A Role for a Low Level Mechanism in Determining Plaid Coherence

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A number of recent studies have suggested that the “intersection of constraints” model of two dimensional motion perception, put forward by Adelson and Movshon [(1982) Nature, 300, 523-525], is incomplete. Evidence has been mounting that there is a second two-dimensional motion sensitive mechanism which is monocular and which appears to respond directly to the movement of the intersections (or “blobs”) in a two-dimensional image. The current study extends these findings by demonstrating that the perceived coherence of a drifting plaid is largely under the control of a monocular mechanism. Prior exposure to a similarly drifting grating or plaid substantially raises the coherence threshold of a test plaid only if the same eye is adapted and tested. The threshold elevation is much more modest if the test plaid is presented to the unadapted eye, suggesting that coherence judgements are primarily based on the activity level of a monocular process—possibly the “blob tracking mechanism”. The results of Expt 2 suggest the possibility that this monocular mechanism is inhibited by binocular exposure.

Recently, strong evidence has been provided suggesting that the perception of rigid, translational, two-dimensional motion (typically a plaid, constructed from two superimposed sine-wave gratings) is mediated by at least two mechanisms. The first is a two stage process which combines one-dimensional (1-D) motion signals in a manner which appears to be consistent with the intersection of constraints (IOC) model originally put forward by Adelson and Movshon (1982) (Burke & Wenderoth, 1993a). The second is a low level (Derrington & Badcock, 1992), monocular (Burke & Wenderoth, 1993b) process presumably responding to the motion of the “blobs” caused by the spatial intersection of the component gratings (the “blob tracking”, or BT, mechanism).

Given the co-existence of the two-stage mechanism and the monocular mechanism, it is important to discover what role each has to play in two-dimensional (2-D) motion perception. There are essentially three features of a moving 2-D image to which the visual...
system must be sensitive; its direction of motion, its speed of motion, and whether or not it is a single, coherently moving object. It is a legitimate question to ask what role, if any, is played by each mechanism in performing these perceptual tasks.

Evidence has already been gathered suggesting that a part is played by both a two stage mechanism (Burke & Wenderoth, 1993a; Derrington & Suero, 1991; Kooi, DeVlois & Wyman, 1988; Stone, Watson & Mulligan, 1990) and a blob tracking mechanism (Alais et al., 1994; Mingolla, Todd & Norman, 1992; Rubin & Hochstein, 1993) in determining the direction in which a 2-D pattern appears to drift, making it difficult not to concur with Gorea and Lorenceau (1991) and conclude that direction judgements can be influenced by the activation of either mechanism.

While the data have not been previously interpreted in this way, those studies which have examined the perceived speed of 2-D motion have produced results which are most easily explained by assuming that they are due to the activation of the BT mechanism. The first such study (Welch, 1989) actually produced data which were interpreted as being consistent with a two-stage model, but in light of subsequent findings it appears that this conclusion was premature (Welch & Bowne, 1990). The only study which has addressed the issue of the perceived speed of a drifting plaid in an unconfounded way was conducted by Fererra and Wilson (1991). Reliable speed matches were possible only when the drifting plaid was compared with a single grating (drifting in the same direction) with the same spatial frequency as the “nodes” of the plaid. The “nodes” of the plaid are caused by the intersections of the component gratings and are formally identical to the blobs which are tracked in the BT model.

Perhaps the most fundamental “decision” the visual system has to make about moving 2-D scenes is whether or not the various moving edges are part of the same object. This has traditionally been studied by measuring the likelihood of subjects judging the two components of a plaid to be moving as a single, coherent pattern (as opposed to dissociatively drifting gratings), and any such judgements have typically been interpreted as reflecting activation of the IOC mechanism, or at least, some sort of two-stage mechanism. Indeed, it has been almost universally assumed that those manipulations which degrade coherence (using components with very different spatial frequencies, contrasts, velocities, directions of motion, colour, etc) do so because they prevent an integration of the component motion signals (Adelson & Movshon, 1982; Movshon, Adelson, Gizzi & Newsome, 1985; Krauskopf & Farell, 1990; Smith, 1992). This view has been challenged recently (although not explicitly) by studies which have shown that coherence is affected by various “higher order” factors (Kooi, DeVlois, Switkes & Grosol, 1992), and particularly by competing depth stratification cues (Stoner, Albright & Ramachandran, 1990; Vallortigara & Bressan, 1991; Trueswell & Hayhoe, 1993; Bressan, Ganis & Vallortigara, 1993). These studies raise the possibility that coherence judgements are modulated by signals arising outside the motion processing system itself, and therefore that not all manipulations which influence coherence judgements necessarily reflect the characteristics of the 2-D motion sensitive mechanisms per se. It may be, for instance, that components which are very different in contrast, spatial frequency or velocity (direction or speed) do not cohere because these are all monocular depth cues, and so are “labelled” by those mechanisms subserving figure-ground segregation as being at different depth planes, preventing the activation of a 2-D motion sensitive mechanism. Obviously, if this active veto mechanism is what accounts for non-coherence (as opposed to the incidental failure to stimulate the pattern sensitive mechanism, favoured by early researchers), then no strong conclusions can yet be drawn about whether coherence judgements are based on activity in a two-stage or the BT mechanism. The present study was designed to investigate this issue.

**EXPERIMENT 1**

Both Movshon et al. (1985) and von Grünau and Dubé (1991) have reported that the coherence threshold or the amount of perceived coherence (in a fixed inspection time) for a drifting plaid is influenced by prior exposure to a pattern moving in the same direction. Adaptation to a single grating or a plaid, drifting in the same direction as the test plaid, lowers the likelihood of seeing coherent motion, and exposure to the alternating components of the test plaid raises the likelihood of judging the test plaid to be moving coherently. These changes in coherence judgements are presumably due to adaptation of, respectively, the 2-D motion sensitive mechanisms (either or both of the pattern sensitive and blob tracking mechanisms), and the 1-D motion sensitive mechanisms responding to the movements of the components. Coherence judgements are less likely if 2-D sensitive mechanisms have been adapted, and so are less likely to be activated (or will be activated less vigorously), but such judgements are more likely if the cells signalling the component motions are fatigued, because this will lead to a predominance of the 2-D motion signal. This finding alone poses problems for the belief that the perception of coherent motion is due solely to the activation of a two stage mechanism because reducing the output of the component sensitive cells should also lower the output of the 2-D sensitive cells, since their activity depends on the 1-D input. Indeed, it is difficult to see how reducing the strength of the 1-D signals could lead to more coherence judgements if 2-D activity is dependent only on 1-D input (as in a two-stage mechanism). This result only seems explicable if there is another process impacting on coherence judgements which is activated independently of the 1-D signals. The BT mechanism is such a process, since it responds directly to the motion of the blobs.

Based on Burke and Wenderoth’s (1993b) discovery that adaptation of the BT mechanism does not transfer interocularly [recently elaborated (Alais et al., 1994)], we decided to use this procedure to assess the contribution
of the BT mechanism to coherent 2-D motion perception. We did so by using a modified version of the procedures of Movshon et al. (1985) and von Grünau and Dubé (1991). Subjects were exposed binocularly or monocularly to an upwardly drifting grating or plaid, or to the alternating components of the plaid, and were subsequently required to adjust the contrast of one of the components of a test plaid (moving in the same direction) until the whole pattern was just at the threshold of switching from appearing to drift as a coherent whole or breaking up into its components. The adjustment was done while subjects viewed the test plaid binocularly (BIN-BIN) or monocularly using the eye which had previously been exposed to the adaptation stimulus (MON-MON) or the eye which had not previously been adapted [interocular transfer (IOT)]. The critical condition for revealing a role for the monocular BT mechanism is IOT. If this method of measuring coherence threshold is comparable to those used previously, then the coherence threshold should be raised (relative to pre-adaptation adjustments) following exposure to the grating or the plaid. This is because adaptation of the BT mechanism will result in transparent, or non-coherent, motion perception with smaller component contrast differences than prior to adaptation. However, the contrast threshold should be lowered following exposure to the alternating components in both the MON-MON and BIN-BIN conditions because adaptation of the 1-D mechanisms will render the 2-D mechanisms relatively more sensitive, requiring a larger contrast difference to produce non-coherence. A similar pattern of results should occur for IOT, but depending on the size of the contribution of the BT mechanism to coherence judgements, the magnitude of the threshold elevation should be smaller (relative to MON-MON and BIN-BIN) following exposure to the grating or the plaid. This is because the adapted BT process will not be tested in the IOT condition, because it is monocular. Conversely, the unadapted BT mechanism in the tested eye will contribute normally to the percept of coherent 2-D motion. Since the BT motion signal does not depend on activity in the 1-D channels, the amount of threshold decrement following exposure to the alternating components should be the same in the MON-MON and IOT conditions.

Methods

All stimulus displays were presented on the flat screen of a Tektronix 608 display monitor (P31 phosphor), interfaced with an Innisfree ("Picasso") image generator and a PDP 11/73 minicomputer. Plaid patterns were generated by temporally interleaving the two frames bearing the drifting components at 188 Hz. The Michelson contrast of each of the adapting plaid components, defined as \((L_{\text{max}} - L_{\text{min}})/(L_{\text{max}} + L_{\text{min}})\), was 0.2, making the contrast of the adapting plaid 0.4. All patterns were displayed in a computer-generated aperture 6.5 deg in diameter (at the viewing distance of 57 cm), seen through a circular black mask, 6.75 deg in diameter. The test stimulus was a plaid constructed from sine wave gratings with a spatial frequency of 1.5 c/deg, drifting at 0.75 deg/sec. We decided to have the components of the test plaid drift in directions 75 deg either side of vertically upwards (in directions 150 deg apart) for two reasons. Firstly, this encourages non-coherence, and secondly, so that the directions of motion of the components were very different from the direction of motion of the plaid. This made it very likely that the adaptations induced by the alternating components and by the vertically drifting grating were of essentially non-overlapping populations of neurons (Levinson & Sekuler, 1976). The contrast of one of the components of the test plaid was held at 0.2, and the contrast of the other component was adjustable. The three adaptation patterns were a plaid with the parameters specified above, the components of the plaid appearing in alternation every 10 sec, and a single, horizontal grating (with the same contrast as the plaid) drifting upwards. Because of the directional relationship of the components, the adapting plaid drifted at 2.9 deg/sec, and the adapting grating was set to match this speed.

There were 11 subjects, all with emmetropic or suitably corrected vision, and all were naïve as to the aims of the experiment. They sat in a darkened laboratory where the only light came from the display screen, and during the test phases of the experiment could adjust the contrast of one of the components of the test plaid using a control box on the desk in front of them. Holding down the leftmost button continuously increased the contrast of the adjustable grating (around a constant mean luminance of 10.8 cd/m²), and the rightmost button continuously decreased it. Subjects pressed the middle button when they were satisfied that the plaid had been set to the point of changeover from coherence to non-coherence. Although judging the changeover point proved to be not particularly difficult (subjects produced reliable pretest judgements), each subject was given 10-15 practice trials to learn to adopt a constant criterion and to be able to make the adjustment fairly rapidly. Subjects were instructed to fixate the small fixation spot in the centre of the display, throughout the experiment. The subject’s head was held in a constant position by a chinrest and padded head clamp.

Following the practice trials, subjects made one adjustment of each of the two pretest plaids, in random order. There were two different pretest plaids because the adjustable grating started at a contrast of either 0.2 (well above the coherence threshold) or 0.02 (well below threshold). The second pretest adjustment was followed (after 1 sec) by an adaptation pattern, selected at random from the three available. The first exposure to the adapting grating or plaid was for 60 sec. The first exposure to the alternating components was for 120 sec. The first exposure period was followed by the presentation of one of the two adjustable patterns (selected at random), signalled by a 1 sec blank screen. The subject adjusted this pattern to the coherence changeover point and pressed the middle button, initiating another 20 sec (40 sec for the alternating components) exposure to the adapting stimulus, which was followed by another
adjustable pattern. After five postadaptation adjustments had been made, the screen went blank for 3 min, and subjects were instructed to rest. This procedure was repeated using the two remaining adaptation patterns, until each subject had made the two preadaptation and five postadaptation adjustments with each of the adapting stimuli. This entire procedure was repeated three times to obtain measurements in the BIN-BIN, MON-MON and IOT viewing conditions. The order in which these were conducted was randomised between subjects. Changes in viewing condition were effected by liquid crystal shutters, mounted in front of the subject's eyes.

The dependent variable was the contrast of the adjustable grating at the perceived coherence crossover point. This point could not be directly demonstrated to subjects, since each observer has a different threshold, but the percepts were explained to them as they performed practice adjustments. The consistency of the preadaptation settings suggested that they had understood the instructions.

Results

The mean of the postadaptation settings minus the mean of the preadaptation settings, for each subject in each viewing condition and following each adaptation pattern, was calculated. These were analysed in a 3 (adaptation patterns) x 3 (viewing conditions) factorial ANOVA. The results are plotted in Fig. 1. The most obvious results are that prior exposure to the grating or to the plaid raised the coherence threshold (the components of the test plaid had to be more similar in contrast to one another to be just judged to be moving coherently), and that prior exposure to the alternating components lowered the coherence threshold. These findings are consistent with those of Movshon et al. (1985) and von Grünau and Dubé (1991). The ANOVA revealed significant main effects of viewing condition ($F_{3,27} = 6.19; P < 0.01$), adaptation pattern ($F_{2,28} = 46.27; P < 0.0001$) and a significant interaction between these two variables ($F_{6,54} = 3.57; P < 0.02$), but the most important result is the smaller threshold elevation in the IOT viewing condition. Specific tests between means of interest, which were devised prior to conducting the experiment (planned contrasts). These tests compared the IOT means with the average of the BIN-BIN and MON-MON means revealed significant differences following adaptation to the grating and to the plaid, but not following exposure to the alternating components ($F_{1,40} = 15.91, P < 0.0005; F_{1,40} = 5.45, P < 0.05$; and $F_{1,40} = 0.212, P = 0.65$, respectively).

Discussion

These results are entirely consistent with the hypothesis that the perceived coherence of a moving plaid depends heavily on the activation level of the hypothesised monocular BT mechanism. Prior adaptation of this mechanism, by exposure to the drifting grating or plaid, substantially increased the coherence threshold only in the MON-MON and BIN-BIN viewing conditions. When the unadapted BT mechanism was used in making a coherence judgement, as in the IOT condition,
the threshold elevation was much more modest. Since the threshold elevation was not, however, reduced to zero, this suggests that coherence judgements are also affected by adaptation of a binocularly responsive 2-D motion sensitive mechanism.

The same modulation is not seen following exposure to the alternating components, also as predicted. The planned contrast comparing the average of the MON-MON and BIN-BIN means with the IOT mean, in this viewing mode, was not significant. Obviously, the IOT and MON-MON means are not different, and neither are the IOT and BIN-BIN means, tested with an unplanned contrast (since the apparent difference was not predicted; \( F_{1,40} = 0.64, P = 0.74 \)). We must conclude, on the basis of this, that the amount of threshold reduction following exposure to the alternating components of the plaid is not modulated by viewing condition. This suggests, unsurprisingly, that the BT mechanism is not adapted by exposure to the alternating components. This does not mean, however, that it has no role to play in determining the coherence thresholds obtained in this exposure mode. Indeed, a careful analysis of the reduction of the coherence threshold following exposure to the alternating components suggests that it can only be due to the activation of the unadapted BT mechanism in the test phase.

It has already been noted that the threshold elevation following exposure to the grating or the plaid is probably explained by the relatively exclusive adaptation of the 2-D mechanisms (both two-stage and monocular), leading to a postadaptation predominance of the 1-D signals, making coherence judgements less likely (or raising the coherence threshold in this case). We can be fairly sure that such exposure does not greatly affect the strength of the 1-D signals because the components are drifting in directions 75 deg away from the adaptation direction (at least in the case of adaptation to the grating—the special effects of exposure to the plaid will be examined later). Conversely, exposure to the alternating components selectively fatigues the 1-D channels, leading to a predominance of the 2-D signals, and a reduction of the coherence threshold. It has also already been noted that the unadapted 2-D mechanism in this case must be the BT mechanism, because the activation of a two-stage mechanism is dependent on the 1-D signals. If they are weakened by adaptation, then so will be the 2-D signal. This suggests that we should predict no change in the coherence threshold following alternating adaptation to the components if there were no BT mechanism. Any reductions in coherence threshold which do occur must, therefore, be due to the activation of another mechanism, presumably the unadapted BT mechanism.

The only unpredicted result of this experiment was the difference between the effects of exposure to the grating in the BIN-BIN and MON-MON conditions. While it is not possible, at this stage, to entirely account for this effect, certain considerations suggest likely explanations. Given that exposure to the components lowers the coherence threshold, and that exposure to motion in the 2-D direction (straight up) raises the coherence threshold, we might expect the effect of exposure to the plaid to be a compromise between these two effects, since both component and pattern motions are present in a plaid. The grating contains no component motions in the 1-D directions, and so might be considered as a cleaner measure of the effect of fatiguing the 2-D sensitive mechanisms. The pattern of results obtained in the MON-MON viewing condition is consistent with these considerations. The threshold elevation following exposure to the plaid is possibly smaller than that following exposure to the grating because of the additional adaptation of the 1-D signals in the former condition. This leaves us with the task of explaining the fact that the threshold elevation following exposure to the grating is smaller in the BIN-BIN condition than in the MON-MON condition. One possibly is that binocular viewing causes greater activity (during the test phase) in one of the 2-D mechanisms due to binocular synergism, diluting the effect of the adaptation of those mechanisms (Burke & Wenderoth, 1989). This can only be the two-stage mechanism, since the BT mechanism is monocular. This explanation hinges on two factors. The first is the claim that binocular viewing preferentially activates a two-stage mechanism, and we have obtained independent evidence that this is the case (Alais et al., 1994). The second is the unknown effect of binocular viewing during the adaptation phase. Experiment 2 was designed to investigate this.

### EXPERIMENT 2

This experiment is concerned with accounting for the surprising difference obtained between the MON-MON and BIN-BIN conditions following exposure to the grating in Expt 1. The result is surprising because in traditional motion aftereffect studies no differences have been reported between aftereffects induced in these two adapt/test modes (Moulden, 1980). Why such a difference occurs when the dependent variable is the coherence threshold of a drifting plaid (as in Expt 1) is not obvious, but knowing whether the effect is due to differences in viewing mode during adaptation or during testing will help rule out some potential explanations. The present experiment examined this question by exposing subjects to the vertically drifting grating monocularly and binocularly, and testing the subsequent threshold elevation monocularly (with each eye) and binocularly. There were, thus, five conditions: MON-MON, BIN-BIN, IOT, BIN-MON and MON-BIN.

The first three conditions of this experiment are replications of the conditions in Expt 1, and are included for comparison. The last two adapt/test modes will reveal whether the smaller threshold elevation following BIN-BIN exposure than that following MON-MON exposure is due to adapting binocularly or testing binocularly. If the difference is due only to an effect active during adaptation then BIN-MON should produce the same amount of threshold elevation as BIN-BIN, and MON-BIN the same amount as MON-MON. If the difference is due only to an effect active during
testing, then MON-BIN and BIN-BIN should produce the same amount of threshold elevation, as should BIN-MON and MON-MON. Any other pattern of results will require a more complicated explanation, involving factors active during both adaptation and testing. Since IOT is the only condition in which an unadapted mechanism is tested (one of the monocular BT processes) and an adapted mechanism is not tested (the other BT process), it should produce the smallest threshold elevation, as in Expt 1.

**Methods**

The methods were, for the most part, identical to those in Expt 1. Only the grating adaptation was used, since it was this adapting pattern which produced the unexpected results in Expt 1. The procedure was exactly the same as in Expt 1; practice adjustments followed by pretests, followed by a series of five adaptations and posttest adjustments in alternation. Each of the 14 new, naive subjects was exposed to the MON-MON, BIN-BIN, IOT, MON-BIN and BIN-MON in random order.

**Results**

The dependent variable was, again, the contrast of the adjustable grating at the coherence threshold. The mean of the posttest settings minus the mean of the pretest settings, for each adapt/test mode, was entered into a one factor, repeated measures ANOVA. The results are graphed in Fig. 2. The result of note is the replication of the findings of Expt 1. Following adaptation to the grating, the magnitudes of the threshold elevations are in the order MON-MON > BIN-BIN > IOT. On the basis of these differences alone, it was not surprising that the overall ANOVA was significant ($F_{5,52} = 6.69$, $P = 0.0002$). Of more interest are the comparisons between pairs of means. As is suggested by Fig. 2, planned contrasts comparing MON-MON with BIN-MON and MON-BIN both revealed significant differences at the 0.05 a level ($F_{1,52} = 4.29$, $P = 0.043$ and $F_{1,52} = 11.62$, $P = 0.0013$, respectively). Contrasts comparing BIN-BIN with BIN-MON and MON-BIN, however, revealed no significant differences ($F_{1,52} = 0.271$, $P = 0.6047$ and $F_{1,52} = 0.667$, $P = 0.4178$). BIN-MON and MON-BIN were not significantly different from one another ($F_{1,52} = 1.789$, $P = 0.1868$).

**GENERAL DISCUSSION**

The results of Expt 2 are not consistent with either of the simple predictions put forward earlier. The fact that BIN-BIN, BIN-MON and MON-BIN all produce smaller threshold elevations than MON-MON indicates that binocular viewing reduces the magnitude of the threshold elevation, irrespective of whether it occurs during the adaptation phase or the test phase. Consideration of the likely reasons for this result, together with the rejection of unworkable explanations, suggest that the monocular BT mechanism might be inhibited by another mechanism which is maximally activated when viewing is binocular. Presumably, the mechanism most likely to be inhibiting the BT mechanism is the two-stage mechanism (since there will be occasions when the
signals from these two mechanisms will be in conflict—see below), but this is far from implicated by the data.

The simplest of the new conditions to explain is MON-BIN. There are potentially two reasons for the threshold elevation in this condition being smaller than that in MON-MON. The first is that binocular viewing in the test phase exposes a monocular BT mechanism which has not been adapted. This will obviously lower the coherence threshold, since the unadapted BT mechanism will be producing a normal 2-D motion signal. The other possible reason depends on the well known tendency of binocularly sensitive cortical neurons to show binocular synergism—to respond much more vigorously to binocular input than to monocular input (e.g. Hubel & Weisel, 1977). Testing binocularly will cause the mostly binocular pattern sensitive cells in MT (Fellerman & Kaas, 1984) to fire synergistically and partially overcome their adaptation, thus reducing the magnitude of the threshold elevation, relative to MON-MON. Unfortunately, neither of these possibilities can be a complete explanation because adapting binocularly (as in the BIN-BIN and BIN-MON conditions) will fatigue both monocular BT mechanisms, and testing monocularly (as in the BIN-MON condition) cannot cause synergistic dilution in the test phase. Taken together, these considerations suggest that there must be something about binocular adaptation itself which accounts for the BIN-BIN and BIN-MON conditions producing smaller threshold elevations than MON-MON.

One possibility (no others occur to us*) is that smaller threshold elevations were obtained in the BIN-BIN and BIN-MON conditions because of inhibition of the monocularly sensitive BT mechanisms by some binocularly sensitive mechanism—possibly a two-stage mechanism. This proposal is only new with respect to the processing of 2-D motion. Anstis and Duncan (1983) conducted an experiment in which subjects viewed a disk rotating clockwise with their left eye and right eye, successively, in alternation, interspersed with binocular exposure to a disk rotating anticlockwise. Subjects reported an anticlockwise motion aftereffect when they viewed the stationary disk monocularly, but a clockwise motion aftereffect when they viewed it binocularly. It is difficult to imagine any explanation of this finding other than that suggested by Anstis and Duncan: that they had adapted largely independent populations of monocular and binocular neurons and that there was an inhibitory connection from the binocular process to the monocular ones. If there was no inhibitory connection then viewing the stationary disc binocularly would have produced no motion aftereffect, because the binocular process would have been signalling clockwise motion and the monocular processes would have been signalling anticlockwise motion. In the absence of an inhibitory connection, these competing signals would presumably have cancelled each other out, as occurs if opposite aftereffects are induced in each eye.

It remains to be demonstrated how a proposed inhibition of the BT mechanisms by binocular viewing helps to explain the results of Expt 2. The as yet unexplained finding is that binocular adaptation causes a reduction in the coherence threshold elevation, relative to MON-MON. This can be simply explained by the suggestion that in the BIN-BIN and BIN-MON conditions, the strong activation of the binocular inhibiting mechanism (due to binocular synergism) in the adaptation phase, causes a significant inhibition of the BT mechanisms, reducing their firing rate, and thus lowering their level of adaptation. As a consequence of this, they produce a stronger 2-D signal in the test phase, causing a reduction of the threshold elevation, relative to MON-MON. This effect is less marked in the MON-MON condition because the inhibiting mechanism is only activated monocularly during the adaptation phase, and so fires at a sub-optimal rate. This leads to less inhibition of the BT mechanisms, and therefore to their becoming more adapted. Of course, the inhibition of the BT mechanisms should also occur in the test phase of the experiment, and this would act to increase the coherence threshold, particularly when the testing is done binocularly. The magnitude of the MON-BIN threshold elevation presumably reflects a balance between the threshold-reducing contribution of the unadapted BT mechanism and the threshold-raising effect of the inhibition of this signal by the synergistically activated inhibiting mechanism. The effect of this inhibition will, of course, be less marked than normal because of the prior adaptation.

If it is true that binocular viewing (in any way) inhibits activity of the BT mechanisms, as is suggested by the results of this experiment, then this holds interesting implications for the unadapted viewing of moving 2-D images. Viewing such a pattern monocularly will cause sub-optimal activation of the two-stage mechanism (because it is largely binocular), little inhibition, and therefore to the predominance of the BT mechanism signals. Conversely, viewing a moving 2-D image binocularly will cause synergistic activation of the two-stage mechanism, and strong inhibition of the BT mechanisms, leading to a largely two-stage mechanism mediated motion signal. Since the two-stage mechanism depends on 1-D signals, which may interact or be otherwise altered (Burke & Wendelken, 1993a, Derrington & Suero, 1991), it will often be signalling a direction of motion different from that being signalled by the BT mechanism. Under these circumstances the signals of the two mechanisms will be in conflict, and which signal dominates will be partially determined by whether viewing is monocular or binocular. We have already gathered evidence that the perceived direction of drift of type II plaids [where such interactions do occur

*It is also possible that the BT mechanisms are exclusively monocular, and so are not activated by binocular viewing, and are not fatigued, therefore, by binocular adaptation. Since an arrangement of this nature must depend on inhibition of the BT mechanisms by some binocularly sensitive mechanism, however, it reduces to a stronger version of what we are suggesting.
(Burke & Wenderoth, 1993a)] is affected by monocular or binocular viewing (Alais et al., 1994), and we are currently exploring the applicability of this line of reasoning to type I patterns.

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