Vision Research 51 (2011) 479–488

Contents lists available at ScienceDirect

Vision Research

journal homepage: www.elsevier.com/locate/visres

Similar adaptation effects on motion pattern detection and position discrimination tasks: Unusual properties of global and local level motion adaptation

Benjamin M. Harvey [a,b,*], Oliver J. Braddick [b]

[a] Department of Experimental Psychology, Utrecht University, Netherlands
[b] Visual Development Unit, Department of Experimental Psychology, Oxford University, Oxford, UK

ARTICLE INFO

Article history:
Received 5 August 2010
Received in revised form 28 November 2010
Available online 9 January 2011

Keywords:
Motion
Adaptation
Psychophysics
Global motion

ABSTRACT

Here we examine adaptation effects on pattern detection and position discrimination tasks in radial and rotational motion patterns, induced by adapting stimuli moving in the same or opposite directions to the test stimuli. Adaptation effects on the two tasks were similar, suggesting these tasks are performed by the same population of neurons. Global motion specific adaptation was then induced by presenting adaptation stimuli and test stimuli in different parts of the visual field. Again, adaptation effects on the two tasks were similar, but neither same-direction nor opposite-direction motion produced any adaptation effect on contracting motion patterns. Finally, adaptation stimuli were compared that should have similar effects on local motion processing neurons, but different effects on global motion processing neurons. Again, adaptation effects on the two tasks were similar. However, when global-level adaptation was avoided, no adaptation effects were seen with adaptation patterns moving in the opposite direction to the test pattern. Together, these last two experiments suggest that adaptation to opposite directions of motion from the test motion affects global motion processing but not local motion processing neurons.

1. Introduction

Our recent psychophysical studies (Harvey & Braddick, 2008) have shown different spatial summation characteristics for pattern detection and centre of motion position discrimination tasks performed on rotating, expanding and contracting motion patterns. This raises the possibility that the neural substrate representing the position of this centre of motion is separate from that representing the type and direction of this motion pattern. This possibility is supported by reports of a stroke patient who is unable to determine the direction of radial motions, but is still able to localize the centres of these patterns accurately (Beardsley & Vaina, 2005). However, in macaques, MST has also been implicated in position discrimination (Duffy & Wurtz, 1995), and several models of heading discrimination propose a population-coded representation in MST (Lappe & Rauschcker, 1993; Page & Duffy, 2003; Perrone & Stone, 1998). Human MST also has a well-established role in detection and direction discrimination of rotating, expanding and contracting patterns (Morrone et al., 2000; Smith, Wall, Williams, & Singh, 2006; Wall, Lingnau, Ashida, & Smith, 2008). It is therefore possible that the same population of neurons performs both pattern detection and position discrimination tasks.

Adaptation effects on motion perception occur after viewing a motion pattern for a long time. When the pattern is removed, and a pattern with no net motion is presented, it appears to move in the opposite direction to the adapting stimulus. This is called a motion after-effect (MAE), and is the most perceptually obvious manifestation of a motion adaptation effect. However, adaptation effects can also occur in the absence of an MAE, for example when the adapting and test motions are presented in different areas of the visual field (Whitney & Cavanagh, 2003), where no visible MAE occurs, but performance is still affected.

If different populations of neurons are involved in performing pattern detection and position discrimination tasks, it might be possible to show different motion adaptation effects on the two tasks. If similar adaptation effects were seen on both tasks, this would suggest that the same populations of neurons are involved in performing them. However, this situation would be complicated if adaptation effects occur at an early level of neural processing which provides the inputs into two separate areas that perform the two tasks. In this case, similar adaptation effects would be seen, although different areas might process both tasks. In the human visual system, the striate cortex (V1) provides the main input into all other areas, and processes motion signals. Adaptation effects occurring at V1 would therefore affect subsequent motion processing, without selectivity for particular populations of neurons.

While it has not been conclusively established that adaptation effects on V1 exist in humans, it is certainly possible that they

---

* Corresponding author at: Department of Experimental Psychology, Utrecht University, Netherlands.
E-mail address: b.m.harvey@uu.nl (B.M. Harvey).

0042-6989/$ - see front matter © 2011 Elsevier Ltd. All rights reserved.
doi:10.1016/j.visres.2011.01.002

do. Adaptation effects on V1 neurons are well established in cats (for example (Vautin & Berkley, 1977; von der Heydt, Hanny, & Adorjani, 1978)). Studies of the level of interocular transfer in humans show the MAE is transferred incompletely in subjects with good stereopsis (Anstis & Duncan, 1983; Mitchell, Reardon, & Muir, 1975; Moulden, 1980). The strength of interocular transfer with spiral motion stimuli typically ranges from 40% to 80% across studies with a wide range of conditions. Figures are typically lower for translational motion stimuli (Heller & Ziefle, 1990; Steiner, Blake, & Rose, 1994). This incomplete transfer suggests that at least some of the MAE is mediated by cells which process motion monocularly, such as those in V1. However, the view that interocular transfer is a direct measure of the binocularity of the adapted neurons has been called into question. Some observers show a larger MAE in the non-adapted eye than in the adapted eye (Nishida & Ashida, 2001), for directionally ambiguous counterphase gratings.

There is more conclusive evidence that adaptation effects occur in human MT+. After adaptation to expanding patterns, the time course of the BOLD effect on MT follows the perceptual effect (Tootell et al., 1995). Furthermore, fMRI analysis of activity of MT+ during and after MAE storage shows that, mirroring the perceptual effect, MT+ BOLD activity dropped during storage, then rebounded to an increased level after storage (Culham et al., 1999). Also, the considerable interocular transfer of the MAE suggests that higher-level, binocularly activated neurons, such as those in MT+, are involved. Finally, rTMS delivered over MT+ early in MAE storage or during the perceptual MAE disrupts the MAE (Theoret, Kobayashi, Ganis, Di Capua, & Pascual-Leone, 2002). Despite the reservations of some investigators (Huk, Ress, & Heeger, 2001), who note that many of the fMRI effects in MT+ can be explained by attentional effects, there is a considerable body of evidence that MT+ is involved in the MAE.

The responses of optic flow pattern-specific neurons in macaque MST also decrease after prolonged exposure to their preferred flow pattern (Duffy & Wurtz, 1997), and the authors suggest this adaptation may contribute to MAEs. This has also been shown in humans, first as a reduced sensitivity to oscillatory motions changing in size (mixed expansion and contraction), which are different to those changing in position (translating) (Regan & Beverley, 1978). A more comprehensive analysis of this phenomenon has shown adaptation to upward and downward parts of a rotational motion pattern causes an after-effect containing leftward and rightward motion to complete the pattern in humans (Snowden & Milne, 1997). The same result was found with intermixed expanding and contracting motions. In this case, this "phantom" optic flow MAE is about half the strength of the effect of the normal MAE observed. The MAE found after adaptation to optic flow patterns also has stronger effects than the MAE produced by similar translating patterns (Bex, Metha, & Makous, 1999). Furthermore, the optic flow MAE was stronger than the corresponding translational MAE in parts of the visual field far from the adapting stimulus. This suggests that the neurons mediating the optic flow MAE have very large receptive fields, like those seen in macaque MST optic flow-sensitive neurons. Moreover, interocular transfer has been observed for MAEs to expanding and rotating motions, and this is more complete than the effect for translating motions (Steiner et al., 1994). Together, these results suggest that an optic flow-specific MAE is also present in humans, and this arises from the optic flow-sensitive cells of human MT+, the putative human MST homologue.

Whether the motion after-effect (MAE) and other motion adaptation effects occur earlier than MT+ or not, some of the MAE clearly originates from neurons whose responses do not reflect binocular processing, at the least. It is thus likely that some of the MAE observed originates in cells which only process motion very locally, before considerable spatial summation has occurred. Those neurons that process only very local motion, such as those in V1, should have a very locally acting adaptation effect. Furthermore, later extrastriate cortical areas such as MT+ might mediate MAEs with more globally acting effects (Wenderoth & Johnstone, 1987). Therefore, this study aimed to separate MAEs occurring in global and local motion processing substrates by differentiating between adaptation patterns that would affect global and local processing differently in Experiments 2 and 3.

2. Methods

2.1. Observers

Four observers participated overall, with three in each experiment. All had normal vision. BH, AA and CB participated in Experiment 1. In Experiments 2 and 3 and part of Experiment 1, CB was unavailable and JS acted as the third observer. BH is an author of this study, whereas AA, CB and JS are paid volunteers who were naïve to the purpose of the experiment.

Further subjects were not used, as results from the three subjects used were qualitatively very similar for all experiments.

2.2. Apparatus and stimuli

Although each experiment had different stimuli, all consisted of random dot kinematograms (RDKs) presented on a Sony GDM-FW900 monitor in a 13.33° by 10.16° (17.97° diagonal) rectangular region. Dynamic sequences were generated on-line at 60 Hz and at 1600×1200 resolution using custom software written in Lua (Ierusalimschy, 2003). Each stimulus consisted of 3000 circular white dots (4.4 min of visual angle diameter) on a black background. Stimuli were viewed binocularly at a distance of 150 cm. Observers sat in a quiet, dimly lit room.

All dots moved at the same speed of 1.9°/s, irrespective of distance from the centre of motion. No radial speed gradients were used, and so motions did not simulate the motion of a rigid object. The choice of velocity and lack of a speed gradient is discussed more fully in (Harvey & Braddick, 2008).

Dots had a lifetime of five frames (0.083 s). To minimize coherent stimulus flicker, dots were replaced asynchronously by randomly distributing initial dot lifetimes among the first five frames.

Incoherently moving dots followed the same motion pattern as coherently moving dots, but around a randomly placed centre of motion, so that for rotating patterns, discriminations could not be made based on the local curvature of single dot paths. If the movement of a coherently moving dot caused it to exceed the boundaries of the coherent part of the display, reach the centre of motion, or at the end of the dot's lifetime, it was replaced at a new, random position with a full, five-frame lifetime.

In radial motion stimuli, if the starting locations of dots had been randomly distributed, there would have been a net movement of randomly placed dots towards or away from the centre of motion. This would respectively increase or decrease dot density at the centre of motion. Therefore, in radial stimuli, the random location was assigned to the third (middle) frame of the dot's lifetime.

In all of these experiments, adaptation patterns were viewed first to induce a motion after-effect (Fig. 1). At the start of each trial, adaptation was induced by a 100%-coherent adaptation pattern for 30 s, topped up with 10-s adaptation intervals between test stimuli. In the control condition, a 0%-coherent RDK was shown, which should induce no directionally specific adaptation effect. The centre of the adaptation pattern was always exactly in the centre of the display. To show the subject that the adaptation time had passed, a high beep sounded and a small green fixation

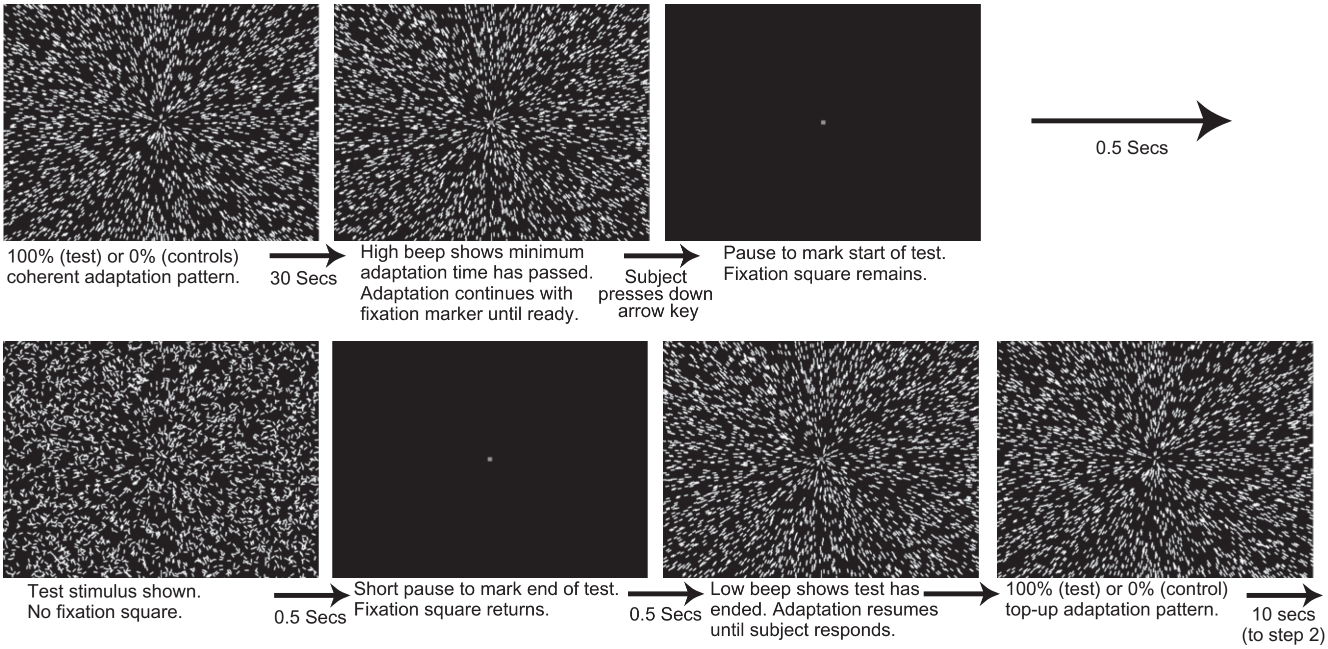

Fig. 1. Stimulus types and timings for adaptation stimuli. The frames in this figure show the superimposition of five consecutive movie frames, giving the impression of global structure with lines, instead of the moving dots that were present in the stimulus.

marker appeared in the centre of the screen, which the subject had been instructed to fixate, while the adaptation pattern continued. When ready, the subject pressed a button on a keyboard (the down arrow key) to start the test stimulus presentation. For a 0.5-s pause, the adaptation pattern was replaced with a plain black screen, on which the fixation marker persisted. This clearly demarcated the start of the test pattern. After this pause, this screen was replaced by the test pattern, with no fixation marker, for 0.5 s. The test pattern differed between the pattern detection and position discrimination tasks. This was followed by another black pause screen with a fixation marker for 0.5 s to demarcate the end of the test period. The adapting stimulus then appeared again, accompanied by a lower beep and with a fixation marker. This sequence was designed to show the adaptation pattern for as much time as possible between test patterns.

Here the fixation marker performed several functions. First, it showed the position of the centre of the screen accurately, important for position discrimination tasks. This was also shown by small white lines in the centre of the top and bottom edges of the screen, but it is unlikely these were used for position discrimination here as the discrimination distance was very fine and these lines were far from the centre of motion, reducing both their visibility and accuracy as a position discrimination cue. The fixation marker also allowed the subject to fixate the centre of the display before the stimulus was presented, as the short presentation time did not allow much eye movement and accurate position discrimination required the subject to foveate the centre of motion. Finally, it let the subject know a key-press was required, either to start the test stimulus when ready (red fixation marker) or to choose which type of stimulus they perceived (blue fixation marker). The fixation marker was not shown during the test stimulus presentation because having a static object in the middle of an RDK (which is designed to contain only motion cues, with no form information) might affect motion processing. Furthermore, it would cover over some of the centre of the display, which contains important information, particularly for position discrimination, as shown in our previous experiment (Harvey & Braddick, 2008).

All coherent motion adaptation and test patterns moved in fixed directions throughout each block of trials to allow adaptation effects to be examined without interference from adaptation to patterns moving in opposite directions. As no differences between the processing of clockwise and anti-clockwise patterns are known, clockwise rotation was used for all test patterns. Anti-clockwise rotation was only used for opposite-direction adaptation patterns.

Coherence thresholds were measured seven times for each condition by an adaptive staircase (Kontsevich & Tyler, 1999) run over a block of thirty trials. A mean, standard deviation, and standard error of the mean were calculated. The standard error of the mean is given as the error bars on the figures. The mean and standard deviation were used to perform a Welch's *t*-test (Welch, 1947) for significant differences in performance between conditions.

The blocks of trials were presented in a random order until each condition had been tested, and then blocks were repeated in another random order. Subjects were informed before each block whether the task involved pattern detection or position discrimination and which motion pattern would be used for the test stimulus.

2.3. Pattern detection task

During the test pattern period, a single interval of a partially coherent RDK or an RDK with 0% coherence was shown. The subject indicated whether they *believed a partially* coherent pattern *was shown,* by pressing the left arrow key if they *thought a partially* coherent pattern *was shown*, or the right arrow key if they did not. The centre of motion of the RDK was always 0.1° to the left or right of the centre of the screen (as in the position discrimination task) to avoid differences in adaptation effect in the two tasks based on differences in pattern position. It was possible that the positional uncertainty introduced by this manipulation might increase the area being attended to and thus affect performance.

Pattern detection tasks often follow a two-interval forced choice design, with one interval containing dynamic noise and the other containing a partially coherent pattern. As adaptation effects decrease with time, the two intervals could not be shown sequentially as this might bias choices. Topping up adaptation between intervals would have further increased the trials' duration and been very attentionally demanding for subjects. Therefore, a one interval yes/no design was chosen.

2.4. Position discrimination task

During the test pattern period, a partially coherent RDK was shown with its centre of motion 0.1° to the left or right of the centre of the display. The subject indicated on which side they perceived the centre of motion by pressing the left or right arrow key.

3. Experiment 1: Interactions between different full-field adaptation patterns

The first experiment examined which directions of circular motion (rotating, expanding and contracting) adaptation affected performance on which test patterns. This would show whether these effects differed between detection and position discrimination tasks.

3.1. Methods

In this experiment, adaptation patterns were shown over the entire display. Test patterns were confined to a 9.5°-diameter circular region centred on the centre of the display (to prevent the position of this circle being used as a position discrimination cue). Areas outside of this circle were filled with dynamic noise. As such, the adaptation pattern was larger than the test pattern and so should easily cover the test pattern display area during test pattern presentation.

This experiment had intended to test all rotating, expanding and contracting patterns as adaptation patterns for all test patterns. However, in pilot experiments conducted on BH, adaptation to rotating patterns had no effect on performance at either task with radial test patterns, and vice versa. As such, tests involving a radial test pattern and a rotational adaptation pattern, or vice versa, were not used for other subjects. This leaves only three adaptation patterns for each test pattern: same as the test pattern (Same), opposite direction to test pattern (Opposite), and adaptation to 0% coherence (Noise, the control condition).

As the motion after-effect causes the visual scene to appear to move, there was a possibility that effects on position discrimination could be results of such apparent changes in position caused by the MAE, rather than a direct effect on the sensitivity to location of the optic flow centre. Changes in perceived position after motion adaptation have been reported by other investigators (Snowden, 1998) even when this effect could not be attributed to a visible MAE (Whitney & Cavanagh, 2003). To test for such an effect on this experiment, a further control experiment was conducted in which the test stimulus was replaced with an analogous static form stimulus. This stimulus did not contain moving dots, but instead had randomly-placed streaks in which the path of each moving dot was integrated across five frames (the moving dots' lifetime) to produce a line. In all other respects, these static form stimuli were the same as the motion stimuli. If positional effects were not specific to the motion processing systems being investigated here, an adaptation effect on these static form patterns would also be expected. As all of the motion adaptation effects seen were present for rotational motion, only concentric form patterns were examined. Only BH was used as a subject for this control experiment.

4. Results

For both pattern detection (Fig. 2, light gray) and position discrimination (Fig. 2, dark gray) tasks, and for all subjects, coherence thresholds for detecting rotating, expanding and contracting patterns were increased when the adaptation pattern was the same as the test pattern. Coherence thresholds were also increased when the adaptation pattern was in the opposite direction to the test pattern, except for contracting test patterns (with one exception: an opposite-direction adaptation effect for contracting patterns was just significant in the position discrimination task with subject CB). The effect of adaptation to the opposite direction of motion, when it was found, was typically significantly smaller than the effect of adaptation to same-direction patterns, although this difference was not always found.

Coherence thresholds were 1.7–4.6 times higher for position discrimination than pattern detection tasks when adapted to noise, with no clear trend of subject or motion type. Adaptation increased the range of this difference to 1–5.7 times higher, although with no clear trend towards bigger or smaller differences. Adaptation effects increased coherence thresholds for pattern detection by 2.8–6.1 times (same-direction adaptation) or 1.2–1.9 times (opposite-direction adaptation, excluding contraction), so opposite-direction adaptation typically affected performance far less. Adaptation effects increased coherence thresholds for position discrimination by 1.4–2.4 times (same-direction adaptation) or 1.2–1.9 times (opposite-direction adaptation, excluding contraction), so again opposite-direction adaptation typically affected performance less. Overall, adaptation effects on position discrimination tasks were smaller, but the coherence threshold when adapted to noise was larger to begin with.

4.0.1. Non-specific effects of motion adaptation on static form test stimuli

No direction of adapting motion had any significant effect on BH's performance at pattern detection or position discrimination tasks on concentric form patterns (Fig. 3).

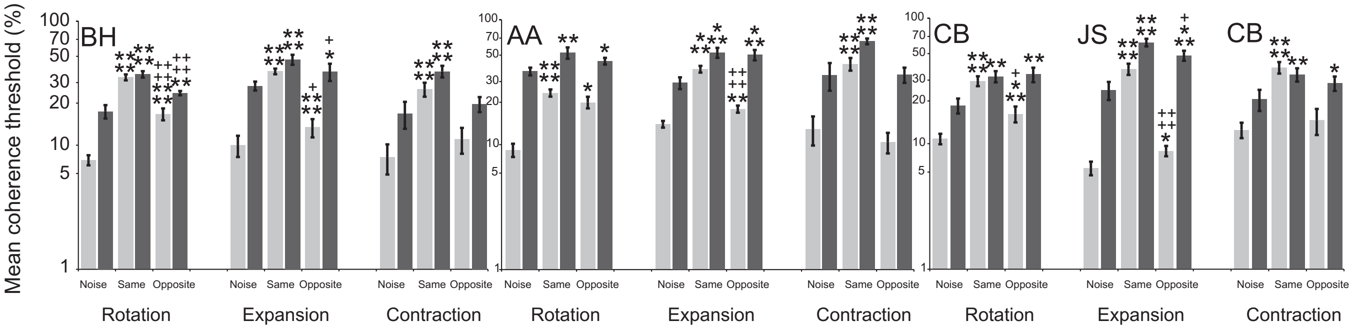

Fig. 2. Effects of adaptation on coherence thresholds for the pattern detection (light gray) and position discrimination (dark gray) tasks. Note: Significantly greater than adaptation to Noise: $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$, $^{****}p < 0.0001$. Significantly less than adaptation to Same motion: $^{+}p < 0.05$, $^{++++}p < 0.0001$.

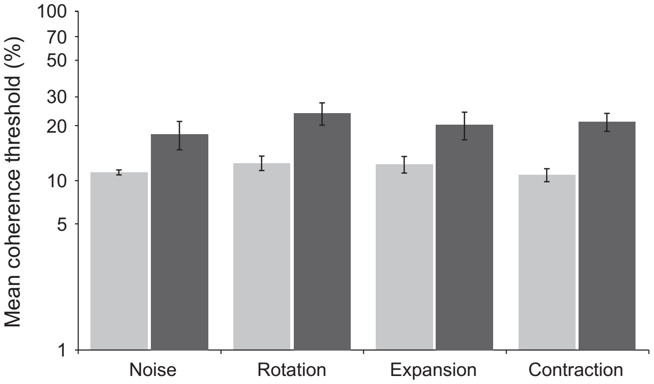

Fig. 3. Motion adaptation effects on concentric form detection (light gray) and position discrimination (dark gray) tasks for subject BH. No statistically significant effects of motion adaptation were seen.

5. Discussion

These results show statistically significant adaptation effects that were very similar for pattern detection and position discrimination tasks. Adaptation effects were significant when the same motion was used for adaptation and test patterns. When the opposite direction of motion was used for adaptation and test patterns, this produced significant adaptation effects, although not for contracting test patterns, except for position discrimination with CB. For BH and JS, the adaptation effects produced by the opposite direction of motion were always significantly smaller than those produced by the same direction of motion. This difference was also seen in pattern detection tasks for CB and for expanding patterns for AA. A similar difference is seen when adaptation to rightwards motion reduced the perceptibility of rightwards, but not leftwards, motion (Raymond & Braddick, 1996). Although the Raymond and Braddick experiment does not use coherence thresholds, its result suggests that processing of translational motion is not affected by the activity of cells tuned to the opposite direction.

There were few differences between adaptation effects for the two tasks, and these were minor when they were found. First, an adaptation effect was produced by an opposite direction of motion for contraction detection, but not contraction position discrimination, for CB. This difference was only significant in the detection task at a probability 4.40%, only slightly below the limit for accepting the null hypothesis, 5%. Second, opposite-direction adaptation effects for rotating patterns for CB and expanding patterns for AA were significantly smaller than same-direction adaptation effects for detection, but not position discrimination tasks. Although this difference is not seen in these two cases, it is consistent across both tasks for BH and JS.

It is interesting that (for both tasks) performance on contracting patterns is typically unaffected by adaptation to expanding motions, while other patterns are affected by adaptation to patterns moving in the opposite direction. The results of Experiment 2 suggest a possible neural basis for this difference.

No significant effects of motion adaptation on subsequent form processing were found here. It is therefore unlikely that the adaptation effects seen here are due non-specific effects, such as the introduction of motion signals into any system examining position, which could, for example, cause position to be distorted in the direction of motion.

There is one major problem with the interpretation of this experiment. It was a useful starting point to examine a broad set of adaptation effects for pattern detection and position discrimination tasks, and their similarities and differences. However, adaptation effects probably affect neurons at various levels of the visual processing hierarchy. This may include the brain's first level of visual motion processing, the motion sensitive cells of V1. If adaptation effects occurring here were affecting these results, then any downstream processing would be affected. Even if different areas performed processing of the two tasks, they would both be affected by adaptation effects on the neurons providing their input. As such, this experiment does not provide useful information about which areas of the brain are determining the level of performance in these tasks. Experiments 2 and 3 examine this more carefully.

6. Experiment 2: Spatially separated adaptation and test patterns, adaptation effects specific to global motion processing

In Experiment 1, it is possible that the effects seen in our results stem from adaptation effects on the cells of V1, which feed into all subsequent motion processing. This experiment avoided these effects by exploiting the fact that V1 neurons only process motions very local to their part of the visual field. On the other hand, downstream processing areas such as MT and MST integrate motion over a large part of the visual field. Thus, this experiment presented adaptation and test stimuli in spatially separate areas of the visual field. In this way, adaptation effects on the V1 neurons that would process the test stimulus are avoided. However, the MT and MST neurons that process the test area should be affected because they should also have inputs signaling motion within the area in which the adaptation pattern was presented.

Furthermore, given the psychophysical differences in spatial summation shown in our previous study (Harvey & Braddick, 2008), adaptation in spatially restricted areas may separate the mechanisms underlying pattern detection and position discrimination tasks.

6.1. Methods

In this experiment, adaptation patterns were shown over the entire display, except for a 3.5°-diameter circular region centred on the centre of the display (Fig. 4, left). This area contained random dot motion of 0% coherence. In the centre of the display, a small fixation marker was shown, which the subject was instructed to fixate throughout adaptation, so that adaptation occurred only in peripheral areas of the visual field. Test patterns were confined to a 3°-diameter circular region centred on the centre of the display (Fig. 4, right). Areas outside of this circle were filled with dynamic noise. As always, during test pattern presentation, no fixation marker was shown.

This experiment tested each subject with expanding, contracting and clockwise rotating test patterns, with adaptation to the same direction pattern and opposite direction patterns.

7. Results

For both pattern detection (Fig. 5, light gray) and position discrimination (Fig. 5, dark gray) tasks in all subjects, coherence thresholds for rotating and expanding (but not contracting) patterns were increased when the adaptation pattern was the same as the test pattern, or in the opposite direction. The effects of adaptation to the opposite direction of motion (where they occurred) were not significantly different the effect of adaptation to same-direction patterns.

Coherence thresholds were 1.1–2.7 times higher for position discrimination than pattern detection tasks when adapted to noise, with no clear trend of subject or motion type. With adaptation, this range was very similar, 1.2–2.5 times higher. Adaptation effects increased coherence thresholds for pattern detection by 1.3–1.9 times (same-direction adaptation, excluding contraction) or

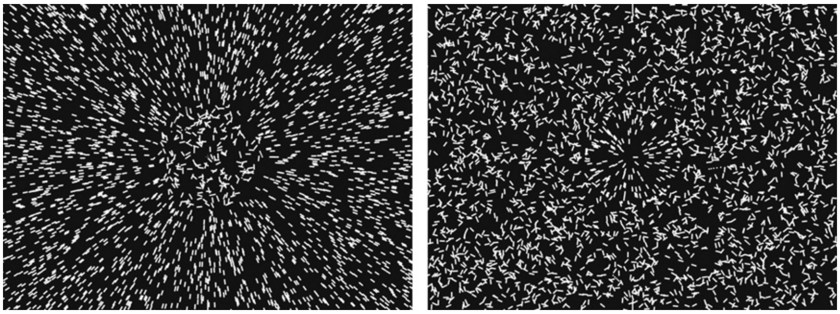

Fig. 4. Examples of adaptation (left) and test (right) stimuli used in Experiment 2. This figure shows the superimposition of five consecutive movie frames, giving the impression of global structure with lines, instead of the moving dots that were present in the stimulus. In the adaptation stimulus, the central 3.5° contains 0%-coherent dynamic noise, while the rest of the stimulus area contains 100%-coherent motion. In the test stimulus the central 3° contains partially coherent motion, while the rest of the stimulus area contains 0%-coherent dynamic noise.

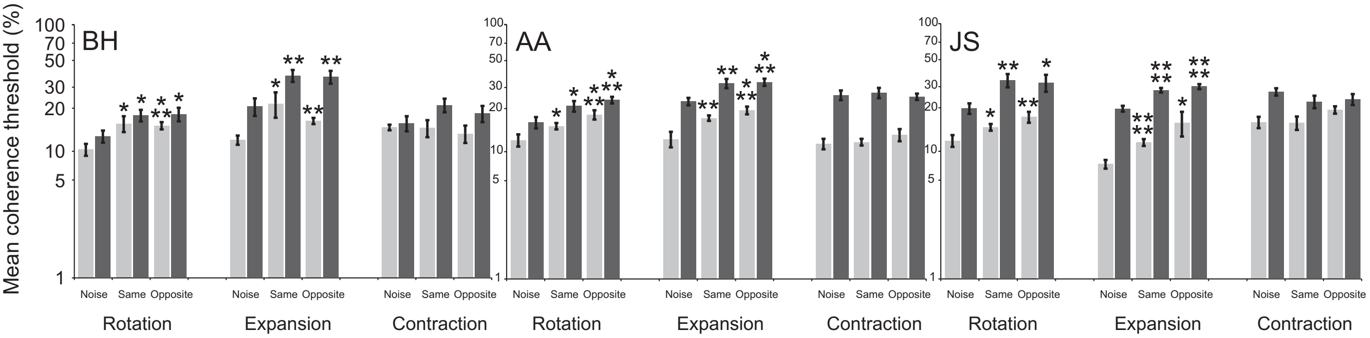

Fig. 5. Effects of adaptation in peripheral vision on coherence thresholds for the pattern detection (light gray) and position discrimination (dark gray) of rotating, expanding and contracting patterns in central vision. Note: Significantly greater than adaptation to Noise: $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$, $^{****}p < 0.0001$.

1.4–2.1 times (opposite-direction adaptation, excluding contraction), so opposite-direction adaptation has a very similar effect to same-direction adaptation here. Adaptation effects increased coherence thresholds for position discrimination by 1.3–1.8 times (same-direction adaptation, excluding contraction) or 1.4–1.7 times (opposite-direction adaptation, excluding contraction), so again opposite-direction adaptation has a very similar effect to same-direction adaptation here. Overall, adaptation effects on position discrimination tasks of similar magnitude to those on pattern detection.

8. Discussion

In this experiment, where stimuli were designed to avoid adaptation effects on the local motion processing cells of V1, the adaptation effects found were very similar for pattern detection and position discrimination tasks. Performance on either task for contracting patterns was not affected by adaptation to same or opposite-direction motion, while for rotating and expanding patterns performance on both tasks was affected by adaptation to either direction, with no significant differences between these effects.

The differences between the two tasks seen in Experiment 1 were not seen here, but CB (for whom many of these differences were seen) was unavailable for this experiment.

In this experiment, no adaptation effects were seen for contracting test patterns. This suggests that the adaptation effects seen for contracting patterns in Experiment 1 result from adaptation of local processing cells such as those in V1. Also, no differences between the magnitude of same and different direction adaptation effects were seen in this experiment. This lack of significant adaptation effects acting at the global motion processing level for contracting motions may help to explain the result of Harris, Morgan and Still (1981). This study found that the MAE caused by expanding motions is smaller when the motion display is accompanied by forward motion of the observer than when stationary or accompanied by backwards motion. However this effect is smaller or absent for contracting motions accompanied by backwards motion. If adaptation effects on contracting motion patterns act only at the local processing level, it is unlikely that they would be affected by vestibular inputs activated by subject motion.

Together, the differences between these results and those of Experiment 1 suggest that much of the same-direction adaptation effect seen in Experiment 1 come from adaptation effects in local motion processing neurons. For contracting test motions, these appear to have been the only adaptation effects seen. So while rotation- and expansion-sensitive detectors seem to be affected at a global processing level by adaptation, contraction-sensitive detectors seem to be unaffected. However, there is clear evidence from macaques (Duffy & Wurtz, 1991; Graziano, Andersen, & Snowden, 1994; Tanaka & Saito, 1989) that contraction-sensitive global motion detectors exist in MST, and human behavioral studies show that global summation occurs with contracting motion (Burr, Morrone, & Vaina, 1998; Morrone, Burr, Di Pietro, & Stefanelli, 1999) suggesting these detectors are also present in humans. So while contraction-sensitive global motion detectors are very likely present in humans, they appear to be invulnerable to adaptation effects on their performance. Further investigation of this results by neurophysiological and fMRI studies would be valuable.

Global, optic flow-specific adaptation effects have been shown before (for example (Snowden & Milne, 1996; Snowden & Milne, 1997) that do not vary with test stimulus position. Our experiment confirms that global-level adaptation occurs, but shows a different effect on contraction test patterns, which Snowden & Milne's experiments would have missed. In the 1996 paper, test patterns were shown inside the adapted area, so the adaptation effect they see on contracting test patterns could be explained by local-level adaptation, as in Experiment 1 here. In their 1997 paper, expanding and contracting test patterns were shown in the same block (where here they were separated), so the effects seen may be due only to the global-level effects on expanding test patterns.

While this result clearly shows adaptation effects at a global motion processing level, it does not show how much of the adaptation effect comes from this stage and how much comes from the local motion processing level. The stimulation of the global processing stage seen here is sub-optimal as it relies on the test pattern being spatially separated from the adaptation pattern. Experiment 3 aims to produce a fairer comparison of the adaptation effects occurring at each level, and provide further evidence of the similarities and differences between global-level adaptation effects on the two tasks.

9. Experiment 3: Changing adaptation patterns to examine adaptation effects specific to global motion processing

A further experiment is conducted here to provide more insight into how much of the adaptation effect acted through global motion processing areas. This experiment compared two altered adaptation patterns, which both alternated between two states every 500 ms. In the first, the adaptation pattern switched between full screen 100%-coherent and dynamic noise (0%-coherent) patterns. The second consisted of half of the display area containing a coherent pattern, and the other half containing dynamic noise, with the pattern in the two areas alternating. A local motion processing neuron should have the same response to these two manipulations, as at any one point the motion will simply switch between coherent and incoherent. However, a neuron that responds to motion over a large area should respond differently. In the first case, it will process coherent motion alternating with incoherent motion. In the second, it will always process some coherent motion. Even though the part of the display that contains that motion will vary, there will always be coherent motion somewhere in its receptive field. As such, the second condition should have larger adaptation effects acting at the global processing level than the first.

9.1. Methods

This experiment only examined expanding test patterns as examining all motion patterns would have been vary time consuming, and all test patterns had been addressed in Experiment 2. Again, coherence thresholds for detection and position discrimination of the pattern were compared after adaptation to full screen same direction (expanding) and opposite direction (contracting) motion with adaptation to dynamic noise. Adaptation patterns with same or opposite-direction motion alternating with dynamic noise every 500 ms (On–Off adaptation) (Fig. 6) were compared to these adaptation conditions. In the final adaptation condition, the display was divided into eight wedges of 45° radial angle (Wedges adaptation) (Fig. 7). Half of these contained coherent motion and the other half contained dynamic noise. Every 500 ms the wedges containing dynamic noise and the wedges containing coherent motion switched.

10. Results

This experiment found that adaptation with alternating wedges produced a larger adaptation effect than adaptation with alternating 100% coherence and dynamic noise, for all subjects and both tasks, and for adaptation to motion in the same or opposite direction to the test motion (Fig. 8). For both tasks, opposite-direction adaptation alternating between full screen coherence and dynamic noise did not produce any significant adaptation effect for any subject or task.

For pattern detection tasks, factorial ANOVA of the results shows significant main effects for adaptation stimulus (Wedges vs. On–Off) for BH ($p < 0.001$), AA ($p = 0.002$) and JS ($p = 0.007$), with the Wedges condition giving significantly higher coherence thresholds.

For position discrimination tasks, factorial ANOVA also shows significant main effects for adaptation stimulus (Wedges vs. On–Off) for BH ($p < 0.001$), AA ($p = 0.005$) and JS ($p = 0.005$), with the Wedges condition giving significantly higher coherence thresholds.

In all cases for position discrimination tasks, and most cases for pattern detection tasks, adaptation effects were larger when the full adaptation stimulus was displayed than in the Wedges or On–Off adaptation conditions. This difference was often significant, but not consistently.

In most cases, the adapted condition produced a significantly higher coherence threshold than adaptation to noise only. However, for all subjects and both pattern detection and position discrimination tasks, the On–Off adaptation condition with opposite directions of adaptation and test motion was not significantly different to adaptation to noise.

Coherence thresholds were 2.1–4.1 times higher for position discrimination than pattern detection tasks when adapted to noise.

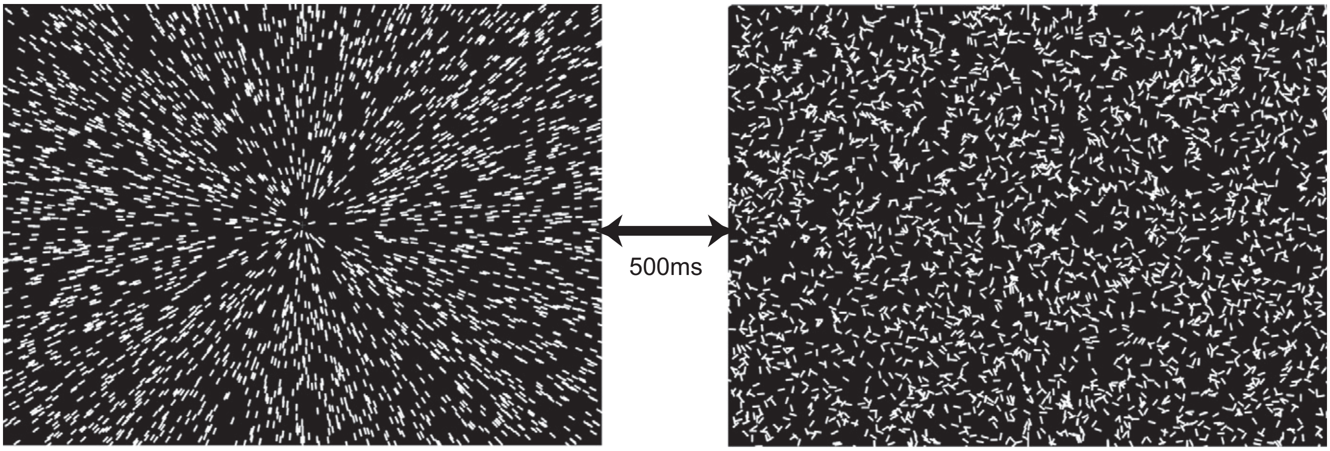

Fig. 6. On–Off adaptation patterns. This figure shows the superimposition of five consecutive movie frames, giving the impression of global structure with lines, instead of the moving dots that were present in the stimulus. The display alternated between a 100%-coherent motion pattern and a 0%-coherent dynamic noise pattern every 500 ms.

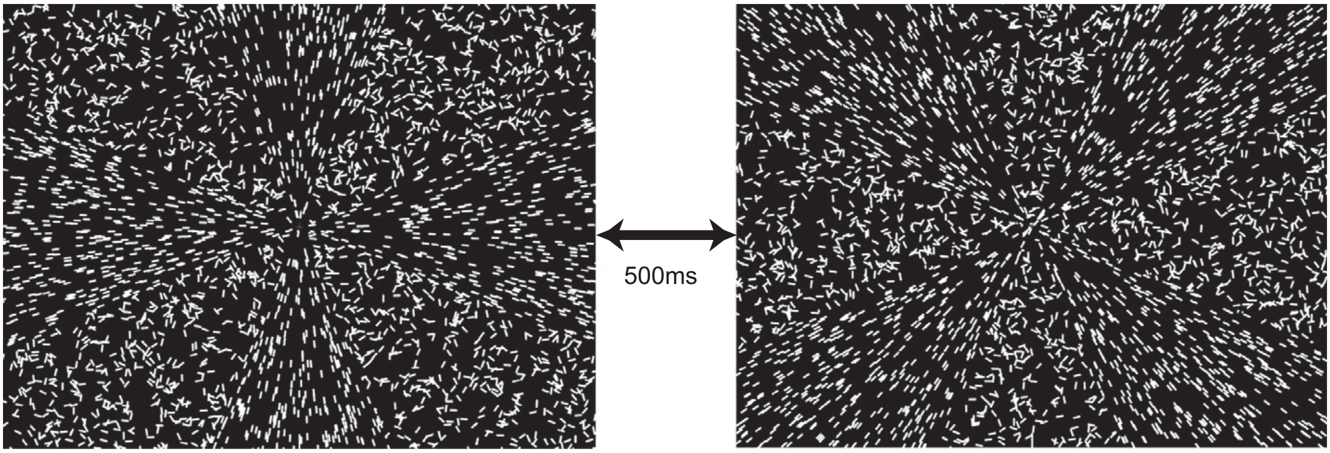

Fig. 7. Wedges adaptation patterns. This figure shows the superimposition of five consecutive movie frames, giving the impression of global structure with lines, instead of the moving dots that were present in the stimulus. The display alternated between 100%-coherent motion in half of the wedges and 100%-coherent motion in the other half of the wedges every 500 ms. The other wedges contained 0%-coherent dynamic noise.

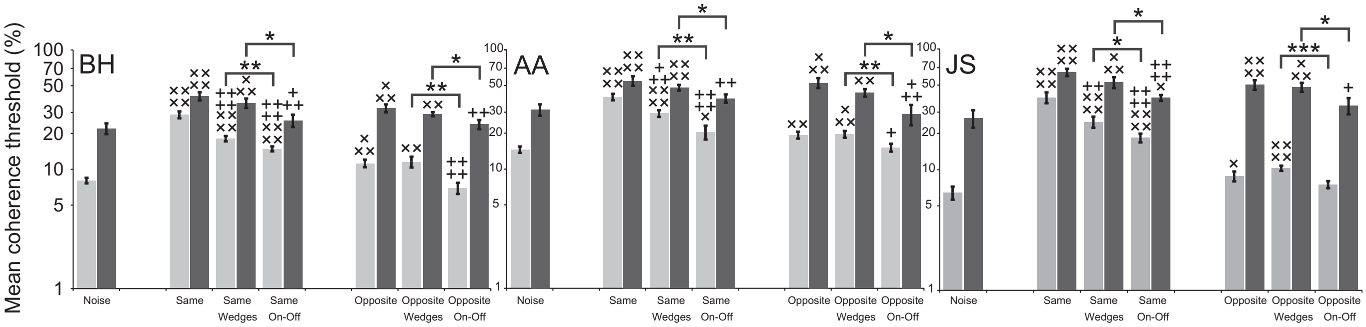

Fig. 8. Effects of adaptation to full screen, Wedges and On–Off adaptation stimuli in both the same and opposite direction to the expanding test pattern, on coherence thresholds for the detection (light gray) and position discrimination (dark gray) of expanding patterns. Note: Significantly greater than adaptation to Noise: $^{\times}p < 0.05$, $^{\times\times}p < 0.01$, $^{\times\times\times}p < 0.001$, $^{\times\times\times\times}p < 0.0001$. Significantly less than adaptation to full pattern: $+p < 0.05$, $^{++}p < 0.01$, $^{+++}p < 0.001$, $^{++++}p < 0.0001$. Significantly less than adaptation to wedges pattern: $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$.

Adaptation increased the range of this difference to 1.4–5.7 times higher, although with no clear trend towards bigger or smaller differences, as seen in Experiment 1. The effects of full-field adaptation on coherence thresholds were quantitatively very similar to those seen in Experiment 1.

Adaptation to the wedges pattern increased coherence thresholds for pattern detection by 2.0–3.9 times (same-direction adaptation, less than the 2.8–6.1 times seen for full-field patterns) or 1.3–1.6 times (opposite-direction adaptation, similar to the 1.3–1.4 times seen for full-field patterns).

Adaptation to the wedges pattern increased coherence thresholds for position discrimination by 1.5–2.0 times (same-direction adaptation, less than the 1.7–2.4 times seen for full-field patterns) or 1.3–1.8 times (opposite-direction adaptation, similar to the 1.5–1.9 times seen for full-field patterns).

So opposite-direction adaptation typically affected performance less than same-direction adaptation, as seen in Experiment 1, but this effect was similar for full-field and wedges adaptation, whereas for same-direction adaptation, wedges adaptation was weaker than full-field adaptation.

Adaptation to the On–Off pattern increased coherence thresholds for pattern detection by 1.4–2.9 times (same-direction adaptation). The same adaptation increased coherence thresholds for position discrimination by 1.2–1.5 times. In both cases, this was less than seen for full-field or wedge patterns. For both task, opposite-direction adaptation in the On–Off pattern condition had no significant effect.

11. Discussion

Together with the results from Experiment 2, these results demonstrate that for adaptation from both same direction and opposite direction stimuli, a significant amount of the adaptation effect occurs at a processing level after considerable spatial summation has occurred. The adaptation in wedges condition was designed to stimulate global expansion-sensitive neurons throughout the adaptation period, while only stimulating any local processing neuron half of the time. The adaptation stimulus which alternated between full screen coherent motion and dynamic noise would stimulate both populations only half of the time, and so should produce less global adaptation, but the same local adaptation.

It was expected that adaptation effects would be larger when the full adaptation stimulus was displayed than in the Wedges or On–Off adaptation conditions. In these latter adaptation conditions the average coherence of the adaptation display was only half of that in the full display condition.

When the adaptation stimulus was in opposite direction to the test pattern and in the On–Off condition, no significant adaptation effects were seen. As this On–Off condition was design to have less effect on global motion detectors, it may be that opposite-direction adaptation effects require effects on global motion detectors to affect performance.

These results also show that the global adaptation seen affects performance on both tasks in a very similar way, again providing further evidence that they are performed by the same global processing cells.

12. Conclusions

These experiments were not able to find separable adaptation effects for pattern detection and position discrimination tasks. The differences seen were small, when they were seen, and did not greatly affect interpretation of the results.

Much of the adaptation effects seen apparently occur at a global processing level, after considerable spatial summation has occurred. Experiment 2 shows this particularly clearly, as adaptation effects were seen (for expanding and rotating patterns) when the patterns were not presented in the same part of the display. Any neuron that responds to both the adaptation and test stimulus must have had a large receptive field, such as those seen in MT+. Experiment 3 also suggests that global adaptation effects are seen here as differences are seen between two conditions to which local motion sensitive cells should respond identically. The differences seen here are easily attributed to motion sensitive cells whose responses show considerable spatial summation.

Importantly, these global adaptation effects are very similar for pattern detection and position discrimination tasks. This suggests that the adaptation effects occur at the same global processing stage. Given that this global processing area is probably area MT and/or the human MST homologue for the pattern detection task, this is also likely to be the case for the position discrimination task. It therefore seems that the centre of motion position is represented in human MT+, supporting models of population coding of position here. However, several studies suggest that area VIP may contain a more straightforwardly coded representation of this centre of motion, particularly useful for heading judgments. First, macaque VIP neurons respond most strongly to preferred headings, and maintain these responses despite changes in gaze (Bremmer, Duhamel, Ben Hamed, & Graf, 2002; Duhamel, Bremmer, Ben Hamed, & Graf, 1997; Zhang, Heuer, & Britten, 2004). These heading responses seem to be clustered in a columnar organization (Zhang & Britten, 2004). Furthermore, an area putatively identified as the human homologue of VIP gives a stronger BOLD response to optic flow stimuli with a single centre of motion than one containing several centres, while MST does not (Wall & Smith, 2008). If VIP does directly represent heading, any adaptation effects in global motion processing areas may feed forward to affect the centre of motion representation in VIP. Our experiments did not address whether centre of motion position was represented in VIP and optic flow direction in MST, but it is certainly a possibility. If this is the case, however, it nevertheless seems likely that MST contains, at a population-encoded level, the information from which this heading representation is derived.

In considering the similarity of the adaptation effects on pattern detection and position discrimination tasks, it must be remembered that pattern detection could be achieved with a far lower coherence threshold than position discrimination. Therefore, in any position discrimination task there was a clearly detectable motion pattern visible. We have not been able to make a stimulus of this type where position discrimination is possible without the motion pattern being clearly detectable. This means that any position discrimination may rely on pattern detection mechanisms, which may underlie the similarity of adaptation effects. This in itself may reflect a common mechanism being involved in both tasks, but it could also be seen as an inherent limitation in any experiment comparing these two tasks, as the subject can never perform a position discrimination task independently of pattern detection.

The results of Experiment 2 (and to a lesser extent Experiment 1) strongly suggest that adaptation effects on processing of contracting patterns occur only at local processing levels. Global contracting motion detectors seem unaffected by motion adaptation in any direction, while detectors for rotating and expanding motions are strongly affected. Further investigation of this results by neurophysiological and fMRI studies would be valuable.

Various results suggest that while same-direction adaptation effects seems to act on both global and local processing levels, the opposite-direction effect may only act at a global level. First, opposite-direction adaptation typically had no effect on either task for contracting test patterns in Experiment 1. A locally acting adaptation effect should work equally well regardless of the pattern examined. Second, while in Experiment 1 same-direction adaptation effects were often smaller than opposite-direction adaptation effects, this was not the case for global adaptation effects in Experiment 2. Finally, Experiment 3 showed no opposite-direction adaptation effect with alternation between fully coherent and fully incoherent motion (On–Off adaptation), while this effect was seen for alternation between wedges and for same-direction motion in both adaptation patterns. So while same-direction adaptation is typically effective under these conditions, apparently by a primarily local motion adaptation effect, this effect was not seen for opposite-direction motion. If the opposite-direction adaptation effect only acts at a global level, this would be supported by the inability of some investigators to find an opposite-direction adaptation effect in translational motion (Raymond, 1996).

This interpretation also fits with neurophysiological studies of translating stimuli (Van Wezel & Britten, 2002), which shows only weak, inconsistent adaptation effects to anti-preferred translational motions in macaque MT neurons. So while this opposite-direction adaptation effect is weak or absent in the processing of translating motions by MT, it is clearly present, at least for expanding and rotating motions, by the analysis of complex motions, presumably by MST.

If this is the case we can extend the finding that opposite-direction adaptation effects are not seen for contracting test motions. One could again conclude that global adaptation effects are unlikely to act on contraction selective neurons. While it is unknown why this should be, it is an interesting finding. This finding has important implications concerning the importance of optic flow motions and their adaptation for the behavior of an animal. Adaptation to expanding optic flow motions is very useful when an animal is moving forward for a long time. If contraction-sensitive global motion detectors are not subject to adaptation (as the presented results suggest) and the local-level adaptation effects acting downstream of these global motion detectors are for same-direction motion only (as the results also suggest), detectablity of contracting motions will not be reduced during exposure to expanding flow fields. This may prevent reduced detectability of independently-moving objects during locomotion, which might be disadvantageous for survival.

Acknowledgments

This work was supported by an MRC research studentship to BMH, and by MRC grants G7908507 and G0601007 to OJB.

References

Anstis, S., & Duncan, K. (1983). Separate motion aftereffects from each eye and from both eyes. *Vision Research, 23*(2), 161–169.

Beardsley, S. A., & Vaina, L. M. (2005). How can a patient blind to radial motion discriminate shifts in the center-of-motion? *Journal of Computational Neuroscience, 18*(1), 55–66.

Bex, P. J., Metha, A. B., & Makous, W. (1999). Enhanced motion aftereffect for complex motions. *Vision Research, 39*(13), 2229–2238.

Bremmer, F., Duhamel, J. R., Ben Hamed, S., & Graf, W. (2002). Heading encoding in the macaque ventral intraparietal area (VIP). *European Journal of Neuroscience, 16*(8), 1554–1568.

Burr, D. C., Morrone, M. C., & Vaina, L. M. (1998). Large receptive fields for optic flow detection in humans. *Vision Research, 38*(12), 1731–1743.

Culham, J. C., Dukelow, S. P., Vilis, T., Hassard, F. A., Gati, J. S., Menon, R. S., et al. (1999). Recovery of fMRI activation in motion area MT following storage of the motion aftereffect. *Journal of Neurophysiology, 81*(1), 388–393.

Duffy, C. J., & Wurtz, R. H. (1991). Sensitivity of MST neurons to optic flow stimuli. I. A continuum of response selectivity to large-field stimuli. *Journal of Neurophysiology, 65*(6), 1329–1345.

Duffy, C. J., & Wurtz, R. H. (1995). Response of monkey MST neurons to optic flow stimuli with shifted centers of motion. *Journal of Neuroscience, 15*(7 Pt 2), 5192–5208.

Duffy, C. J., & Wurtz, R. H. (1997). Multiple temporal components of optic flow responses in MST neurons. *Experimental Brain Research, 114*(3), 472–482.

Duhamel, J. R., Bremmer, F., Ben Hamed, S., & Graf, W. (1997). Spatial invariance of visual receptive fields in parietal cortex neurons. *Nature, 389*(6653), 845–848.

Graziano, M. S., Andersen, R. A., & Snowden, R. J. (1994). Tuning of MST neurons to spiral motions. *Journal of Neuroscience, 14*(1), 54–67.

Harris, L. R., Morgan, M. J., & Still, A. W. (1981). Moving and the motion after-effect. *Nature, 293*(5828), 139–141.

Harvey, B. M., & Braddick, O. J. (2008). Psychophysical differences in processing of global motion and form detection and position discrimination. *Journal of Vision, 8*(7:14), 1–18.

Heller, D., & Ziefle, M. (1990). Zur Bedingungsanalyse von Bewegungsnacheffekten. *Schweizerische Zeitschrift fur Psychologie, 49*, 139–149.

Huk, A. C., Ress, D., & Heeger, D. J. (2001). Neuronal basis of the motion aftereffect reconsidered. *Neuron, 32*(1), 161–172.

Ierusalimschy, R. (2003). *Programming in Lua*. Rio de Janeiro: Lua.org.

Kontsevich, L. L., & Tyler, C. W. (1999). Bayesian adaptive estimation of psychometric slope and threshold. *Vision Research, 39*(16), 2729–2737.

Lappe, M., & Rauschcker, J. P. (1993). A neural network model for the processing of optic flow from ego-motion in higher mammals. *Neural Computation, 5*, 374–391.

Mitchell, D. E., Reardon, J., & Muir, D. W. (1975). Interocular transfer of the motion after-effect in normal and stereoblind observers. *Experimental Brain Research, 22*(2), 163–173.

Morrone, M. C., Burr, D. C., Di Pietro, S., & Stefanelli, M. A. (1999). Cardinal directions for visual optic flow. *Current Biology, 9*(14), 763–766.

Morrone, M. C., Tosetti, M., Montanaro, D., Fiorentini, A., Cioni, G., & Burr, D. C. (2000). A cortical area that responds specifically to optic flow, revealed by fMRI. *Nature Neuroscience, 3*(12), 1322–1328.

Moulden, B. (1980). After-effects and the integration of patterns of neural activity within a channel. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences, 290*(1038), 39–55.

Nishida, S., & Ashida, H. (2001). A motion aftereffect seen more strongly by the non-adapted eye: Evidence of multistage adaptation in visual motion processing. *Vision Research, 41*(5), 561–570.

Page, W. K., & Duffy, C. J. (2003). Heading representation in MST: Sensory interactions and population encoding. *Journal of Neurophysiology, 89*(4), 1994–2013.

Perrone, J. A., & Stone, L. S. (1998). Emulating the visual receptive-field properties of MST neurons with a template model of heading estimation. *Journal of Neuroscience, 18*(15), 5958–5975.

Raymond, J., & Braddick, O. (1996). Responses to opposed directions of motion: continuum or independent mechanisms? *Vision Research, 36*(13), 1931–1937.

Regan, D., & Beverley, K. I. (1978). Looming detectors in the human visual pathway. *Vision Research, 18*(4), 415–421.

Smith, A. T., Wall, M. B., Williams, A. L., & Singh, K. D. (2006). Sensitivity to optic flow in human cortical areas MT and MST. *European Journal of Neuroscience, 23*(2), 561–569.

Snowden, R. J. (1998). Shifts in perceived position following adaptation to visual motion. *Current Biology, 8*(24), 1343–1345.

Snowden, R. J., & Milne, A. B. (1996). The effects of adapting to complex motions: Position invariance and tuning to spiral motions. *Journal of Cognitive Neuroscience, 8*(5), 435–452.

Snowden, R. J., & Milne, A. B. (1997). Phantom motion after effects – Evidence of detectors for the analysis of optic flow. *Current Biology, 7*(10), 717–722.

Steiner, V., Blake, R., & Rose, D. (1994). Interocular transfer of expansion, rotation, and translation motion aftereffects. *Perception, 23*(10), 1197–1202.

Tanaka, K., & Saito, H. (1989). Analysis of motion of the visual field by direction, expansion/contraction, and rotation cells clustered in the dorsal part of the medial superior temporal area of the macaque monkey. *Journal of Neurophysiology, 62*(3), 626–641.

Theoret, H., Kobayashi, M., Ganis, G., Di Capua, P., & Pascual-Leone, A. (2002). Repetitive transcranial magnetic stimulation of human area MT/V5 disrupts perception and storage of the motion aftereffect. *Neuropsychologia, 40*(13), 2280–2287.

Tootell, R. B., Reppas, J. B., Dale, A. M., Look, R. B., Sereno, M. I., Malach, R., et al. (1995). Visual motion aftereffect in human cortical area MT revealed by functional magnetic resonance imaging. *Nature, 375*(6527), 139–141.

Van Wezel, R. J., & Britten, K. (2002). Motion adaptation in area MT. *Journal of Neurophysiology, 88*(6), 3469–3476.

Vautin, R. G., & Berkley, M. A. (1977). Responses of single cells in cat visual cortex to prolonged stimulus movement: neural correlates of visual aftereffects. *Journal of Neurophysiology, 40*(5), 1051–1065.

von der Heydt, R., Hanny, P., & Adorjani, C. (1978). Movement aftereffects in the visual cortex. *Archives Italiennes De Biologie, 116*(3–4), 248–254.

Wall, M. B., Lingnau, A., Ashida, H., & Smith, A. J. (2008). Selective visual responses to expansion and rotation in the human MT complex revealed by functional magnetic resonance imaging adaptation. *European Journal of Neuroscience, 27*(10), 2747–2757.

Wall, M. B., & Smith, A. T. (2008). The representation of egomotion in the human brain. *Current Biology, 18*(3), 191–194.

Welch, B. L. (1947). The generalization of "Student's" problem when several different population variances are involved. *Biometrika, 34*, 28–35.

Wenderoth, P., & Johnstone, S. (1987). Possible neural substrates for orientation analysis and perception. *Perception, 16*(693–709).

Whitney, D., & Cavanagh, P. (2003). Motion adaptation shifts apparent position without the motion aftereffect. *Perception and Psychophysics, 65*(7), 1011–1018.

Zhang, T., & Britten, K. H. (2004). Clustering of selectivity for optic flow in the ventral intraparietal area. *Neuroreport, 15*(12), 1941–1945.

Zhang, T., Heuer, H. W., & Britten, K. H. (2004). Parietal area VIP neuronal responses to heading stimuli are encoded in head-centered coordinates. *Neuron, 42*(6), 993–1001.