of a pattern moving in the non-preferred direction is (partly) due to the introduction of flicker in the stimulus, and not to a directionally selective mechanism. As a control we measured directional tuning when pattern 2 was a moving RPA and pattern 1 was a dynamic noise pattern presented at various flicker frequencies. As shown in Fig. 4, there is no clear difference between pattern 1 when it is

stationary, and when it is dynamic noise with a temporal frequency equal to the base frame rate (90 Hz). The average ratio of a stationary to a dynamically refreshed pattern 2, when pattern 1 moves in the preferred direction, is 1.04 ± 0.10 ($n = 19$). Other authors have described the same results for the monkey primary visual cortex (Snowden *et al.*, 1991). This is an important finding because it indicates that the suppressive effects as shown in Figs 2 and 3 are due to the motion itself, rather than to the flicker in the stimulus.

Figure 4 also shows that dynamic noise with a temporal frequency of 15 or 23 Hz shifts the direction-tuning curves upwards. The curves are shifted uniformly, with no change in shape, which means that the absolute difference in firing rate remains equal. Theoretically this could have implications for cells that are tuned to low speeds. For speeds smaller than 1 pixel per frame the temporal characteristics of the stimulus change. As shown in Fig. 4, dynamic noise increases the firing rate at frame rate divisors of three or more. None of the cells was, however, tuned to such low speeds, and our data were therefore not affected by sensitivity to dynamic flicker.

DISCUSSION

Motion detection models often contain a stage where signals from two motion detectors tuned to opposite directions are subtracted (Reichardt, 1961; van Santen & Sperling, 1984, 1985; Adelson & Bergen, 1985). Our results show that such a full opponency stage is not present in complex cells of cat area 17. Stimulation of these cells with two patterns which move transparently in opposite directions still elicits a response that is significantly above spontaneous activity. These results are in agreement with the work of Emerson *et al.* (1992) who compared the responses of complex cells with those predicted by computational models. They showed that the cell responses were best predicted by the non-opponent motion energy model (Adelson & Bergen, 1985). To achieve directional selectivity, it is evidently not necessary to introduce explicit suppression among detectors tuned to different directions of motion.

However, our results also show that there is actually a suppressive effect of motion in the non-preferred direction on the response to a pattern moving in the preferred direction. This qualitative finding was already described by Kaji and Kawabata (1985) for cat complex cells, with a comparable experimental design. In their experiments they used textured patterns with a larger pixel-size of 12 min arc and transparency was induced by superimposing a textured pattern on another pattern using mirrors, instead of spatially interleaving the RPAs, as in our experiments. The suppression corresponds fairly well, both qualitatively and quantitatively, with results obtained in monkey V1 (Snowden *et al.*, 1991; Qian & Andersen, 1994). We used almost the same measure for the *SI*, the only difference being that we multiply the index by 100. Snowden *et al.* (1991) state that cells in area V1 respond well to their preferred direction of motion even when one pattern is moving transparently in the opposite direction, because they found an average *SI* of 4 in V1. However, if we use the same criteria as in our study and only take into account their directionally selective cells (e.g. with a $DI > 50$), the majority of this subset of V1 cells had an *SI* of about 30. This value is about the same as reported recently by Qian and Andersen (1994) for monkey V1. Our scatterplot of *SI* against *DI* of cat complex cells looks rather similar to these data for monkey V1, with only slightly higher *SI* values for the cat. Snowden *et al.* (1991) and Qian and Andersen (1994) showed that the amount of suppression is higher in monkey area MT compared to V1. Although area 17 of the cat is often seen as homologous to V1 of the monkey (Payne, 1993), it is also widely accepted that some aspects of motion processing that are observed in area MT of the monkey can be observed in the striate cortex of the cat (e.g. Orban *et al.*, 1987). It would be interesting to know whether suppression is higher in areas PMLS and PLLS, the presumed counterparts of monkey areas MT and MST.

Suppressive mechanisms in cat complex cells

What mechanism underlies the suppressive effect which we found? In electrophysiological literature on cat area 17 cells, a variety of suppressive mechanisms have been described, e.g. end-inhibition, surround-inhibition, cross-orientation inhibition and mechanisms underlying figure-ground segregation. Because we did not adjust the stimulus field to the size of the receptive field, all these mechanisms could have played a role in our measurements.

Our findings are in agreement with the results of Hammond and Smith (1986) for bars moving on moving textured backgrounds. They specifically investigated the characteristics of a similar sample of cells, that is, directionally selective complex cells strongly responsive to moving textured patterns. They reported that responses to a bar in the preferred direction are typically enhanced by backgrounds moving in the preferred direction, and are depressed by backgrounds moving in the non-preferred direction. For bar stimuli in the non-preferred direction, this pattern is reversed. The cell's response to the combination of a moving bar and a moving textured pattern in the preferred direction was significantly stronger than that to either component stimulus alone, yet always less than that anticipated from a straight summation of responses. Similar experiments by Orban *et al.* (1987) showed that the response of about 50% of cat area 17 cells to a moving (solid black or white) bar is modulated by large moving textured backgrounds. They found six different types of visual cortical neurons in area 17, based upon the relative directional selectivity during the in-phase and anti-phase testing with such stimulus combinations. We did not find these different types of cells, which may very well be due to the fact that we selected cells that were specifically responsive to moving RPAs.

Our results for motion suppression show an interesting

similarity to cross-orientation inhibition. It has been shown that the responses of most cortical cells can be suppressed by the superposition of a bar (Bishop *et al.*, 1973) or a sinusoidal grating (e.g. Petrov *et al.*, 1980; Morrone *et al.*, 1982; Bonds, 1989; DeAngelis *et al.*, 1992) presented orthogonally to the cell's preferred orientation. This effect has been proposed as a mechanism for the generation or refinement of orientation selectivity. DeAngelis *et al.* (1992) found that all cortical cell responses can be substantially reduced by an orthogonal grating restricted to the region of the excitatory receptive field, as long as the spatial frequency of the orthogonal grating is appropriate and its contrast is sufficiently high. They found that the strength of the suppression was generally independent of the orientation of the suppressive stimulus. Similar to the finding of DeAngelis *et al.* (1992), we find that the response level of cells during suppression is always clearly above the cell's spontaneous discharge rate. This indicates that the cell's activity was not completely suppressed by the superimposed orthogonal gratings or RPAs moving in a direction deviating more than 45 deg from the preferred direction. The similarity of our results for moving RPAs to the cross-orientation phenomena suggests that a similar type of mechanism may account for both phenomena.

The combination of two moving RPAs in different directions clearly showed that complex cells do not simply sum the response to the individual patterns. This is in agreement with the work of Gizzi *et al.* (1990) who evaluated the directional selectivity of simple and complex cells in cat area 17 to sinusoidal gratings, and to plaids composed of two sinusoidal gratings. The striate neurons always responded independently to each component of the plaid, and never signalled the motion of the whole pattern. For complex cells, the response was independent of the relative phase of the components of the plaids, which is consistent with the nonlinearity of spatial summation and independence of phase for alternating sinusoidal gratings (Movshon, 1978). Gizzi *et al.* (1990) also found that the responses of area 17 cells were, on average, one-third less than predicted by the sum of the responses to the components of the plaid measured separately.

Our results showed extensive suppressive interactions for motion mechanisms underlying the directionally selective responses of complex cells. Facilitation occurs when the directions of two transparently moving patterns differ by less than about 45 deg. For larger differences, we find suppression, even by a moving pattern that yielded a positive response by itself. Several of the previously described mechanisms may play a role in directionally selective suppression. RPAs contain a broad range of spatial and temporal frequencies, and since we stimulated with large fields, many different spatial and temporal interactions probably played a role. Yet the use of transparent RPAs made it possible to manipulate the motion content of the stimuli without affecting the luminance characteristics.

Our result that the suppression for all combinations of different directions can be predicted by the average response can also be thought of as a normalization process. The response to combined stimulation is normalized with respect to the total motion content in the stimulus. The same holds to a first approximation for the facilitation. Responses to the two patterns moving in the same direction always fall short of the combined response to the individual patterns. These findings are in good agreement with models of interaction between complex cells by Heeger (1992). He suggested a general suppression in which complex cells mutually inhibit one another, effectively normalizing their responses. We think this model is also directly applicable to our results. The calculation of the average motion energy content we find can be thought of as a normalization process, with the responses normalized with respect to total movement content.

REFERENCES

Adelson, E. H. & Bergen, J. R. (1985). Spatiotemporal energy models for the perception of motion. *Journal of the Optical Society of America A, 2*, 284–299.

Baker, J., Petersen, S., Newsome, W. & Allman, J. (1981). Visual response properties of neurons in four extrastriate visual areas of the owl monkey (*Aotus trivirgatus*): A quantitative comparison of medial, dorsomedial, dorsolateral and middle temporal areas. *Journal of Neurophysiology, 45*, 397–416.

Bishop, P. O., Coombs, J. S. & Henry, G. H. (1973). Receptive fields of simple cells in the cat striate cortex. *Journal of Physiology (London), 231*, 31–60.

Bishop, P. O., Kato, H. & Orban, G. A. (1980). Direction-selective cells in complex family in cat striate cortex. *Journal of Neurophysiology, 43*, 1266–1283.

Bonds, A. B. (1989). Role of inhibition in the specification of orientation selectivity of cells in the cat striate cortex. *Visual Neuroscience, 4*, 41–55.

Clarke, P. G. H. (1977). Subjective standstill caused by the interaction of moving patterns. *Vision Research, 17*, 1243.

Crook, J. M. (1990). Directional tuning of cells in area 18 of the feline visual cortex for visual noise, bar and spot stimuli: A comparison with area 17. *Experimental Brain Research, 80*, 545–561.

DeAngelis, G. C., Robson, J. G., Ohzawa, I. & Freeman (1992). Organization of suppression in receptive fields of neurons in cat visual cortex. *Journal of Neurophysiology, 68*, 144–163.

van Doorn, A. J. & Koenderink, J. J. (1982). Spatial properties of the visual detectability of moving spatial white noise. *Experimental Brain Research, 45*, 189–195.

Edelsteyn, N. M. J. & Hammond, P. (1988). Relationship between cortical lamination and texture sensitivity in complex neurones of the striate cortex in cats. *Journal of Comparative Neurology, 278*, 397–404.

Emerson, R. C., Bergen, J. R. & Adelson, E. H. (1992). Directionally selective complex cells and the computation of motion energy in cat visual cortex. *Vision Research, 32*, 203–218.

Fredericksen, R. E., Verstraten, F. A. J. & van de Grind, W. A. (1993). Spatio-temporal characteristics of human motion perception. *Vision Research, 33*, 1193–1205.

Gizzi, M. S., Katz, E., Schumer, R. A. & Movshon, A. (1990). Selectivity for orientation and direction of motion of single neurones in cat striate and extrastriate visual cortex. *Journal of Neurophysiology, 63*, 1529–1543.

Hammond, P. (1978). Directional tuning of complex cells in area 17 of the feline visual cortex. *Journal of Physiology, 285*, 479–491.

Hammond, P. & MacKay, D. M. (1975). Differential responses of cat visual cortical cells to textured stimuli. *Experimental Brain Research, 22*, 427–430.

Hammond, P. & MacKay, D. M. (1977). Differential responsiveness of simple and complex cells in cat striate cortex to visual texture. *Experimental Brain Research, 30*, 275–296.

Hammond, P. & Smith, A. T. (1986). Relative motion sensitivity in cat striate cortex as a function of stimulus direction. *Brain Research, 386*, 93–104.

Heeger, D. J. (1992). Normalization of cell responses in cat striate cortex. *Visual Neuroscience, 9*, 181–197.

Hubel, D. H. & Wiesel, T. N. (1962). Receptive fields, binocular interaction, and functional architecture in the cat's visual cortex. *Journal of Physiology, 160*, 106–154.

Kaji, S. & Kawabata, N. (1985). Neural interactions of two moving patterns in the direction and orientation domain in the complex cells of cat's visual cortex. *Vision Research, 25*, 749–753.

Molenaar, J. G. & van de Grind, W. A. (1980). A stereotactic method of recording from single neurons in the intact *in vivo* eye of the cat. *Journal of Neuroscience Methods, 2*, 135–152.

Morrone, M. C., Burr, D. C. & Maffei, L. (1982). Functional implications of cross-orientation inhibition of cortical visual cells. *Proceedings Royal Society of London B Biological Science, 216*, 335–354.

Movshon, J. A. (1978). Receptive field organization of complex cells in the cat's striate cortex. *Journal of Physiology London, 283*, 79–99.

Noest, A. J. & van den Berg, A. V. (1993). The role of early mechanisms in motion transparency and coherence. *Spatial Vision, 72*, 125–147.

Orban, G. A., Gulyás, B. & Vogels, R. (1987). Influence of a moving textured background on direction selectivity of cat striate neurons. *Journal of Neurophysiology, 57*, 1792–1812.

Orban, G. A., Kennedy, H. & Maes, H. (1981). Response to movement of neurons in areas 17 and 18 of the cat: Direction selectivity. *Journal of Neurophysiology, 45*, 1059–1073.

Payne, B. R. (1993). Evidence for visual cortical area homologs in cat and macaque monkey. *Cerebral Cortex, 3*, 1–25.

Petrov, A. P., Pigarev, I. N. & Zenkin, G. M. (1980). Some evidence against Fourier analysis as a function of the receptive fields in cat's striate cortex. *Vision Research, 20*, 1023–1025.

Qian, N. & Andersen, R. A. (1994). Transparent motion perception as detection of unbalanced motion signals II. Physiology. *Journal of Neuroscience, 14*, 7367–7380.

Reichardt, W. (1961). Autocorrelation: A principle of the evaluation of sensory information by the central nervous system. In Rosenblith, W. A. (Ed.) *Sensory communication*. New York: Wiley.

van Santen, J. P. H. & Sperling, G. (1984). Temporal covariance model of human motion perception. *Journal of the Optical Society of America, A1*, 451–473.

van Santen, J. P. H. & Sperling, G. (1985). Elaborated Reichardt detectors. *Journal of the Optical Society of America, 2*, 300–321.

Skottun, B. C., Zhang, J. & Grosof, D. H. (1994). On the directional selectivity of cells in the visual cortex to drifting dot patterns. *Visual Neuroscience, 11*, 885–897.

Snowden, R. J., Treue, S., Erickson, R. G. & Andersen, R. A. (1991). The response of area MT and V1 neurons to transparent motion. *Journal of Neuroscience, 119*, 2768–2785.

Wagner, H.-J., Hoffmann, K.-P. & Zwerger, H. (1981). Layer-specific labelling of cat visual cortex after stimulation with visual noise: A [^{3}H]2-deoxy-d-glucose study. *Brain Research, 224*, 31–43.

Acknowledgements—Richard van Wezel and Frans Verstraten are supported by the Life Sciences Foundation of the Dutch Organization for Scientific Research (NWO). We thank Eric Fredericksen for helping with the use of the custom stimulus generation hardware. We are also grateful for the helpful comments on the manuscript by David Alais and Mike Rowe and two anonymous reviewers.