Interactions Between ON and OFF Signals in Directional Motion Detectors Feeding the NOT of the Wallaby

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Ibbotson, M. R. and C.W.G. Clifford. Interactions between ON and OFF signals in directional motion detectors feeding the NOT of the wallaby. J Neurophysiol 86: 997–1005, 2001. An apparent motion stimulus is used to probe the interactions between signals representing brightness increments (ON stimuli) and decrements (OFF stimuli) in the directional motion detectors forming the input to the nucleus of the optic tract (NOT) of the wallaby, Macropus eugenii. Direction-selective NOT neurons increase their firing rates during image motion from temporal-to-nasal over the contralateral eye (preferred direction) and their spontaneous activities are inhibited by motion in the opposite, anti-preferred direction. An apparent motion stimulus, consisting of neighboring vertical bars, where the brightness can be manipulated independently, also produces directional responses. Preferred direction sequences of brightness changes of like polarities (ON-ON or OFF-OFF) produce increased firing rates while sequences of opposite polarities (ON-OFF or OFF-ON) in the same direction produce relatively small excitatory responses or inhibit the spontaneous rate. For apparent motion in the anti-preferred direction, these directional properties are reversed, showing that signals for brightness increments and decrements provide inputs to the same motion detectors. There is no evidence for segregation of motion detectors into those receiving only half-wave rectified inputs. Interactions between ON and OFF signals utilize the sign of the incoming signals. An array of Reichardt-type motion detectors receiving inputs represented as positive and negative values for ON and OFF stimuli, respectively, are used to simulate the NOT responses. The brightness signals enter band-pass temporal filters prior to motion detection. By altering the time constants of these prefilter, it was possible to accurately simulate the time courses of each cell’s responses.

INTRODUCTION

Direction-selective neurons have been identified in a wide range of brain regions and species (for early examples, see: frog retina: Barlow 1953; Lettvin et al. 1959; rabbit retina: Barlow and Levick 1965; Barlow et al. 1964; cat cortex: Hubel and Wiesel 1962, 1965; insect optic lobe: Hausen 1976). In most cases, the signals are generated by motion detectors in which nonlinear interactions occur between signals from neighboring regions of the visual image after introducing a temporal asymmetry (Borst and Egelhaaf 1989; Emerson et al. 1987, 1992; Poggio and Reichardt 1973). Although the response characteristics of a motion detector depend to a large extent on the internal structure of the detector itself, the final response is also dependent on the way in which the incoming signals are modified by earlier processing stages (Nakayama 1985). For example, it is likely that incoming signals are acted on by spatiotemporal band-pass filters producing large responses to brightness changes and either small or no responses when the brightness level is constant (e.g., Egelhaaf and Borst 1992). Also, brightness increments (ON stimuli) and decrements (OFF stimuli) in the image might be processed separately (Kuffler 1953; Schiller et al. 1986).

It is well established that vertebrate photoreceptors are hyperpolarized by light and their outputs are fed into bipolar cells. Sign-conserving synapses feed OFF bipolar cells while sign-inverting synapses feed ON bipolar cells (Werblin and Dowling 1969). Further processing occurs in the retina to produce a wide diversity of response properties in the ganglion cells, including direction-selective neurons (DeVries and Baylor 1997; Levick and Thibos 1983). The most commonly encountered cells have receptive fields divided into center and surround regions that respond to opposite contrast polarities (Kuffler 1953). Two types of center-surround cells exist, ON-center cells, which increase their activity when bright bars are presented in their receptive fields, and OFF-center cells, which are excited by bars darker than the background. Importantly, the background activities of ON- and OFF-center cells are inhibited by dark and bright bars, respectively (e.g., Enroth-Cugell and Robson 1966; Hochstein and Shapley 1976). Schiller et al. (1986) suggest that both ON and OFF channels exist in the mammalian visual system to supply information to the CNS about light increments and decrements through an excitatory process. This is necessary because the spontaneous activities of retinal ganglion cells are low, so the information about a light increase in an OFF-center cell or decrease in an ON-center cell is highly compressed. Therefore the existence of ON and OFF channels greatly improves the efficiency of information transfer for increments and decrements.

The present paper studies the responses to brightness increments and decrements of direction-selective neurons in the nucleus of the optic tract (NOT) of the wallaby, Macropus eugenii (Clifford et al. 1997; Hoffmann et al. 1995; Ibbotson 2001; Ibbotson and Mark 1996; Ibbotson et al. 1994, 1998, 1999). The NOT is a pretectal structure containing horizontally tuned direction-selective neurons that control the slow phases of optokinetic eye movements (Simpson 1984). While experiments conducted in the cat...
visual cortex show that signals coding brightness increments and decrements interact with each other in the motion detectors of that system (e.g., Emerson et al. 1987, 1992), little is known about the sensitivity to brightness increments and decrements and their effect on the response properties of neurons in the NOT of any species. Here we use an apparent motion stimulus consisting of neighboring vertical bars that can increase or decrease their brightness relative to a mean level of background luminance. The apparent motion stimuli are used to observe interactions between brightness increments and decrements in neighboring regions of the receptive fields of NOT neurons. The polarity sensitivity of the prefilter that provide the input to motion detectors has a profound influence on their directional tuning properties and, therefore, the directional tuning of any downstream neurons, such as those in the NOT. What are these directional properties and what do they tell us about the structure of the motion detectors that provide the input to NOT neurons?

METH ODS

Physiology

Recordings were made from the NOT of anesthetized, paralyzed wallabies (M. eugenii). The physiology and anatomy of the wallaby visual system is generally similar to more common laboratory mammals, such as cats (Mark and Marotte 1992). Recordings were obtained from four wallabies weighing 4.5–7.0 kg. All procedures were approved by the animal experimentation ethics committee of the Australian National University and followed the guidelines of the National Health and Medical Research Council of Australia. Anesthesia, surgery, and extracellular recording methods have been described in detail (Ibbotson et al. 1994). The stimuli were presented on a display monitor (CCID7551: Barco Industries) and were generated by a computer controlled video display driver (AT Vista: True Vision). The refresh rate of the monitor was 97.7 Hz, and each frame contained 480 lines (512 pixels/line). The screen subtended 67° x 52° at the eye, and the display monitor could be moved to any location within the visual field of the animal. The display screen was positioned for each neuron so its center was as close as possible to the most responsive region of the cell’s receptive field. Experiments were conducted with a stimulus consisting of 10 pairs of bars spread across most responsive region of the cell’s receptive field. Experiments were tioned for each neuron so its center was as close as possible to the eye, and the display monitor could be moved to any location contained 480 lines (512 pixels/line). The screen subtended 67° x 52° at the eye, and the display monitor could be moved to any location within the visual field of the animal. The display screen was positioned for each neuron so its center was as close as possible to the most responsive region of the cell’s receptive field. Experiments were conducted with a stimulus consisting of 10 pairs of bars spread across 27.5° of the stimulus screen. All bar pairs were identical and consisted of two vertical areas (bar A and bar B) subtending 52° (vertically) by 0.7°. Bar A was on the left and bar B on the right when viewing the screen. The two bars were horizontally abutting, and the separation between neighboring bar-pairs was 1.5°. All areas of the screen surrounding the bar-pairs were gray (45 cd/m²). Bars A and B could be either the same gray as the surround or have a brightness of 85.5 cd/m² (contrast increment) or 8 cd/m² (contrast decrement). The stimulus sequence was as follows: one of the bars in each pair would appear on the screen (either bright or dark) in a selected frame and remain on the screen for 10 s, thus generating step changes in contrast at those screen locations. The second bar in each pair would appear on the screen a certain number of frames later and remain on the screen until the trial finished, again producing a step change in brightness. The interval between the appearance of the bars is referred to as the inter-stimulus interval (ISI). The ISI could be any number of frames, each frame lasting 10.23 ms. Typical ISIs were from 10 frames to 100 frames.

Theoretically, the experiment could have been conducted with just one bar pair but the responses were small. By having 10 bar pairs operating in synchrony, it was possible to elicit quite large responses from the neurons. Due to the proximity of the bar pairs (1.5° separation), it is possible that there were some interactions between slits in neighboring pairs. However, except in magnitude, differences in the responses obtained with a single bar pair and 10 bar pairs were negligible. Due to the relatively small areas of the visual field occupied by the stimulus bars, the responses of the neurons to the apparent motion stimulus could be small even with 10 bar pairs. Consequently the background activity of the neurons was not always driven to zero by apparent motion in the anti-preferred direction.

Model

Responses were simulated using a five-stage model: prefiltering, delay filtering, multiplication, subtraction and spatial integration (Fig. 1). In the first stage, the image is operated on at all points by causal temporal filters that have a transient response to changes in image intensity. The transient response is achieved by subtracting the responses of a pair of first-order low-pass filters of equal gain but different time constants (τ₁, τ₂). The impulse responses, h(t), of the first-order low-pass temporal filters were given by

\[ h(t) = \begin{cases} \frac{1}{\tau} \exp\left(-\frac{t}{\tau}\right), & t \leq 0 \\ 0, & t > 0 \end{cases} \]

where τ is either τ₁ or τ₂. Inclusion of the initial 1/τ term equates the gains of the two low-pass filters, ensuring that their sustained responses cancel each other on subtraction. The transient response of the resulting band-pass temporal filter (BPTF, Fig. 1) is achieved by subtracting the responses of the first-order low-pass filters. The resultant difference filters have bi-phasic temporal impulse responses with τ₁ controlling the initial excitatory component and τ₂ controlling the duration of the inhibitory tail (Fig. 2A). The inputs had contrast values ranging from 1 to −1. Positive contrast values indicate brightness increments and negative values decrements. To show the time courses of the filter outputs, we present the impulse responses and step responses of the filters to brightness increments (Fig. 2, —) and decrements (Fig. 2, - - -). In the experiments presented here, we use step changes in brightness, so the step responses (Fig. 2B) are representative of the inputs to the motion detectors used to generate the simulations illustrated in Figs. 8 and 9.
The responses in Fig. 3 were from a neuron that responded optimally to the continuous motion of a sinusoidal grating at temporal frequencies of 6–12 Hz. The cell had a background activity of 35 spikes/s, which is represented by the horizontal line in Fig. 3. The spontaneous activity is represented in the same way in Figs. 4 and 5 for two other neurons. Phi motion in the preferred direction produced a small excitatory discharge to the brightness change in the first bar and a larger response to the brightness change in the second bar (Fig. 3, A and B). The response magnitudes generated by the ON-ON and OFF-OFF sequences were very similar. Reverse phi motion in the preferred direction produced a similar response to the first brightness change, followed by a reduction of the cell’s background firing rate after the second bar appeared (Fig. 3, C and D). For apparent motion in the anti-preferred direction, phi motion generated an excitatory response to the first bar, followed by a reduction in background firing rate when the second bar appeared (Fig. 3, E and F). Reverse phi motion in the anti-preferred direction generated a short-lived excitation to the appearance of the first bar and a larger excitatory response to the appearance of the second bar (Fig. 3, G and H).

Figure 4 shows the directional responses of a cell that was maximally sensitive to grating motion at 12–18 Hz. The apparent motion stimulus produced large but very transient responses from the cell. As with the cell in Fig. 3, the neuron produced a small response to the appearance of the first bar in all tests. During phi motion in the preferred direction, the response to the second bar was facilitated (Fig. 4, A and B) while for phi motion in the anti-preferred direction, the response to the second bar was attenuated (Fig. 4, E and F). Unlike the cell in Fig. 3, however, the response during phi motion in the anti-preferred direction did not fall below the level of spontaneous background activity. Even though the response was not inhibited below the background level, the motion component of the response was negative because the response to apparent motion was smaller than the response to that bar when it was presented alone (see Fig. 6 for details on

FIG. 3. Responses of an NOT neuron to phi motion (A, B, E, and F) and reverse phi motion (C, D, G, and H) in the preferred (P) and anti-preferred (AP) directions. The cell’s firing rate increases in response to the 2nd bar for P direction phi motion and for AP direction reverse phi motion. It is inhibited during AP phi motion and for P direction reverse phi motion. The peristimulus time histograms (PSTHs) in each panel are the average responses to identical stimuli. The peristimulus time histograms are shown for the same 50 ms time window as in Fig. 2.

FIG. 2. Impulse responses (A) and step responses (B) of the prefilters used in the model to ON stimulation (—) and OFF stimulation (— — ). The prefilters are causal band-pass temporal filters that have a transient response to changes in image intensity. The transient response is achieved by subtracting the responses of a pair of first-order low-pass temporal filters of equal gain but different time constants \( \tau_1 = 1.2 \text{ ms} \) and \( \tau_2 = 24 \text{ ms} \).

The responses of the BPTFs are fed into a one-dimensional array of correlation-based Reichardt detectors. Each motion detector consists of two subunits tuned to opposite directions of motion. These subunits also give some motion-independent responses (Egelhaaf et al. 1989). The output of each subunit may be thought of as the correlation of two spatially and temporally displaced samples of the image. The prefiler response from a given location is passed through a temporal delay filter (stage 2, Fig. 1) and multiplied (stage 3, Fig. 1) with the signal from a neighboring location. The temporal displacement between the signals is determined by the time constant of the motion detector delay filter, itself a causal first-order low-pass temporal filter. In stage 4 (Fig. 1), the motion detector response is obtained from an opponent combination of its sub-units. If the opponent combination is unbalanced, some motion-independent signals are transmitted. We quantify the balance, \( 0 \leq \beta \leq 1 \), of a motion detector according to the equation: 

\[
R(t) = P(t) - \beta \cdot A(t),
\]

where \( P(t) \) and \( A(t) \) are the outputs of the subunits responsive to preferred and anti-preferred motion, respectively, and \( R(t) \) is the motion-detector response.

In the fifth stage of the model, the response of the spatial array of motion detectors is summed to represent the input to a wide-field NOT cell. If the response of the motion-detector array is positive, the model neuron will respond above its baseline level. If the array response is negative, the response level will be below the resting level (simulating inhibition). The model does not produce individual spikes but rather a response level that simulates the spike rate. Quantitatively, the spiking rate of the model NOT cell is a linear function of its input between a floor of 0 Hz (no spiking) and its maximum firing rate.

RESULTS

The results presented are based on recordings from 22 direction-selective neurons in the NOT. The responses of three neurons are shown as peristimulus time histograms in Figs. 3–6. These cells were chosen because they clearly show the general directional properties that were evident in all 22 neurons, and they show the range of temporal characteristics that were found. None of the cells showed an absolute selectivity for brightness increments or decrements.

Eight stimulus conditions were used. In four of the conditions, both bars had the same contrast polarity and the apparent motion is referred to as phi motion. These would be ON-ON and OFF-OFF sequences in the preferred and anti-preferred directions. In the remaining four conditions, the bars had opposite contrast polarities and the apparent motion is referred to as reverse phi motion, i.e., ON-OFF and OFF-ON sequences in the preferred and anti-preferred directions. The terms preferred and anti-preferred describe the directional tuning of the neurons during phi motion.

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Fig. 4. Responses of a 2nd NOT neuron to the stimuli described in Fig. 3. The cell’s firing rate increases in response to the 2nd bar for P direction phi motion and for AP direction reverse phi motion. The responses to the 2nd bar presentation during AP phi motion and P direction reverse phi motion are attenuated relative to the responses to the 2nd bar being presented alone. The PSTHs are the averages from 32 trials. The 1st bar appeared at 0.91 s and the 2nd bar at 1.77 s.

Fig. 5 shows the responses of a neuron that was maximally sensitive to grating motion at low temporal frequencies of 0.4–0.8 Hz. This cell produced sluggish, long-lasting responses to the presentation of a brightness change in either bar when presented in isolation. The cell responded to both brightness increments and decrements but the responses to the latter tended to be larger. For phi motion in the preferred direction, the response to the second bar was facilitated (Fig. 5, A and B). For phi motion in the anti-preferred direction, the appearance of the second bar produced a quite complex but characteristic

calculating motion components). The directionality was inverted during reverse-phi motion (Fig. 4, C, D, G, and H).

Figure 5 summarizes the directional properties of all 22 neurons. The data plotted in these graphs were calculated by taking the mean motion component (MC) of the response in each of the eight directional tests. The mean MC was the mean response across a selected number of bins in the PSTH (i.e., the sum of the responses per bin divided by the number of bins). The exact magnitude of the response was less important than its polarity so no statistical measure was used to calculate the beginning or end of the responses. Rather for each cell, the duration of the excitatory motion component to the ON-ON sequence was judged by eye from the PSTHs (starting at the response. This consisted of a small, short-lived inhibition below the background firing rate followed by a prolonged excitatory discharge (Fig. 5, E and F). The excitation was smaller than the response produced by a brightness change in that bar when presented in isolation. As with all the other cells tested, the directionality was inverted for reverse phi motion (Fig. 5, C, D, G, and H).

Prior to each of the eight stimulus conditions shown in Figs. 3–5, we measured the responses of the neurons to the presentation of the first and second bars in isolation. These responses are the flash responses of the cells. To obtain the motion components of the responses, the flash responses were subtracted from the apparent motion responses. We present the results of this analysis for the cell shown in Fig. 3 (Fig. 6). The horizontal line in Fig. 6 represents zero, so values above that line are positive motion components and values below the line are negative values. This analysis confirms that apparent motion in the preferred and anti-preferred directions with phi motion produce positive (Fig. 6, A and B) and negative (Fig. 6, E and F) motion components, respectively. Conversely, motion in the preferred and anti-preferred directions with reverse phi motion produce negative (Fig. 6, C and D) and positive (Fig. 6, G and H) motion components.

Figure 6 summarizes the directional properties of all 22 neurons. The data plotted in these graphs were calculated by taking the mean motion component (MC) of the response in each of the eight directional tests. The mean MC was the mean response across a selected number of bins in the PSTH (i.e., the sum of the responses per bin divided by the number of bins). The exact magnitude of the response was less important than its polarity so no statistical measure was used to calculate the beginning or end of the responses. Rather for each cell, the duration of the excitatory motion component to the ON-ON sequence was judged by eye from the PSTHs (starting at the response. This consisted of a small, short-lived inhibition below the background firing rate followed by a prolonged excitatory discharge (Fig. 5, E and F). The excitation was smaller than the response produced by a brightness change in that bar when presented in isolation. As with all the other cells tested, the directionality was inverted for reverse phi motion (Fig. 5, C, D, G, and H).

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beginning of the onset transient and ending at the approximate point where the response returned to the background level). This duration was used for all eight conditions for each cell. For example, the durations used to measure the mean MCs for the cells in Figs. 3–5 were 200, 80, and 1,100 ms, respectively. The MC is the spike rate summed over a fixed time window, so is measured in the number of spikes (Fig. 7).

The values obtained from phi motion were plotted on the y axis while those for reverse phi motion were plotted on the x axis. Student’s t-tests were used to find if the mean MCs were significantly above or below zero. Preferred direction ON–ON and OFF–OFF sequences (Fig. 7A and B) produced MCs significantly above zero (t-test, $P < 0.01$). For anti-preferred motion with ON–ON sequences (Fig. 7C), one cell had an MC significantly above zero (t-test, $P < 0.01$), while four cells had MCs not significantly different from zero. However, the most striking result was that 17 neurons (77%) had MCs significantly below zero (t-test, $P < 0.01$). For anti-preferred motion with an OFF–ON sequence (Fig. 7C), one cell produced an MC not significantly different from zero, two cells gave MCs significantly below, and 19 cells (86%) showed MCs significantly above zero (t-test, $P < 0.01$). For anti-preferred motion with an OFF–OFF sequence (Fig. 7D), three cells had MCs significantly above and 19 cells (86%) significantly below zero (t-test, $P < 0.01$). For anti-preferred motion with an OFF–ON sequence (Fig. 7D), three cells produced MCs significantly below and 19 cells (86%) significantly above zero (t-test, $P < 0.01$).

In summary, preferred direction phi motion generated positive motion components in all the neurons, while reverse phi motion in the same direction generated negative motion components in all the neurons (Fig. 7, A and B). The motion components were negative for anti-preferred direction phi motion (Fig. 7, C and D) in all but five cells. All but three neurons generated positive values for anti-preferred reverse phi motion (Fig. 7, C and D). From these results, it is clear that interactions do occur between signals registering brightness increments and decrements in the motion detectors.

### Modeling the directional responses of the neurons

Figure 8 shows a simulation that was designed to mimic the response characteristics of the neuron shown in Fig. 3. The variables used in the model were as follows. The prefilter time constants were 1.2 ms ($\tau_1$) and 120 ms ($\tau_2$), the delay filter time constant was 267 ms, and the balance, $\beta$, was 0.7. The prefilter time constants were chosen so that the waveforms of the motion detector responses had similar time courses to those of the neuron. The ISI was chosen to be 200 ms, which is close to the value used to produce the responses in Fig. 3, and the spontaneous activity of the neuron was arbitrarily set at a value of 50. The simulations show similar characteristics to those evident in the responses of the neuron. The first brightness change in the apparent motion sequence produced a small excitatory response, evident in all eight stimulus conditions. Phi motion in the preferred direction produced a facilitated response that decayed away in approximately 200 ms (Fig. 8, A and B). Reverse phi motion in the preferred direction produced a transient reduction in background activity when the second brightness change occurred (Fig. 8, C and D). As with the neuron of Fig. 3, motion in the anti-preferred direction produced the inverse of these directional properties (Fig. 8, E–H).

By changing the parameters that govern the prefiltering and subtraction stages of the model, motion detector arrays were produced that simulated the responses of most cells. For example, we simulated the responses of the neuron shown in Fig. 5 using prefilter time constants of 1.2 ms ($\tau_1$) and 480 ms ($\tau_2$), a delay filter time constant of 267 ms, and $\beta$ of 0.6 (the spontaneous activity was set at 50). The ISI used for these simulations was 900 ms, which is close to the value used to produce the responses in Fig. 5. The increased length of the second prefilter time constant, $\tau_2$, produced sluggish responses...
to the brightness changes as seen in the responses of the neuron. The responses to anti-preferred motion illustrate the accuracy of the simulations. The neuron’s response in the anti-preferred direction is a short-lived inhibition followed by a prolonged excitation (Fig. 5F). The same pattern is seen in the response of the simulation (Fig. 9F). A difference between the simulations and the biological data for this cell is that the responses to an off-off sequence were stronger than the responses to an on-on sequence in the neuronal output but were the same in the simulated output. This property could also be simulated by reducing the gain of the on signal, e.g., by incorporating a saturation mechanism. However, it was felt that introducing another variable was inappropriate, as the purpose of the modeling was to simulate the general directional properties of the biological data.

**DISCUSSION**

Neurons in the nucleus of the optic tract of the wallaby (Ibbotson et al. 1994), as in other species (e.g., rabbit: Collewijn 1975; cat: Hoffmann and Schoppmann 1981), summate the outputs of many small-field motion detectors. Here we used an apparent motion bar-stimulus to stimulate neighboring regions of the receptive fields of the motion detectors. Similar stimuli have been used in recent studies of direction-selective neurons in a range of species (e.g., insects: Egelhaaf and Borst 1992; rabbit: Amthor and Grzywacz 1993; Grzywacz and Amthor 1993; wallaby: Ibbotson 2001; Ibbotson et al. 1999). Exner (1875), who showed that sequential flashing of neighboring light sources generates a percept of motion in humans, first used apparent motion stimulation in psychophysical experiments. Sequences of brightness changes of the same polarity, referred to as phi motion (Wertheimer 1912), are seen as motion in the direction of the second brightness change. When brightness changes in neighboring locations are of opposite polarities, motion in the reverse direction is seen: reverse phi motion (Anstis 1970; van Santen and Sperling 1984).

The reversal of directional tuning can be explained if one considers the motion of a grating. If the grating shifts a quarter cycle to the right, a human viewer perceives rightward motion. If the grating simultaneously reverses its contrast, leftward motion will be perceived. The effect is explained because a contrast reversal equals a half-cycle shift, which combined with the quarter cycle movement produces a three quarter-cycle displacement. Since this displacement is equal to a quarter-cycle shift to the left, the grating appears to move leftward. With a full-wave rectified input, the observer would not see motion whether there was a contrast reversal or not. This is because a quarter-cycle shift of a grating effectively becomes a half cycle shift of the full-wave rectified signal. If the motion detectors received input selectively from half-wave rectifying prefilters, the reverse-phi phenomenon would be perceived with a grating stimulus. However, with the stimulus used in the present experiments, half-wave rectifying prefilters would prevent the motion detector from computing a directional signal. For example, if the prefilters only responded to brightness increments, an on-off sequence in the preferred direction would produce a response only to the appearance of the initial brightness increment. The appearance of the brightness decrement a short time later would not produce a response from the ON-selective prefilters, so no motion would be detected.

In the NOT neurons of the wallaby, phi motion produces positive and negative motion components for motion in the preferred and anti-preferred directions, respectively. Reverse phi motion inverts these directional properties. These response characteristics are suggestive of the reverse-phi phenomenon observed in human vision. The response to reverse-phi motion shows that there is no segregation of motion detectors into those that receive half-wave rectified inputs from pure ON or OFF channels. Also it is clear that the motion detector input is not full-wave rectified. Rather increments and decrements produce signals that interact within the motion detectors so that the signs of the incoming signals are utilized.

**Implications for motion detector models**

The model presented here consists of an array of Reichardt motion detectors, and it accurately predicts the responses of the NOT neurons. In the model, step changes darker than the background luminance generate negative signals at the prefilter stage while brighter steps generate positive values (Fig. 2B), so the polarity of the original image is maintained. As described in the next section, ON- and OFF-center ganglion cells with these properties are found in the mammalian retina (Kuffler 1953). As the fundamental nonlinearity in a Reichardt detector is a multiplication, the directionality of the detector’s output will depend on the brightness polarity of the input (Reichardt 1961). Importantly, even though the inputs to the motion detectors are positive and negative for ON and OFF stimuli, respectively, the detector produces positive output signals to static ON and OFF stimulation (flashes or brightness steps). That is, the motion detector output appears full-wave rectified when presented with static brightness changes. The prefilters are not the reason for the apparent full-wave rectification of the detector output. Rather the multiplication stage in the detector effectively squares the signals, so both ON and OFF stimulation produce positive responses.

The neurons in the NOT produce direction-selective time-
bars are presented in their receptive fields, and OFF-center cells, regions that are excited by opposite contrast polarities. These cells that have receptive fields divided into center and surround direction-selective motion detectors.

Modeling the time courses of the responses

There are only four free parameters in our model, and we could replicate the response properties of most cells by changing only the second prefiler time constant ($\tau_2$) and the balance, $\beta$. For example, the responses presented in Fig. 5 have quite complex waveforms for phi motion in the anti-preferred direction and reverse phi motion in the preferred direction. The motion component of the response consists of an initial transient inhibition followed by a prolonged excitation. Adjusting only the prefiler time constants in the model allowed us to replicate both the flash and motion responses. In many neurons, the responses to ON and OFF stimulation had different magni-
tudes (Figs. 4 and 5). The present model could be modified easily by compressing the responses of the prefilters to either brightness increments or decrements. In this way, the responses could be biased so that either ON or OFF stimulation provided a stronger input.

A major governing parameter in the model was the balance, \( \beta \), of the final subtraction stage. In general, we found that values between 0.4 and 0.8 were needed to simulate the responses. Simulating responses like those in Fig. 4 required lower \( \beta \) values. In these neurons, apparent motion in the anti-preferred direction did not inhibit the background activity of the cells but did reduce the size of the flash response to presentation of the second bar alone. In this case, anti-preferred motion did have an inhibitory influence, but it was not sufficient to inhibit the spontaneous rate. Simulating responses like those in Fig. 3 required higher values of \( \beta \) (i.e., 0.7–0.8) because in these neurons the spontaneous firing rate was inhibited by anti-preferred motion.

**Polarity sensitivity of directional neurons in other species**

Goodwin and Henry (1975) showed that complex cells in the cat cortex always have the same preferred direction for moving light and dark bars. To study the directional properties of complex cells further, Emerson et al. (1987, 1992) used a random bar “white noise” stimulus that consisted of 16 contiguous 0.5° wide bars, each of which could change its luminance randomly and independently between three levels in each video frame (16 ms). As the stimulus could contain all possible combinations of light and dark bars in each frame, it consisted of bright or dark bars moving to-and-fro in short sequences in each part of the receptive field. The responses to the motion sequences were calculated, and a spatiotemporal receptive field map was derived for the cells. They found that phi motion in the preferred direction produced strong facilitation, while reverse phi motion produced strong suppression. Sequences of motion in the anti-preferred direction also showed inversion of the response for reverse phi motion. These results from the cat suggest that a product function operates on the signed stimulus brightness. The results strongly resemble those obtained from the wallaby NOT. In the insect visual system, the retinal image is not separated into ON and OFF pathways. Studies on wide-field direction-selective summing neurons in the fly optic lobe have shown that the motion detectors forming the input to these cells receive inputs from prefilters that maintain brightness polarities (Egelhaaf and Borst 1992). The responses of the directional summing neurons in the fly to apparent motion sequences are very similar to those observed in the wallaby NOT neurons.

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