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POLARITY SPECIFIC ADAPTATION TO MOTION IN THE HUMAN VISUAL SYSTEM

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Abstract—Three experiments investigated polarity specific adaptation to movement. Experiment 1 tested for *temporal* polarity specific adaptation, using counterphase sawtooth gratings as adapting and test stimuli. Each counterphase grating contained oppositely moving sawtooth components, and was thus balanced for direction, but both components of the adapting grating created only one polarity of luminance change over time, whereas the components of the test grating presented different signs. After adaptation, only the test component containing the unadapted temporal change was visible. A second experiment, using an analogous procedure, found evidence for *spatial* polarity specific adaptation. Experimental results can be explained by motion detectors which preserve information about spatial and temporal polarity. A third experiment found that spatial and temporal polarity specific adaptation differ in their dependence on temporal frequency.

Motion detection   Counterphase gratings   Polarity specific adaptation

INTRODUCTION

Light reflected from surfaces in the external world is brought into focus as a two-dimensional pattern of light and dark on the retina. The steepest gradients of intensity over space in the retinal image (edges) generally define the borders of the surfaces. One fundamental task of any vision system is to segregate those surfaces and boundaries which go together (because they belong to one external object) from those that belong to other parts of the visual scene. Only then can the processes of object identification proceed. One potent cue to figure-ground articulation is relative motion between the object and its background, either as a consequence of its own motion or because of motion parallax. Information about image motion is thus of great value to the visual system. But how is it extracted?

When objects move, the corresponding intensity edges in the retinal image also move, with the result that intensities in the region of those edges are modulated with respect to time. In order to detect movement, the visual system must put together the spatial (luminance) information and the temporal information which is available in the image. For the sake of simplicity, the following discussion of motion detection will be limited to simple one-dimensional stimuli, but the logic applies equally to two-dimensional images.

Figure 1a depicts the intensity variation across a vertical edge, dark on the left and bright on the right, which we shall refer to as having a positive spatial slope ($S+$). When the edge moves leftward, shown by the large open arrow, local intensity rises over time in the vicinity of the edge ($T+$, small solid arrows). If the edge moves rightward (Fig. 1b) local intensity falls over time ($T-$). The remaining two panels in Fig. 1 depict the changes which occur when the edge has a negative spatial slope ($S-$). Four conjunctions of spatial intensity change and temporal intensity change are uniquely associated with the two possible motion directions of a vertical edge which can have either of two possible luminance polarities: $S+T+$ and $S-T-$ conjunctions both arise from leftward motion, and $S-T+$ and $S+T-$ conjunctions arise from rightward motion.

A number of theoretical models have been proposed for motion detection, and they differ particularly in the way they use spatial and temporal information. Some models, such as Marr and Ullman's (1981) gradient model, rely upon preserving and comparing the signs of local spatial and temporal intensity change. Motion to the left in Fig. 1 can be inferred when the two signs match, and motion to the right can

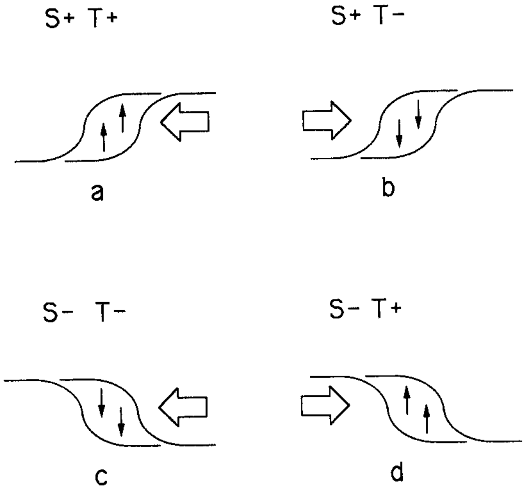

Fig. 1. Changes in luminance over space and time created by moving edges. (a) Luminance profile across a vertical intensity edge which is dark on the left and bright on the right (a positive spatial gradient, $S+$). The edge is shown moving to the left (open arrow) in two successive positions. The movement creates rising intensity over time in the vicinity of the edge (solid arrows), which we term $T+$. If the edge moves rightward instead (b), intensity falls over time in the neighbourhood of the edge ($T-$). (c) and (d) Spatial and temporal luminance changes created by an edge of the opposite spatial polarity ($S-$) moving either to the left or to the right. Note that movement direction can be specified by the conjunction of spatial luminance change and temporal luminance change.

be inferred when they do not match. Marr and Ullman made specific proposals concerning mechanisms to extract spatial and temporal polarity. Other models do not rely upon preservation of polarity. Van Santen and Sperling's (1984) Elaborated Reichardt Detector performs a "non-linear comparison of temporal modulations in adjacent locations", and its spatiotemporal phase invariance rules out polarity specificity. Adelson and Bergen's (1985) spatiotemporal energy detector is built from polarity specific filters, though their outputs are combined to construct a motion detector whose response is "sensitive to the direction of motion but insensitive to the sign of the stimulus contrast".

Thus a fundamental empirical question arises: are motion detectors selectively tuned to spatial and temporal polarity? The answer to this question should lead to the elimination (or revision) of certain detector models as plausible candidates for motion detection in the human visual system.

If motion detectors are selectively tuned to polarity, it should be possible to demonstrate polarity specific adaptation (PSA) to motion. If they are not tuned to polarity, there should be no PSA. Moulden and Begg (1986) claimed to have demonstrated PSA, and on this and other grounds interpreted their findings as being consistent with the predictions of the Marr–Ullman (1981) gradient model. However, Webb and Wenderoth (1991) have taken issue with these conclusions. In particular, they failed to discover any evidence for spatial PSA, and argued that Moulden and Begg's effect could be explained in terms of adaptation to direction and temporal polarity. The experiments described here were prompted by their arguments. We shall show that under appropriate conditions PSA can in fact be demonstrated, both for spatial polarity and for temporal polarity. A more detailed discussion of Webb and Wenderoth's experiments will be given in the Discussion.

The first two experiments described below tested for the presence of temporal PSA (expt 1) and spatial PSA (expt 2). Stimuli in both experiments consisted of counterphase gratings containing two sawtooth components.* The two components always moved in opposite directions at the same velocity, and could either have the same spatial profile (*same* counterphase) or mirror-reversed profiles (*opposite* counterphase), as shown in Fig. 2. The contrast of the two components was always equal.

EXPERIMENT 1: TEMPORAL PSA

The adapting stimulus consisted of an *opposite* counterphase (Fig. 2c). It contained both directions of movement at matched velocity, so that any directional bias in the perception of the test stimulus could not arise from directional bias in the adapting stimulus. Similarly, since the counterphase contained both signs of spatial polarity, any adaptation effect could not be attributable to an imbalance in this attribute during adaptation. However, because of the pairing of direction and spatial polarity, each component of the counterphase produced only one kind of temporal luminance modulation—a repetitive slow increase in luminance over time followed by a rapid decrease. Can this modulation alter the perceived direction of the test stimulus, in the absence of any effects attributable to direction or spatial polarity? Earlier experiments by Krauskopf (1980) found that the

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*Conventionally, counterphase gratings are sinusoidal, consisting of matched waveforms moving in opposite directions. Here we apply the term to sawtooth gratings to emphasise that the two components are always identical in spatial frequency, contrast and velocity.

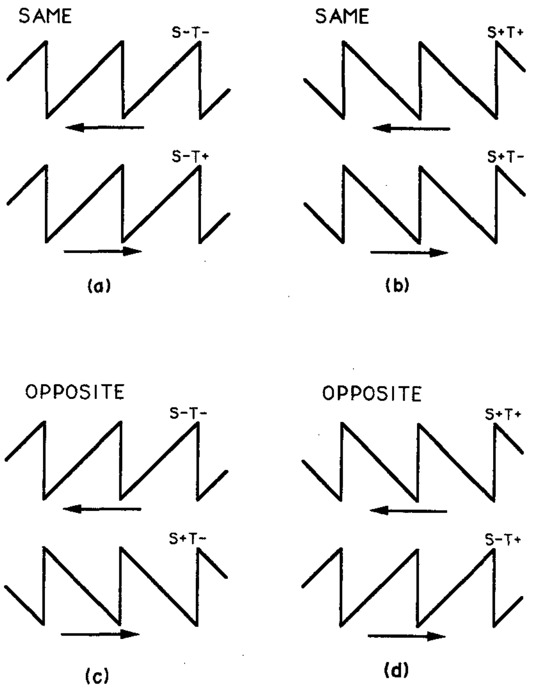

Fig. 2. Luminance profiles of counterphase gratings used in the experiments. Each consisted of two sawtooth components, matched for contrast and spatial frequency, moving in opposite directions (arrows). The two components could either have the same spatial profile (top), or opposite profiles (bottom). Assuming that visual response to sudden changes in luminance over space or time is greater than response to linear ramps (due to band-pass filtering), each component in each grating supplies one particular conjunction of spatial change and temporal change, shown by the S and T symbols. The *same* counterphases each give both signs of temporal luminance change but only one sign of spatial change, vice versa for the *opposite* counterphases.

detectability of sudden increases (or decreases) in luminance was reduced after adapting to sawtooth modulation involving sudden increases (or decreases).

The test stimulus consisted of a *same* counterphase, either the compound shown in Fig. 2a or that shown in Fig. 2b (randomly selected from trial to trial). Taking Fig. 2a, before adaptation there is no tendency to see one directional component any more than the other (often both can be seen in a transparency effect). The leftwards moving component pairs a rapid decrease in luminance over space with a rapid decrease in luminance over time, while the rightward component pairs a rapid decrease over space with a rapid increase over time.

As described in the Introduction, if the adapting stimulus activates detectors which do not preserve information about temporal polarity, there should be no alteration in the apparent directional properties of the test counterphase gratings after adaptation. However, if motion detectors *are* selective for temporal polarity, then after adaptation the test counterphase in Fig. 2a should appear to move rightwards because the rightwards component contains an unadapted rapid increase over time. The counterphase shown in Fig. 2b should appear to move leftwards after adaptation because here the leftward component contains the unadapted temporal polarity ($T+$). Note that these predictions are counter-intuitive, because they require that adaptation to a counterphase stimulus can make another counterphase stimulus appear to be unidirectional.

Method

Subjects. Six subjects were used, two of the authors and four naive and inexperienced observers.

Apparatus. Vertical one-dimensional gratings were displayed on a Joyce Electronics CRT display (P4 phosphor). z-Modulation voltages were supplied from a CED 502 Interface controlled by a MicroPDP11/73 computer. The frame rate of the CRT was 200 Hz and the Y-scan frequency was 120 kHz. Screen resolution was 25 lines per cm. Digital z-values were read out from a table into a fast DAC, whose output was synchronised to the Y-scan modulation. There were two tables of digital values (corresponding to the two components of the counterphase) each containing an array of 8-bit numbers defining a sawtooth waveform. Every second TV frame the computer switched from one table to the other, to produce a counterphase grating. A cumulative offset was added to the start of each table to create drift. One period of the sawtooth corresponded to 2.4 cm on the CRT screen. Viewing distance was 57 cm (unrestrained), so the fundamental spatial frequency was 0.41 c/deg, with component temporal frequency set at 3.1 Hz. Component Michelson contrast was 0.15 during adaptation (counterphase contrast 0.3) and 0.08 during testing (counterphase contrast 0.16). Mean luminance was 235 cd/m^2. Low contrasts were used to minimise the contribution of any distortions introduced by non-linear luminance response in the visual system (the CRT's response was calibrated and found to be linear). The CRT screen was masked down to a rectangular aperture measuring 12 by 9 cm (12 by 9 deg arc), and a small red central fixation spot was provided. Subjects viewed the CRT binocularly in darkness.

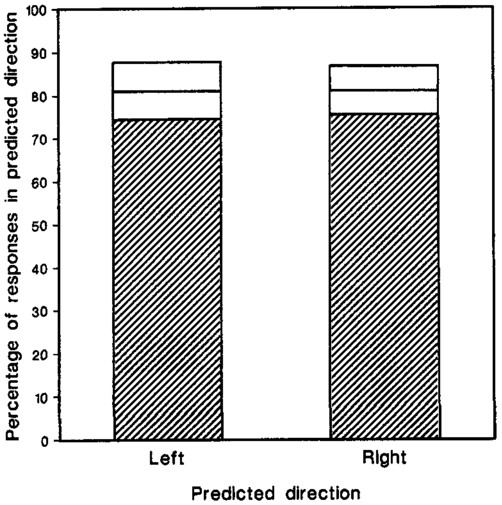

Fig. 3. Data from expt 1 on temporal PSA, showing the percentage of responses in each of the predicted directions, averaged across six subjects. Shaded areas represent one SE either side of the mean.

Procedure. The experimental procedure consisted of a 30 sec adaptation period followed by test/top-up cycling (3 sec test and 10 sec top-up). An audible warning (as well as the change in stimulus contrast) alerted the subject at the onset of the test stimulus. During the test phase either one of the two possible stimuli (Fig. 2a or b) was presented at random, and the observer was required to press one of two keys to denote that the stimulus appeared to move either rightwards or leftwards. A total of 30 trials were presented for each of the two test stimuli (the *same*s in Fig. 2) in random order. Data were collected in two separate sessions, each comprising 30 presentations of a test stimulus (15 for each *same* stimulus).

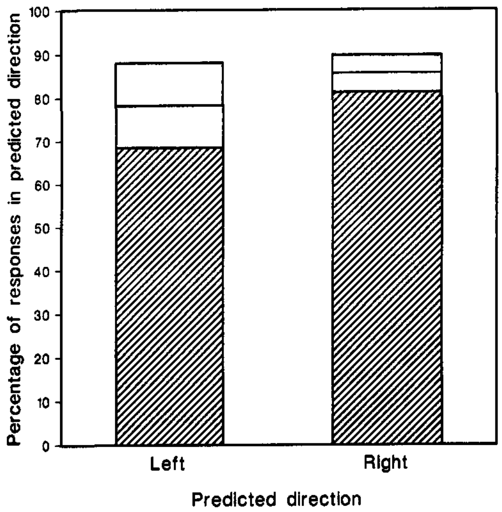

Fig. 4. Data from expt 2 on spatial PSA. Conventions as in Fig. 3.

Results

For both test stimuli (Fig 2a and b), a mean of 81.1% of responses were made in the directions predicted by the presence of temporal PSA. Responses would have been around chance levels (50%) in the absence of PSA. See Fig. 3.

EXPERIMENT 2: SPATIAL PSA

The logic of this experiment was very similar to that of expt 1. The adapting stimulus was a *same* counterphase (Fig. 2a), so the two components were matched in contrast, velocity, and spatial sign but moved in opposite directions. As a result, they generated both signs of temporal polarity, but only one sign of spatial polarity ($S-$, a rapid decrease over space). The test stimulus was an *opposite* counterphase, either Fig. 2c or d. In the case of Fig. 2c, both components create rapid decreases in luminance over time ($T-$), but the leftward component has a rapid *decrease* in luminance over space ($S-$) while the rightward component has a rapid *increase* in luminance over space. If motion perception can be affected by adaptation to one spatial polarity, then the counterphase in Fig. 2c should appear to move rightwards. Similarly, the test stimulus in Fig. 2d should appear to move leftwards because that component contains the unadapted spatial polarity.

Method

Subjects. The same six subjects were used as in expt. 1.

Apparatus and procedure. Stimuli and procedure were identical with those in expt 1, except for the use of different counterphase gratings as described above.

Results

For the stimulus in Fig. 2c 85.8% of responses were as predicted by the presence of spatial PSA, and for the stimulus in Fig. 2d the figure was 78.3%. See Fig. 4.

DISCUSSION OF EXPERIMENTS 1 AND 2

The results of these experiments clearly show that adaptation to movement is specific to the particular polarity of both the temporal and the spatial luminance changes present in the stimulus (the adaptation effects have also been demonstrated to large seminar audiences using video recordings of the stimuli, which gives an informal indication of their robustness).

The data are therefore inconsistent with those of Webb and Wenderoth (1991), who failed to find spatial PSA. This failure may be attributable to their stimulus, which consisted of a single luminance step traversing a 0.9 deg arc window at 1 deg/sec. After each traverse, there was a 100 msec pause before the edge reversed direction to create adaptation to only one sign of spatial change while presenting both signs of temporal change. So the adapting stimulus passed over any one retinal location only once every 2 sec, over a total adapting period of 60 sec. The stimulus is so different from the counterphase gratings used here that it is difficult to make straightforward comparisons. One possibility is that the adapting stimulus was simply too weak to affect the reported direction of the test stimulus (300 msec exposure of an edge moving at 9 min arc/sec), though a significant effect was obtained for temporal polarity.

The results of expts 1 and 2 support the idea that motion detectors in the human visual system which respond to horizontal motion are partitioned into four classes of "conjunction detector". Each class responds selectively to one of the four possible conjunctions of spatial and temporal polarity shown in Fig. 1. A third experiment investigated the internal structure of these detectors. Motion detectors can be constructed in a variety of ways, but the building blocks are usually sustained (X) and transient (Y) mechanisms known to supply the inputs to the visual cortex. X mechanisms are commonly associated with pattern vision, and Y mechanisms are commonly associated with motion perception. Two specific models will be described in detail, to demonstrate how X and Y mechanisms can be used in different ways to construct polarity specific detectors. Marr and Ullman's (1981) gradient detector uses both mechanisms in each of its four polarity-specific detectors, as shown in Fig. 5. Temporal polarity specificity (and adaptation) is mediated by Y inputs, while spatial polarity specificity is mediated by X inputs. A simpler way to construct individual spatial and temporal polarity specific detectors, based on a Reichardt-style correlator (Reichardt, 1961) which uses only Y inputs, is also shown in Fig. 5. Here, two detectors of the four receive inputs from mechanisms which respond selectively to luminance increments, and the other two receive inputs from mechanisms which respond to luminance decrements. Note that in Reichardt's original arrangement, detectors responsive to opposite directions were paired so that they shared the same input receptive fields and their responses were combined at a comparator neuron. If the two opposing correlators in Fig. 5 which have $T+$ (or $T-$) inputs were paired, the comparator output would be selective for temporal polarity but not for spatial polarity. Even if expt 3 supported the correlator arrangement in Fig. 5, it would be difficult to explain the results of expt 2 using the pairings proposed by Reichardt.

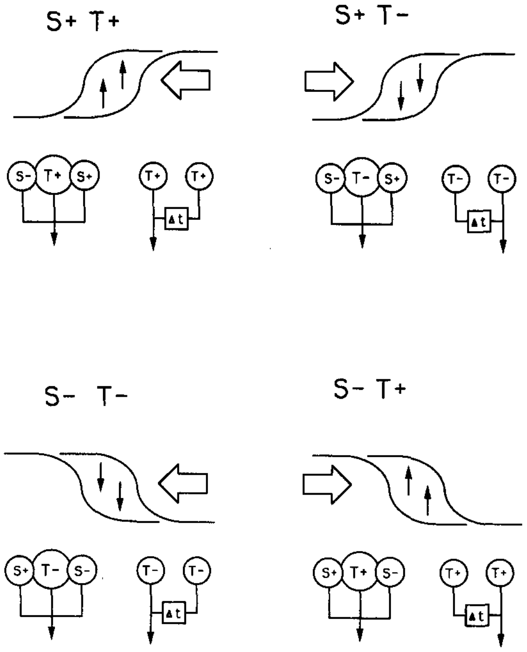

Fig. 5. The four possible conjunctions of spatial change and temporal change generated by a moving edge, and two candidate detectors to detect each conjunction. The left-hand detector below each conjunction is configured according to the gradient model of Marr and Ullman (1981). Each detector receives three inputs, one from a transient mechanism which responds selectively to temporal luminance change ($T+$ or $T-$), and two from sustained mechanisms. The latter's receptive fields (one on-centre, $S+$, and one off-centre, $S-$) are positioned so that their (non-linearly) combined output is selective for spatial polarity. The $S - S+$ pairs respond to positive spatial gradients, while the $S + S-$ pairs respond to negative spatial gradients. The right-hand conjunction detectors are configured as a set of simple Reichardt-type correlators (Reichardt, 1961). The two inputs to each correlator are transient filters which respond selectively either to rising luminance over time ($T+$) or to falling luminance over time ($T-$).

The X and Y systems are known to differ in their temporal properties, with X cells having a low-pass temporal frequency (TF) response and Y cells having a band-pass TF response. A scheme employing both X and Y mechanisms, such as Marr and Ullman's, therefore would predict that the temporal PSA effect found in expt 1 will show a band-pass TF dependence, while the spatial PSA effect found in expt 2 will show a low-pass TF dependence. Since the correlator system shown in Fig. 5 contains only transient units (having Y-type responses), it would predict that the two adaptation effects will vary in the same way with TF, both showing a band-pass TF dependence. Experiment 3 was designed to determine the temporal tuning properties of PSA.

EXPERIMENT 3: TEMPORAL FREQUENCY DEPENDENCY OF PSA

This experiment used the same stimuli as used in expts 1 and 2, except that four different temporal frequencies were employed: 3.1, 6.2, 9.4 and 12.5 Hz. Adapting and test TFs were always the same. After-effect duration was used as a measure of adaptation strength, adopting the standard psychophysical linking hypothesis that stimuli to which visual processes are more sensitive produce deeper and longer-lasting adaptation. This seemed simpler than making assumptions that the adaptation reflects changes in apparent velocity or contrast, and attempting to use velocity or contrast nulling.

Method

Subjects. Four subjects were used, one of the authors (AOH, who was unaware of the temporal frequency predictions), and three naive observers.

Apparatus. The same apparatus was used as in the previous experiments. Differing temporal frequencies were created by varying the number of TV frames for which each counterphase component was presented before replacement by the other component, and/or by varying the size of the between-frame displacement of each component.

Procedure. With two kinds of adaptation procedure (spatial or temporal polarity), and four possible temporal frequencies, there were eight conditions. Four trials were performed in each condition. Each trial consisted of 2 min adaptation followed (after an audible warning) by the test stimulus. The subject was instructed to press a response button as soon as the test stimulus no longer appeared to move consistently in one direction, and the computer recorded the time elapsed. Durations of weaker adapting stimuli (shorter than 2 or 3 sec) were sometimes difficult to record, because the sub-

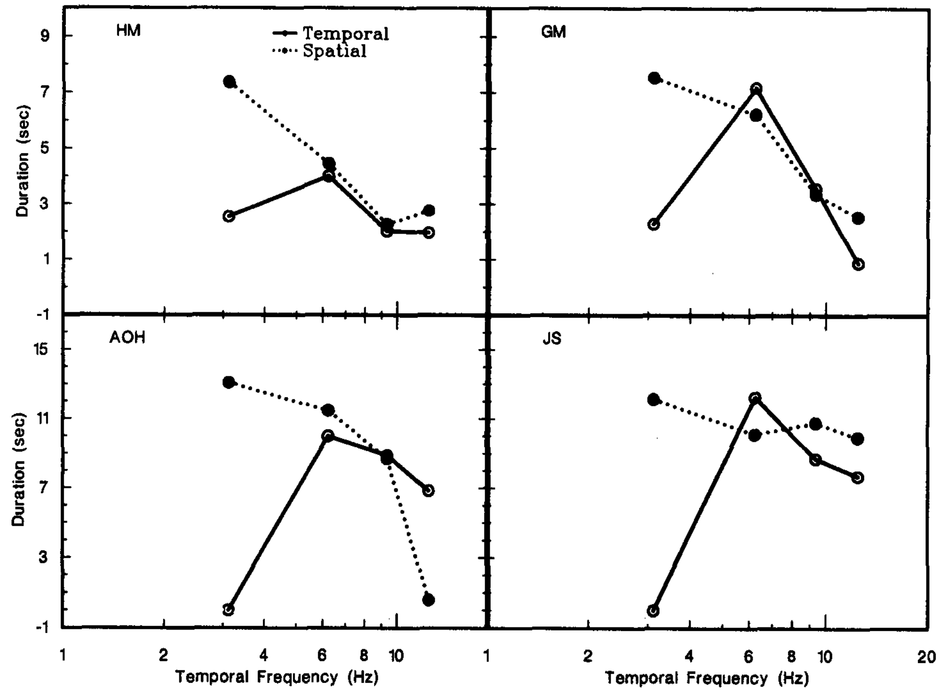

Fig. 6. Results of expt 3. Data from four subjects are shown individually. Dotted lines depict mean duration of spatial PSA as a function of adapting and test temporal frequency. Solid lines depict mean duration of temporal PSA as a function of temporal frequency.

ject allowed the test stimulus to "run on" for a few seconds, unsure of their decision. In these cases, the subject alerted the experimenter about the difficulty of the judgement, and a duration of zero was recorded. The set of 32 trials per subject was performed in random order, with a long inter-trial interval of 15 min or more to avoid carry-over of adaptation. Recall that in expts 1 and 2 there were two possible test stimuli, one that appeared to move left and another that appeared to move right. In expt 3, two of the trials in each condition involved one of these two test stimuli, and the other two trials involved the other test stimulus.

Results and discussion

Data for each subject are shown in Fig. 6. Each point is the mean of four trials. Standard errors have been omitted for clarity, but the average SE across the four trials was 0.94 sec (range of SEs 2.32 sec). Taking first the data shown by (○), representing temporal PSA, the longest adaptation effects were found for intermediate TFs. At lower or higher TFs duration falls away. Turning to the results for spatial PSA (●), it is clear that all subjects show the greatest effect for the lowest TF. At this frequency there is a marked difference between the results for spatial PSA and those for temporal PSA.

The differing effects of TF on spatial and temporal PSA offer support for models in which motion detectors receive inputs from both X and Y mechanisms, such as the Marr–Ullman gradient scheme (Fig. 5). The correlator shown in Fig. 5 cannot account for the data.

The duration of temporal PSA was very short at 3.1 Hz, yet in expt 1 stimuli at this frequency were successful in producing strong directional biases, using three sec duration probes of the test stimuli. However, the duration measure used in expt 3 was conservative, so that durations below 2 or 3 sec were recorded as zero. Presumably adaptation at 3.1 Hz is sufficient to bias subjects' reports of direction in briefly presented test stimuli, but not sufficient to produce after-effect durations measurably longer than 2 or 3 sec.

SUMMARY AND CONCLUSIONS

The first two experiments demonstrated that motion adaptation is specific both to the spatial polarity and to the temporal polarity of luminance change. These results can only be explained by a model of the motion detector which preserves information about polarity, and support the idea that motion detectors are partitioned into four classes which detect conjunctions of spatial change and temporal change. The results of the third experiment are consistent with the proposal that spatial PSA is mediated by sustained or X mechanisms, while temporal PSA is mediated by transient or Y mechanisms.

The spatiotemporal energy model of Adelson and Bergen (1985) includes polarity selective filters, as does the gradient detector of Marr and Ullman (1981). Other data also support the idea that motion detectors respond according to spatial and temporal changes of image intensity (e.g. Mather, 1984, 1987). The present results are difficult to explain in terms of phase-invariant Reichardt correlators.

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