Responses of Complex Cells in Cat Area 17 to Apparent Motion of Random Pixel Arrays

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Received 30 November 1994; in revised form 28 April 1995; in final form 13 June 1996

The characteristics of directionally selective cells in area 17 of the cat are studied using moving random pixel arrays (RPAs) with 50% white and 50% black pixels. The apparent motion stimulus is similar to that used in human psychophysics [Fredericksen et al. (1993). Vision Research, 33, pp. 1193–1205]. We compare motion sensitivity measured with single-step pixel lifetimes and unlimited pixel lifetimes. A motion stimulus with a single-step pixel lifetime contains directional motion energy primarily at one combination of spatial displacement and temporal delay. We recorded the responses of complex cells to different combinations of displacement and delay to describe their spatio-temporal correlation characteristics. The response to motion of RPAs with unlimited lifetime is strongest along the preferred speed line in a delay vs displacement size diagram. When using an RPA with a single-step pixel lifetime, the cells are responsive to a much smaller range of spatial displacements and temporal delays of the stimulus. The maximum displacement that still gives a directionally selective response is larger when the preferred speed of the cell is higher. It is on average about three times smaller than the receptive field size. © 1997 Elsevier Science Ltd. All rights reserved.

Motion detection Apparent motion Visual cortex Complex cell Cat

INTRODUCTION

The use of moving random dot patterns in human psychophysical experiments has greatly contributed to our understanding of the mechanisms involved in motion perception (e.g., Braddick, 1974; Nakayama & Silverman, 1984; van Doorn et al., 1985; van de Grind et al., 1992; Fredericksen et al., 1993, 1994a,b; see for a review Nakayama, 1985). The present work is motivated by the finding of Fredericksen et al. (1993, 1994a,b) that human motion detection mechanisms are sensitive to specific ranges of spatial displacement and temporal delay. They used moving RPAs with a single-step pixel lifetime, containing directional motion energy primarily at a single spatio-temporal combination. They showed that, at any given speed, motion sensitivity was tuned to specific spatial displacements and temporal delays. Their findings were discussed in a framework of ensembles of bilocal detectors, as had been previously proposed by others (van Doorn & Koenderink, 1982a,b; van Doorn et al., 1985; Koenderink et al., 1985; van de Grind et al., 1986, 1992). A bilocal detector has two sub-receptive fields, which might be spatially discrete or partially overlapping, feeding into a coincidence detector. The latter detector signals the coincidence of the delayed signal from one sub-receptive field and the direct signal from the other. This model was introduced into the human psychophysics literature by Schouten (1967) and is a generalized version of the well known Reichardt detector (Reichardt, 1961). Thus, the results of Fredericksen et al. (1993, 1994a,b) would imply that for a given velocity, only a specific subset of bilocal detectors determines motion detection thresholds.

These findings directly motivated the present work. The question we ask is whether a similar rule holds for single cells at an early level in the visual pathway involved in motion detection. To this end we recorded the responses of complex cells to the same stimulus that was used in the cited human psychophysical studies, and analysed how their responses depend on the spatial displacement and temporal delay in the stimulus. For a correct comparison with the human psychophysical work, we must assume that a directionally selective cell contributes to a correct estimate of the motion direction only if the responses to motion in the preferred and non-preferred directions are different. This simple assumption has been demonstrated in other studies in which
psychophysical performance was directly compared with single cell recordings in monkeys (e.g., Britten et al., 1992). If the assumptions that Fredericksen et al. made are correct, one would expect direction-selective responses for only a small range of spatial displacements and temporal delays of their specific stimulus.

Different studies of directional selectivity in primary visual cortex have led to various types of models. Currently, popular models are versions of bilocal or Reichardt correlation detectors (Reichardt, 1961; van Santen & Sperling, 1985) and versions of the so-called energy model (Adelson & Bergen, 1985). It has been shown that bilocal detector models and energy models are basically equivalent (Adelson & Bergen, 1985; Watson & Ahumada, 1985). Recently, however, Emerson et al. (1992) argued that the two types can be distinguished if they are compared on a more detailed level. Emerson et al. (1992) used a reverse correlation technique to determine the spatio-temporal characteristics of motion sensitive neurons in area 17 of the cat. Their results supported the non-opponent stage of the motion energy model and were not consistent with any stage of the classical or elaborated Reichardt detector. The moving RPAs that we use in this study do not allow us, and were not intended, to differentiate between motion energy models and bilocal detector models. Our results on the responses of complex cells can be interpreted within both frameworks, and we concentrate on questions regarding spatial and temporal properties of the correlation stage. An advantage of using RPAs is that the results can be compared more directly to the many psychophysical findings based on random dot patterns and RPAs. In the discussion, we compare our results to related psychophysical results and to other physiological investigations of directional selectivity in the cat primary visual cortex.

Psychophysical motion detection thresholds for apparent motion depend not only on spatio-temporal correlation, but also on temporal integration (e.g., Morgan, 1979; van Doorn & Koenderink, 1984; Burr et al., 1986; Nakayama & Silverman, 1984; Fredericksen et al., 1994a,b). From psychophysical studies it is unclear whether the temporal integration occurs at the level of primary motion detectors or at higher integration levels. To investigate the role of temporal integration and requirements for correlation for directional selectivity of complex cells in cat area 17, we compare their responses to RPAs with a single-step lifetime, and with unlimited pixel lifetime. In previous studies of single cell responses to apparent motion in the primary cortex, researchers have used stereoscopically presented moving bars (Cremieux et al., 1984; Duyens et al., 1987; Mikami et al., 1986; Newsome et al., 1986), two-flash bars (Movshon et al., 1978; Ganz & Felder, 1984; Baker & Cynader, 1986, 1988), multi-flash jumping gratings (Baker et al., 1991), two flash random dot patterns (Mikami, 1991), and the patterns used for reverse correlation techniques (e.g., Jones & Palmer, 1987; Szulborski & Palmer, 1990; Emerson et al., 1987, 1992; DeAngelis et al., 1993; Baker & Boulton, 1994).

An important drawback of some of these two-flash paradigms is that they disregard the importance of temporal integration in motion detection. Evaluation and comparison of responses to moving RPAs with a single-step pixel lifetime and with unlimited pixel lifetime can provide insights regarding the correlation and temporal integration mechanisms that are difficult to obtain with single-flash paradigms or reverse correlation methods.

Our results show that RPAs with unlimited lifetime evoke responses for every spatial and temporal combination that represents the preferred speed of the cell, up to a certain maximum. The maximum displacement that still gives a directionally selective response is larger when the preferred speed of the cell is higher. It is on average about three times smaller than the receptive field size. For moving RPAs with a single-step pixel lifetime, complex cells have a small range of displacement and delay values at which the cell responds differently to the preferred and non-preferred directions. In this case, there is no clear orientation along the preferred speed line in a plot of directional selectivity against delay and displacement.

**METHODS**

**Preparation and recording**

Ten adult cats (2.5–4.5 kg in weight) of either sex were prepared acutely for 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% N2O/O2 mixture, supplemented with 0.1–0.3% halothane. Animals were artificially ventilated at 28 strokes/min, and the end-tidal CO2 concentration was kept between 3.8 and 4.0%. Local anaesthetic (Xylocain) was applied to all wounds and pressure points. Muscle relaxation was initiated with a loading dose of 25 mg/kg i.v. gallamine triethiodide (Flaxedil), and maintained by a steady intravenous infusion at 10 mg/kg/hr in a glucose (1.25%) and Ringer solution. Heart rate, body temperature, blood pressure, inspired and expired gases (N2O, O2, CO2, and halothane), and the O2 saturation in the blood were continuously monitored and regulated within correct ranges.

The corneae were protected by neutral contact lenses with an artificial, elliptical pupil of 1.5 × 6 mm. The pupils were dilated with 1% atropine sulphate. 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 the retina on a tangent screen. The positions of the areae centrales were then estimated from the positions of the optic discs and orientation of major vessels.

The cat was positioned in a stereotaxic apparatus...
ear bars and an upper jaw support with tooth clamps. Extracellular recordings were obtained from single cells in area 17 with tungsten microelectrodes insulated with parylene (World Precision Instruments, Inc.). Electrodes had a tip diameter of 1–2 μm and an impedance of 1–5 MOhm measured at 500 Hz. 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. A cortical receptive field in the dominant eye was first examined with hand-held stimuli and plotted on the tangent screen to determine location, size, direction sensitivity, and preferred orientation. Some cells with stable and long-lasting recordings were more precisely characterized using electronically produced moving bars, and evaluation of the peristimulus time histograms (PSTHs). The receptive fields were located in the lower contralateral quadrant of the visual field, slightly below and lateral to the projections of the area centralis. They were within 10 deg of either area centralis. The width of the receptive fields was, on average, 3.2 ± 1.6 deg. Complex cells were identified according to their response profiles to moving bars (Hubel & Wiesel, 1962) (most importantly the absence of separate “on” and “off” regions) and their responsiveness to a moving textured stimulus (Hammond & MacKay, 1975; Hammond & MacKay, 1977). Only cells with a vigorous response to moving RPAs, and a direction index of more than 0.5 were examined. The direction index is defined as 1–(response in non-preferred direction/response in preferred direction), after subtraction of spontaneous activity (Baker et al., 1981; Orban et al., 1981).

**Stimulus**

The moving RPA (256 × 256 pixels) consisted of 50% black and 50% white pixels. For each stimulus presentation the positions of the black and white pixels were newly determined, e.g., the pattern was never identical. The stimuli were generated by the same type of custom built image generation hardware as used in human psychophysical experiments in our laboratory (e.g., Fredericksen et al., 1993). The frame rate of the P4 phosphor screen was 90 Hz, corresponding to a base frame-exposure duration of 11 msec. All temporal delays used in this study are integer multiples of this base frame duration. For the single-step pixel lifetimes (B), half the pixels move coherently (indicated by the arrows), while the other half is randomly refreshed. The next time-step the other half moves coherently. This results in a stimulus that contains mainly (with 50% probability) one specific step size and delay between the steps (one spatio-temporal displacement). The average luminance was set to 50 cd/m², with an average r.m.s. contrast level of 70%. At a viewing distance of 57 cm the pixel size was 3.3 × 3.3 min of arc.

14 × 14 deg. The mean luminance of the random pixel array (RPA) was 50 cd/m² with an average r.m.s. contrast level of 70%. See Fredericksen et al. (1993) for more technical details about the stimulus.

A practical advantage of using RPAs for studying sensitivity to apparent motion in complex cells, is that an RPA has 50% black and 50% white pixels, thus providing a wide band of spatial and temporal frequencies, with random phases. This makes it much easier to ensure, for any step size, that the entire receptive field is equally well stimulated, as compared to, for instance, flashed bars.

**FIGURE 1.** Schematic diagram of the stimulus design. The complete random pixel array (50% dot density) consisted of 256 × 256 black or white pixels. To explain the difference between the unlimited and single-step pixel lifetimes, we show only one column of 11 pixels moving rightward. The surrounding area, also filled with black or white pixels in the actual stimulus, is colored gray in the figure. For the unlimited lifetime stimulus (A) the pixels move each time step (from t₁ to t₂ and from t₂ to t₃) n pixels to the right (in the figure the step size is one pixel). The speed of the pattern can be changed by either varying the step size (in pixels) or by changing the time between the steps. The duration of each time-step is an integer multiple of the 11 msec duration of the monitor base frame rate. For the single-step pixel lifetimes (B), half the pixels move coherently (indicated by the arrows), while the other half is randomly refreshed. The next time-step the other half moves coherently. This results in a stimulus that contains mainly (with 50% probability) one specific step size and delay between the steps (one spatio-temporal displacement). The average luminance was set to 50 cd/m², with an average r.m.s. contrast level of 70%. At a viewing distance of 57 cm the pixel size was 3.3 × 3.3 min of arc.
As mentioned in the Introduction, we used RPAs with an unlimited pixel lifetime to compare our physiological results with earlier psychophysical results. Figure 1 shows the difference between unlimited and single-step pixel lifetimes. For unlimited pixel lifetime [Fig. 1(A)], all pixels move coherently at each time step (here with a displacement size of 1 pixel). For the single-step pixel lifetime [Fig. 1(B)], each pixel is randomly refreshed after one step. At each time-step, half the pixels are displaced and the other half are refreshed (random black or white). During the next time-step, the pixels that moved coherently during the previous step are now refreshed and vice versa. This results in motion specified by one specific delay and spatial displacement. During the refresh-step, the new luminance of the pixel is not
**CAT COMPLEX CELLS AND APPARENT MOTION**

**preferred direction**  
![Graph showing response histograms for preferred direction](image)

**non-preferred direction**  
![Graph showing response histograms for non-preferred direction](image)

**displacement** (arc min) **delay** (msec)

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**FIGURE 3.** Response histograms of a complex cell (930404) to a moving random pixel array with unlimited pixel lifetime. The spatial displacement and temporal delay of a single sequence of frames for all combinations were changed in equal proportions, as indicated on the right-hand side of the figure, so that the speed remains the same. Tick marks indicate the timing of the steps. The average spike frequencies are shown in the upper right corners. For cell characteristics, see the legend of Fig. 2(A).

The initiation of the stimulus sweeps and the parameter settings of the moving RPAs were performed by a Macintosh IIfx computer. On-line data acquisition and processing were done with the same computer. An experiment consisted of nine or more pseudo-randomly interleaved trials, with different spatial-displacement and temporal-delay combinations. Each experiment was repeated five to ten times and the average firing rate and other statistical parameters were calculated. One trial consisted of a 0.8 sec presentation of a stationary pattern to determine the spontaneous activity, followed by 2 or 3 sec of motion in the preferred direction, then a 0.8 sec stationary pattern, and finally 2 or 3 sec of motion in the non-preferred direction. The non-preferred direction is defined as the direction opposite to the preferred direction. For all cells in this study the direction of minimal response corresponded well with the direction opposite to the preferred direction.

**Measurement protocol and data analysis**

The initiation of the stimulus sweeps and the parameter settings of the moving RPAs were performed by a Macintosh IIfx computer. On-line data acquisition and processing were done with the same computer. An experiment consisted of nine or more pseudo-randomly interleaved trials, with different spatial-displacement and temporal-delay combinations. Each experiment was repeated five to ten times and the average firing rate and other statistical parameters were calculated. One trial consisted of a 0.8 sec presentation of a stationary pattern to determine the spontaneous activity, followed by 2 or 3 sec of motion in the preferred direction, then a 0.8 sec stationary pattern, and finally 2 or 3 sec of motion in the non-preferred direction. The non-preferred direction is defined as the direction opposite to the preferred direction. For all cells in this study the direction of minimal response corresponded well with the direction opposite to the preferred direction.

Constrained by whether the last pixel was black or white. Therefore, there is a 50% chance that the luminance is not changed, meaning that pixels can have lifetimes of two time-steps or more. In that sense our paradigm is comparable to the 50% correlation moving random dot patterns that were used by Newsome & Paré (1988). However, when refreshed, the pixels are distributed in all directions and therefore cannot introduce a difference in response for the preferred and non-preferred directions. Randomly refreshing pixels will introduce motion energy in all other directions. The overall result is net directional motion energy restricted to a single direction and to only a specific spatial displacement and delay.

**FIGURE 3.** Response histograms of a complex cell (930404) to a moving random pixel array with unlimited pixel lifetime. The spatial displacement and temporal delay of a single sequence of frames for all combinations were changed in equal proportions, as indicated on the right-hand side of the figure, so that the speed remains the same. Tick marks indicate the timing of the steps. The average spike frequencies are shown in the upper right corners. For cell characteristics, see the legend of Fig. 2(A).
preference direction from the response in the non-preferred direction, as a measure of the directional selectivity of the cell. Note that this is different from the direction index as described above.

RESULTS

Unlimited lifetime of the pixels

First, we describe the response of complex cells to apparent motion of RPAs with an unlimited pixel lifetime. This corresponds to a "normal" coherently moving RPA. All pixels are displaced with the same step size and delay between the steps. Figure 2 shows results for three representative complex cells from a sample of 25 cells. The response measure is the cell's average firing rate during the 2 or 3 sec of motion presentation as a function of delay and step size, at the preferred speed. The random pixel array (RPA) moved either in the preferred (open squares) or in the opposite, non-preferred direction (closed discs). The horizontal dashed line shows the average spontaneous activity of the cell. The abscissa represents both the step size and the inter-step delay of the RPA movement. Their ratio is constant, which means that the speed is constant [here 5.9 (A), 4.2 (B) and 7.5 (C) deg/sec]. Of course, the motion appears less and less smooth, as the step size and delay values increase.

The response to motion in the preferred direction at first decreases only slightly when both the displacement and inter-step delay in the stimulus increase. For the cells presented in Fig. 2, the curves start declining more sharply at step size and delay combinations of about 31, 39, and 34 min of arc with a delay of about 88, 154 and 77 msec, respectively. The cells do not show a very pronounced inhibition of spontaneous activity in the non-preferred direction. The response to the flicker of the stimulus. No correlation can take place because either the step size is too large or the delay is too long.

Single-step vs unlimited pixel lifetimes

In Fig. 4 we compare the results for unlimited pixel lifetime, as shown in Fig. 2, to a single-step pixel lifetime. The open squares in Fig. 4 show the response in the preferred direction, while the discs show the response in the non-preferred direction. The ratio of spatial displacement and delay is constant. To aid comparing results for single-step and unlimited pixel lifetimes, we include the results for the unlimited lifetime (thin lines). [Compare Fig. 4(A) with Fig. 2(C).]

Only cells that are very responsive to RPAs with an unlimited pixel lifetime give reliable responses to motion with a single-step pixel lifetime (11 out of 25 cells). The two examples from this subset of 11 cells. A difference between the two stimuli is that RPAs with unlimited lifetime contain spatio-temporal correlation required for motion sensitivity. For unlimited pixel lifetime, all cells are correlated (see Fig. 1). This might explain why the maximum response to RPAs with a single-step pixel lifetime is always much smaller than for RPAs with an unlimited lifetime of the pixels.

The most important difference between the two types is that RPAs with unlimited lifetime contain correlation for multiples of the step size and delay combinations, while RPAs with a single-step pixel lifetime mainly contain one specific displacement and delay combination. The difference in response is most clearly seen when the displacement and delay values are small. For short delays and small displacements, there is no response to moving RPAs with a single-step pixel lifetime. At the same spatio-temporal combination, the response to unlimited pixel lifetime is mostly at its maximum. Obviously, with single-step pixel lifetimes the spatio-temporal correlation required for motion sensitivity fails at these step size–delay combinations. For unlimited pixel lifetimes the cell still responds, presumably because it correlates over multiple steps. It is important to note that the temporal characteristics of the two stimuli are the same. Thus, the large difference in
Figure 4. Average responses of two complex cells to a random pixel array (RPA) with a single-step pixel lifetime. The RPA moved in the preferred (open squares) and non-preferred (solid discs) direction and for all spatial and temporal combinations. The thin lines indicate the average response of the cell to an RPA with unlimited pixel lifetime, as shown in Fig. 2. The horizontal, dashed line indicates the average spontaneous activity of the cell. On the abscissa, the displacement size and delay at which the RPA is moved are indicated. The speed was equal for the different displacement and delay combinations [(A) 7.5 deg/sec; (B) 15.3 deg/sec]. The error bars represent ±1 SEM. For cell characteristics of cell A (931302), see the legend of Fig. 2(C). (B) Cell 941402: ipsilateral; receptive field size, 2.4 deg; receptive field position 8 deg from area centralis; preferred speed, 7.7 deg/sec.

Response is due to the fact that for the single-step pixel lifetime no correlation could be established. The curves for RPA with a single-step pixel lifetime in Fig. 4 show tuning to a range of spatial displacements and temporal delays. Even though all combinations represent the same, preferred speed, the curves show an optimum range. The response for single-step pixel lifetime at the larger spatial displacement and longer temporal delays declines similarly to the response for unlimited pixel lifetimes (thin lines in Fig. 4).

The curves as presented in Figs 2 and 4 provide only limited information about the spatio-temporal correlation required for directional selectivity. So far, we have shown results for different combinations of displacement and delay for one speed only. A sequence of displacements of an RPA may fail to elicit direction-selective responses, either because the time interval between flashes is inappropriate, or because the spacing between the flashes is unsuitable, or both. Furthermore, one cannot exclude the possibility of more than one optimal spatial displacement and delay.

For some cells (n = 5) we could carry out a much more extensive series of measurements than those represented in Figs 2 and 4. For these cells, we determined the average response in the preferred and non-preferred directions for a wider range of displacement and delay combinations, also for different speeds. The results for two cells are shown as contour plots in Figs 5 and 6. The figures present the responses to both unlimited (A, C and E) and single-step pixel lifetimes (B, D and F). The shading in the plots represents the average response in the preferred direction (A and B) and the average response in the non-preferred direction (C and D). High activity is shown by darker shading, while low activity is shown by...
FIGURE 5. Contour plots representing the average firing rate during 3 sec stimulus presentations in the preferred (A, B) and non-preferred direction (C, D), as a function of spatial displacement and temporal delay for RPAs. The lower panels (E, F) show the calculated preferred minus non-preferred response. In the left panels, the pixel lifetime of the moving RPA was unlimited and for the right panels a single step. A high firing rate or a large difference in response between preferred and non-preferred direction, is shown by darker shading, as indicated on the right-hand side of the figure (in spikes/sec). All grid points at the tick marks indicated on the axis were evaluated. For the characteristics of this cell (941402) see Fig. 4(B).
FIGURE 6. See the legend of Fig. 5 for a description of the plots. For the characteristics of this cell (931302) see Fig. 2(C).
curves in Fig. 2 [Fig. 6 is the same cell as in Figs 2(C) and 4(A)]. Figures 5(A) and 6(A) show that along this equal speed line, just before the response declines drastically, there is a point of highest response to motion in the preferred direction. For very long delay values, the cell in Fig. 6 still responds to motion at this preferred displacement. The response to motion in the non-preferred direction either does not change [Fig. 5(C)] or shows the same dependency on spatial displacement and temporal delay as to motion in the preferred direction [Fig. 6(C)]. For the unlimited pixel lifetime, subtraction of responses to the preferred and non-preferred direction [Figs 5(E) and 6(E)] does not result in drastic changes of the plots, compared to the response in the preferred direction.

The response to motion of an RPA with a single-step pixel lifetime has different characteristics. The contour plots for the preferred direction [Figs 5(B) and 6(B)] show more localized ranges of displacement and delay combinations to which a cell responds. The cell in Fig. 6 has several optimal peaks both for the preferred and non-preferred direction. However, when the responses to both directions are subtracted [Fig. 6(F)], the plot shows only one clear peak. The conclusion is that the directional selective response (difference between preferred and non-preferred direction) of both cells is tuned to only a small range of displacements and delays. The range of optimal displacements is largely independent of the temporal delay between the steps. The optimal delay values were about 99, 55, 88, 55 and 55 msec and corresponding optimal spatial displacement values 0.68, 0.68, 0.44, 0.42 and 0.42 deg, respectively. These optimal combinations correspond to the optimal speed lines found for unlimited pixel lifetimes. The major difference between an unlimited pixel lifetime and a single-step pixel lifetime is that the response and directional selectivity decrease at small step sizes for a single-step pixel lifetime. For all five cells subjected to this experiment we found a clear change from tuning to speed for unlimited-pixel-lifetime RPAs to tuning to a small range of step sizes and delays for single-step pixel lifetime RPAs.

It would be interesting to gain an overview of the optimal displacement and delay values for a population of these complex cells, and to correlate these values with other cell properties, like receptive field size, eccentricity, and preferred speed. The contour plots with single-step pixel lifetimes, as shown in Figs 5 and 6, give the best information, but are rather hard to obtain because these experiments take a long time. Also, it is clear from a comparison of Figs 2 and 4 that using a single-step pixel lifetime paradigm yields much smaller responses with higher variabilities. To obtain data on a sufficiently extensive population of cells, we calculated the direction index (see Methods section for definition) for each displacement and delay combination only, at the preferred speed and for an unlimited pixel lifetime from the data as shown in Fig. 2. These directional index plots have the same shape as the curves shown in Fig. 2 for the preferred direction, but often with a steeper decline. The displacement value at which the direction index was 50% of the maximum direction index was used as an estimate of the maximum displacement and delay values.

Figure 7 shows two scatterplots of the maximum displacement size and maximum delay against the preferred speed for 25 cells, using an RPA with an unlimited pixel lifetime. Figure 7 shows that cells with lower preferred speeds have a higher maximum delay and a lower maximum displacement. This correlates nicely with other direct demonstrations that neurons preferring lower velocities are those that respond to smaller jump sizes in two-flash apparent motion (Baker & Cynader, 1988).

No significant correlations between either maximum step size or delay with eccentricity or with receptive field size were observed, although it has been reported repeatedly that the largest interflash spacings for directional selectivity occurred in cells with large receptive
fields and high eccentricities (Mikami et al., 1986; Duysens et al., 1987). That we could not confirm such correlations is probably due to the modest number of cells and the restricted cortical region of area 17 from which we recorded. The maximum displacement size of this sample of cells was, on average, 0.92 ± 0.32 deg. This is about three times smaller than the average receptive field size (in the preferred direction) of these cells, which was 3.2 ± 1.6 deg. The maximum delay was, on average, 105 ± 33 msec.

**DISCUSSION**

*Spatio-temporal characteristics of complex cells*

In this study we introduced a new way to evaluate the spatio-temporal requirements for directional selectivity of complex cells in area 17 of the cat. A comparison between RPAs with unlimited lifetime and with a single-step lifetime revealed that the directionally selective response of motion sensitive complex cells is tuned to a small range of specific combinations of spatial displacement and temporal delay, though other combinations yielded the same speed. By a directionally selective response, we mean the difference in response between the preferred and non-preferred directions. We are especially interested in this measure because we are interested in the ability of each cell to discriminate motion in its preferred direction from motion in its non-preferred direction. We assume that the firing rate of a directionally selective cell gives an estimate of the certainty that something is moving in a specific direction. If another cell tuned to the opposite direction has the same firing rate, it is impossible to tell from the responses of these two cells in which direction something is moving. From this point of view it is not the cells' firing rates that are important, but the difference in firing rates between the two cells. We assume that each cell has a virtual, complement cell that is tuned to the opposite direction. This is the same basic assumption that has been widely used by others, for instance, to derive the so-called neurometric functions of directionally selective MT cells (see for example Britten et al., 1992). The preferred minus non-preferred response calculation makes it possible to compare our results more directly with human psychophysical experiments using the same stimulus.

Our sample of area 17 cells was very specific. We selected cells within 10 deg of the area centrals that responded vigorously to moving RPAs. Directional tuning curves and other general cell properties were similar to those described in other studies, in which moving random dot patterns were used to stimulate cat area 17 cells (Hammond & MacKay, 1975, 1977; Orban et al., 1987; Crook, 1990; Bauer & Jordan, 1993; Casanova, 1993; Skottun et al., 1994). Based on the results of extensive investigations by Hammond's group with almost the same type of stimulus, it is likely that these cells are complex cells from layer V of area 17 (e.g., Hammond & Smith, 1982; Hammond, 1985; Edelstejn & Hammond, 1988; but, for a discussion about classification of complex and simple cells with moving random texture patterns, see Skottun et al., 1988; Hammond, 1991). Nonetheless, the maximum spatial displacements for our sample of complex cells fall in the same range as the values found in other studies on area 17 cortex cells. We found maximum displacement values of about 0.4–1.6 deg. The largest distance over which direction-selective effects were obtained with bars was reported to be always greater than 0.3 deg (Emerson & Gerstein, 1977; Duysens et al., 1987), but less than 1.5 deg in cat area 17 (Ganz & Felder, 1984) or monkey V1 (Mikami et al., 1986), although Duysens et al. (1987) reported a maximum value of 4.7 deg. The similarity in absolute values is remarkable because cells were selected differently and they were examined with totally different stimulus paradigms. Furthermore, one has to keep in mind that these maximum displacement values depend not only on stimulus design and sampling biases, but also on differences in the definition of maximum displacement. In agreement with previous findings for the maximal displacement in relation to receptive field size (Cremieux et al., 1984; Ganz & Felder, 1984; Baker & Cynader, 1986, 1988), we found that the receptive field sizes of the complex cells were, on average, about three times larger than the maximal displacement. Baker & Cynader (1986) also showed that for complex cells, the optimal displacement is invariant across the extent of the receptive fields. This would suggest that the receptive field of these complex cells consists of a distribution of motion-processing subunits with the same spatial parameter.

Recent studies in which reverse correlation methods were used (Baker & Boulton, 1994; Emerson et al., 1992) reported ranges of delays that agree with our results (between about 50 and 100 msec). We showed in Fig. 5 that cells are still direction selective at long delays at their optimal spatial displacement. So it seems that cells are broadly tuned in the temporal domain. Other studies (Duysens et al., 1987) also reported cells that remain directionally selective at delays as long as 250 msec. However, it is important to note that the actual delay in the stimulus ranges from zero to twice the delay duration, because in our stimulus there was no interchange interval.

We found that the range of optimal displacements for directional selective responses does not vary with a change in temporal delay. This is consistent with findings that the optimal jump size for a bar is invariant with the temporal parameters of the stimulus (Baker et al., 1991). It suggests that the spatial and temporal requirements for a difference in response to the preferred and non-preferred directions in complex cells are separable. Such a finding of separability for directional selectivity does not contradict other work that shows dependence of directional selectivity on inseparable filters in striate neurons (e.g., Hamilton et al., 1989; Pollen et al., 1989; Emerson et al., 1992; Emerson & Citron, 1992). It has been shown that almost all neurons show space–time separability, when non-separable second order interaction plots are collapsed to show the overall amount of
directional selectivity, by calculating the preferred-minus-null response (Emerson et al., 1987, 1992; Baker, 1994). In other words, our preferred minus non-preferred calculation shows separability, although the underlying mechanism may be inseparable. The separability and the tuning for a specific spatial displacement and delay suggest that it is reasonable to use either bilocal or Reichardt detectors (Reichardt, 1961) or motion energy detectors (Adelson & Bergen, 1985) to describe the motion discrimination ability at the level of complex cells of cat area 17.

**Human psychophysics**

The present study was motivated by the psychophysical work of Fredericksen et al. (1993, 1994a,b), who used the same stimulus paradigm and stimulus generator for studying human motion detection. Of course we realize that one has to be extremely careful when comparing the responses of single cortical cells in the cat with human psychophysics. Yet psychophysical work can provide specific research questions for which one can find answers in physiological studies (and vice versa).

The work of Fredericksen et al. (1993, 1994a,b) suggests that the human motion detection system can be described by a front-end array of correlational devices, bilocal detectors, whose outputs are used to compute higher-level motion information. Such an initial stage of visual motion processing has been successfully used as a unifying framework for a diversity of findings concerning human motion detection (Nakayama, 1985; van de Grind et al., 1992, 1986; van Doorn & Koenderink, 1982a,b, 1985; Koenderink et al., 1985; Borst & Egelhaaf, 1989; Zanker, 1994). In the studies of Fredericksen et al. (1993, 1994a,b), a stimulus was specially designed to isolate detectors tuned to one specific spatial displacement and temporal delay. Here we report responses of area 17 complex cells to the same stimulus (Figs 4 and 5). These complex cells can be considered as an early stage of motion detection of RPAs because they are among the first cells in the visual system of the cat that respond direction-selectively to moving RPAs (Hammond & MacKay, 1975, 1977).

Our present results indicate that direction-selective cells in area 17 of the cat show a large difference in response to moving RPAs with a single step vs with an unlimited lifetime. RPAs with a single-step pixel lifetime elicit strong direction-selective responses only for a small range of displacement and delay combinations. Thus, one has to be careful with the interpretation of results obtained with single-step or limited pixel lifetimes in RPAs or random dot patterns. The reason behind using limited lifetime patterns in human psychophysical experiments or electrophysiological studies with behaving monkeys (e.g., Britten et al., 1992, 1993; Qian & Andersen, 1994) is often to avoid tracking of individual dots or groups of dots. Our results show that one has to keep in mind that these patterns may address only a restricted group of cells tuned to a specific range of displacement and delay combinations in the stimulus. The results show that the basic assumption of the psychophysical studies of Fredericksen et al. (1993) is supported by our physiological results, because the results in Figs 5 and 6 show directionally selective responses for a specific range of displacement and delay combinations in the stimulus.

Our results also provide relevant information to test the plausibility of models for temporal integration in motion perception based on human psychophysical experiments, such as the studies of Fredericksen et al. (1994a,b). The present neurophysiological results support the ideas underlying the leaky integration model of Fredericksen et al. (1994a,b). The stepping RPA provides discrete, pulsatile visual motion information, which is reflected in the discrete responses of area 17 complex cells (see Fig. 3). As the temporal delay is increased the individual bursts of activity become distinguishable. At shorter delays the response pulses merge, a condition approximating the response to a "real" motion stimulus. Furthermore, the cells show an increase in firing rate over time until a maximum firing rate is reached, suggesting temporal integration over time (after the initial burst of firing) (see Fig. 3). At long delays, the cells still show directional selectivity at the optimal displacement, but no temporal integration. This supports psychophysical findings that there is no threshold improvement with longer stimulus presentation, when long delays are used (Fredericksen et al., 1994a,b). At shorter delays the duration of the stimulus is a better measure of temporal improvement of directional motion thresholds in humans than the number of displacements (Fredericksen et al., 1994a,b).

In summary, by comparing responses to single-step and unlimited pixel lifetimes we show that directional selectivity (the difference in response between preferred and non-preferred direction) of cortical cells is tuned to a small range of displacement-delay combinations. Based on these findings, it may be beneficial to further specify the spatial and temporal parameters, for example, as a function of eccentricity. The data also provide a physiological basis for some findings reported in human psychophysical studies of motion detection.

**REFERENCES**


Acknowledgements—Richard van Wezel is supported by the Life Sciences Foundation of the Dutch Organization of Scientific Research (NWO). We are grateful to Bob Emerson and David Alais for helpful comments on the manuscript. Parts of this work have been previously presented in abstract form (van Wezel et al., 1994, 1995).