Available online at www.sciencedirect.com
SCIENCE DIRECT®
Vision Research 46 (2006) 1170–1177
Vision Research
www.elsevier.com/locate/visres

Brief communication

Large shifts in perceived motion direction reveal multiple global motion solutions

Linda Bowns [a,*], David Alais [b]

[a] School of Psychology, University of Nottingham, University Park, Nottingham NG7 2RD, UK
[b] Department of Physiology and Institute for Biomedical Research, School of Medical Science, University of Sydney, NSW 2006, Australia

Received 17 March 2005; received in revised form 5 July 2005

Abstract

Moving objects are thought to be decomposed into one-dimensional motion components by early cortical visual processing. Two rules describing how these components might be re-combined to produce coherent object motion are the intersection of constraints and the vector average rules. Using stimuli for which these combination rules predict different directional solutions, we found that adapting one of the solutions through motion adaptation switched perceived direction to the other solution. The effects were symmetrical: shifts from IOC to VA, and from VA to IOC, were observed following adaptation. These large shifts indicate that multiple solutions to global motion processing coexist and compete to determine perceived motion direction.

Keywords: Motion perception; Adaptation; Global motion; Intersection of constraints

1. Introduction

Early stages of visual cortical motion processing decompose moving objects into a series of one-dimensional Fourier components. Re-combining these to recover the object's velocity is a vital task. Two dominant theories of how one-dimensional Fourier components are combined to determine pattern motion are the intersection of constraints rule (IOC: Adelson & Movshon, 1982) and the vector average rule (VA: Wilson, Ferrera, & Yo, 1992). Fig. 1 illustrates the IOC and VA rules using a velocity space diagram. The angles of the vectors correspond to the components' directions of motion, and vector lengths indicate their speeds. The VA solution is obtained simply by averaging the x- and y-components of each vector. Solving the IOC rule requires velocity constraint lines to be drawn perpendicular to each of the vectors and it is their point of intersection that defines the IOC direction. The IOC rule was initially presented as a solution to the well-known "aperture problem" whereby the motion of a single (featureless) component such as a grating is directionally ambiguous when viewed through a small aperture. The IOC rule is simple but powerful because it provides a veridical solution—a means of recovering the only vector shared by both components.

While there is good psychophysical and physiological support for the IOC rule (Bowns, 1996; Huk & Heeger, 2002; Movshon, Adelson, Gizzi, & Newsome, 1985; Rodman & Albright, 1989; Stone, Watson, & Mulligan, 1990; Stoner & Albright, 1992), it has frequently failed to predict perceived motion direction when a sub-class of stimuli known as "type II" patterns are used at short durations (Alais, Wenderoth, & Burke, 1994; Yo & Wilson, 1992). Type II patterns have velocity components of unequal speeds and similar directions, producing an IOC solution which does not lie between the component directions (see Figs. 1B and C) and which therefore differs from the VA direction. Type II patterns, then, provide a means to test the IOC and VA rules since they make distinct predictions. Studies using type II patterns have indicated that the

---

[*] Corresponding author. Tel.: +44 0 115 951 5283; fax: +44 0 115 951 5324.
E-mail addresses: lbowns@psychology.nottingham.ac.uk (L. Bowns), alaisd@physiol.usyd.edu.au (D. Alais).

0042-6989/$ - see front matter © 2005 Published by Elsevier Ltd.
doi:10.1016/j.visres.2005.08.029

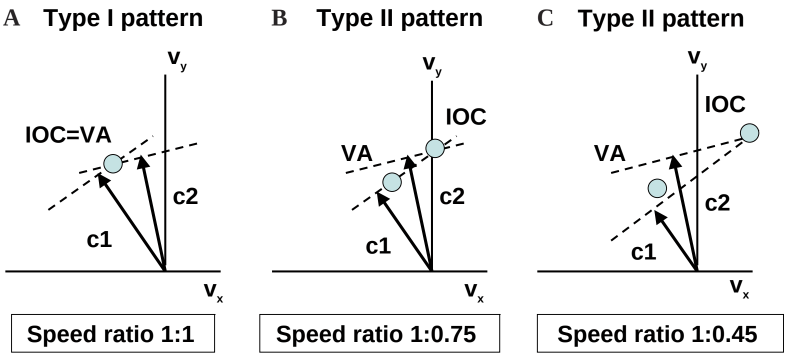

Fig. 1. Velocity space diagrams illustrating the three plaids used in these experiments. The angles of the vectors correspond to the components' directions of motion, and vector lengths indicate their speeds (see Section 2). The perceived direction of the plaid will generally correspond either to the vector average direction (labelled VA) or to the intersection of constraints direction (labelled IOC). Velocity constraint lines are shown (dashed lines perpendicular to motion vectors) and their point of intersection defines the IOC global motion solution.

VA direction is perceived at short durations (150–200 ms: Wilson et al., 1992; Yo & Wilson, 1992) and that the IOC direction is perceived only at longer durations (Yo & Wilson, 1992). A recent study (Bowns, 1996), however, showed that this result did not generalise to all type II patterns, when the component speed ratio was changed some type II plaids were perceived in the IOC direction even at short durations. This suggested that the shift from the VA to the IOC direction is not simple due to the orientation dependency in the early neural response of MT neurons that was recently observed (Pack & Born, 2001).

One way to unify these disparate results is to hypothesise a mechanism that allows both the IOC and VA solutions to coexist, with both potentially contributing to the direction that is ultimately perceived. This hypothesis leads to a clear prediction: if the neural response to one of the directional solutions were to be attenuated (by adaptation, for example), the coexisting solution should then determine perceived pattern direction. In a type II plaid, that should result in large changes in perceived pattern direction. Here, we test our hypothesis using stimuli in which the combination rules predict differing directional solutions. One of the stimuli was created to favour one of the solutions, while the other was created to favour the other solution. For both patterns, attenuating the neural response to the favoured direction through a selective-adaptation paradigm resulted in the perceived direction shifting to the other solution. This large shift indicates that multiple solutions to global motion processing coexist and compete to determine perceived direction. This finding reconciles the theoretical dichotomy in demonstrating that both solutions are neurally implemented, and unifies earlier disparate findings in the motion literature.

We tested our hypothesis that both IOC and VA solutions coexists by using a selective-adaptation paradigm on three specially constructed moving patterns. Each was made by superimposing a pair of one-dimensional components (sinusoidal gratings) to form a so-called 'plaid' pattern (Fig. 1). The first plaid (Fig. 1A) is a control pattern in which both components move at the same speed (speed ratio 1:1), thus yielding identical IOC and VA solutions. The second plaid (Fig. 1B) is similar but differs in that the speed of one of its components is reduced to make a type II pattern (speed ratio 1:0.75). The third plaid (Fig. 1C) is like the second except that the slower component has been further reduced in speed (speed ratio 1:0.45). Our proposal that both VA and IOC solutions coexist and combine to determine perceived direction makes two strong predictions: (i) following VA adaptation, the perceived direction of speed ratio 1:0.75 should shift to the IOC direction and (ii) following IOC adaptation, speed ratio 1:0.45 should shift to the VA direction. Speed ratio 1:1 was also adapted, although no change in direction is predicted since both competing solutions are identical.

2. Methods

2.1. Subjects and stimuli

Three experienced observers and two naïve participants with normal or corrected acuity served as subjects. Their task was to judge the perceived direction of drifting 'plaid' stimuli—translating patterns produced by summing two drifting sinusoidal components. The patterns had a Michelson contrast of 0.95 and appeared on a gamma-corrected video monitor in a central circular aperture 6.3° wide. The surrounding area was set to mean luminance (32.4 cd m^{-2}) and image displacements were synchronised to the vertical refresh rate of 75 Hz. Spatial resolution was 24 pixels deg^{-1} from the viewing distance of 48 cm. The two component gratings were of equal contrast and spatial frequency (0.8 cyc deg^{-1}), with drift directions of 112° and 135°. The speed of the first component (112°) was fixed at 5.25 deg s^{-1}, (a drift rate of 4.2 Hz), while the speed of the second component was proportional to the first, taking a value of either 1, 0.75 or 0.45 of the first component's speed (5.25, 3.94 and 2.36 deg s^{-1}, respectively). In this way three plaids were created, with the 1:1 speed ratio being a type-I plaid, and the 1:0.75 and 1:0.45 ratios being type-II plaids. These three speed combinations were chosen because their VA directions differ only slightly (123.5°, 121.8° and 119.1°) while their IOC directions differ widely (123.5°, 88.4° and 61.7°).

2.2. Procedure

To establish pre-adaptation baselines, observers indicated the direction of each pattern following brief (160 ms) presentations. The three patterns were presented 20 times in a randomised order, i.e., 60 trials in a single block, and the mean direction for each pattern was calculated. In a subsequent experiment, observers again judged the direction of each briefly presented pattern but they were first exposed to 16 s of adaptation by a grating drifting either in the IOC or VA direction of the pattern being tested, and matching its spatial period and speed (adapting spatial frequency for the VA solution was 0.8 cyc deg^{-1}; for the IOC solutions: plaid ratio 1:1 spatial frequency was 0.8 cyc deg^{-1}; plaid ratio 1:0.75 spatial frequency was 0.7 cyc deg^{-1}; plaid ratio 1:0.45 spatial frequency was 0.5 cyc deg^{-1}) The spatial frequency decreases in the IOC conditions because it is the spatial modulation along the axis of the IOC direction which gets increasingly oblique with respect to the pattern's texture.

In a random order, twelve post-adaptation measurements were taken for each pattern following IOC adaptation and twelve following VA adaptation. A recovery period of at least 1.5 times the adaptation duration separated all adaptation trials. Finally, the effectiveness of adaptation in shifting speed ratio 1:0.45 from the IOC to VS direction and speed ratio 1:0.75 from VS to IOC direction was explored in experiments varying the adaptor's spatial frequency over a 7-octave range of [0.1, 0.2, 0.4, 0.8, 1.7, 3.3, 6.6 and 13.2] cyc deg^{-1} and temporal frequency over a 6-octave range of [0.3, 0.5, 1.1, 2.1, 4.2, 8.4 and 16.8] Hz. The time course of adaptation was also explored by testing the following adaptation durations: [0.13, 0.25, 0.5, 1, 2, 4 and 8] s.

3. Results

Confirming an earlier report (Bowns, 1996; Yo & Wilson, 1992), the speed ratio 1:0.75 is reliably perceived to move in the VA direction, while the speed ratio 1:0.45 is perceived to move in the IOC direction (Bowns, 1996) (Fig. 2). With baseline directions established, we sought to attenuate the neural response to either the VA or the IOC direction by exposing observers to 16 s of motion adaptation. This was done for all three patterns in a random sequence. Remember the adapting pattern was a sine-wave grating whose velocity matched that of the pattern being tested (i.e., VA direction for speed ratio 1:0.75; IOC direction for speed ratio 1:0.45), and was followed immediately by a re-test of pattern direction.

The results for five observers reveal directional shifts that are clearly as predicted Fig. 2A shows the data for VA adaptation: speed ratio 1:0.75 shifts from the VA direction (pre-adaptation) to the IOC direction (post-adaptation). The error bars are the standard error of the mean. As predicted, there was no change in direction for plaids with speed ratio 1:1, and neither for speed ratio 1:0.45 since it is already seen in the IOC direction. Fig. 2B shows the data for IOC adaptation: plaids with speed ratio 1:0.45 shifts from the IOC to the VA direction, while plaids with speed ratio 1:1 and 1:0.75 remain unchanged as expected.

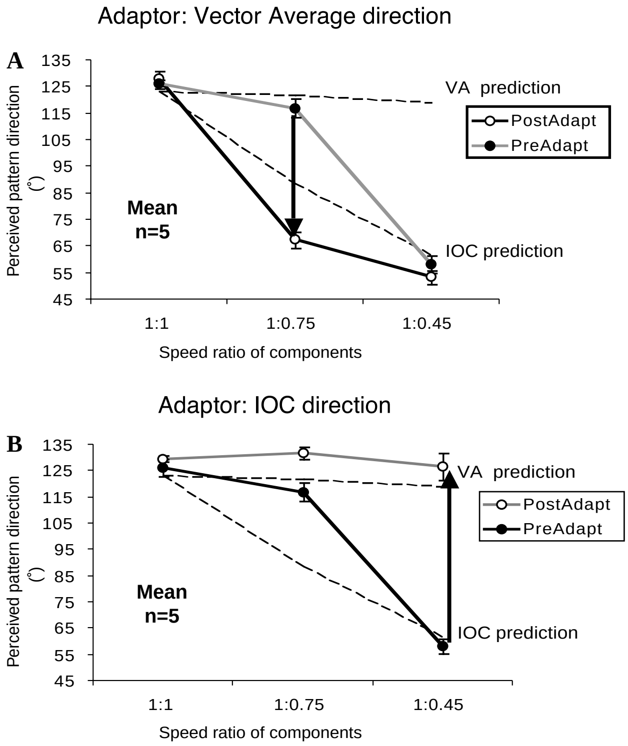

Fig. 2. Average results for five subjects showing large changes in perceived plaid direction following motion adaptation in the VA direction (upper panels) or IOC direction (lower panels). Plaid with speed ratio 1:1 is a type I plaid and so the IOC and VA solutions are the same. Adaptation by either adaptor does not affect the direction of the plaid with speed ratio 1:1. Being type II plaids, the second and third plaids yield different IOC and VA solutions. Prior to adaptation, speed ratio 1:0.75 is perceived in the VA direction, while speed ratio 1:0.45 is seen in the IOC direction. (A) VA adaptation (open circles) caused speed ratio 1:0.75 to change from the VA to the IOC direction. For speed ratio 1:0.45, which was seen to move in the IOC direction prior to adaptation, VA adaptation had little effect. (B) IOC adaptation (open circles) caused speed ratio 1:0.45 to change from the IOC to the VA direction, while speed ratio 1:0.75, seen in the VA direction prior to adaptation, was little affected.

4. Discussion

Inspecting the data for IOC adaptation in Fig. 2B reveals a moderate overshoot relative to the expected VA direction. This is probably due to the well-known motion repulsion effect (Schrater & Simoncelli, 1998). Because both components in a type II pattern lie to one side of the IOC solution, adaptation to a grating moving in the IOC direction would cause both components in a subsequently viewed type II pattern to be repelled away from the adapting direction. This repulsion effect is approximately equivalent to a global rotation of the pattern and would cause direction judgements to overshoot the VA prediction. To ensure that plaid with speed ratio 1:0.45's shift from the IOC to VA direction following IOC adaptation is not due to a large motion repulsion effect, we quantified the magnitude of the effect. A symmetrical (type I) plaid was constructed by taking the component directions of speed ratio 1:0.45 and averaging their speeds. A slight scaling of component speed produced a pattern that moved with the same velocity as the VA prediction for speed ratio 1:0.45. Being a type I pattern, its pre-adaptation direction was accurately perceived. However, following 16 s of grating adaptation in speed ratio 1:0.45's IOC direction, the type I pattern was subsequently repelled away from its pre-adaptation direction by a small amount. For the three observers, this repulsion effect ranged from 7° to 10°, an amount similar to the overshoot visible in Fig. 2B. The modest size of the effect rules out a motion–repulsion account of speed ratio 1:0.45's IOC-to-VA shift following IOC adaptation. Nor could repulsion account for the large directional shift in speed ratio 1:0.75 to the IOC direction following VA adaptation since the adapted direction lies between the two component directions, which would produce approximately equal repulsion effects on each component and therefore little or no directional change in the post-adaptation pattern.

The results shown in Fig. 2 are consistent with our proposal that the visual system is capable of encoding both the IOC and the VA solution for a single moving pattern. Traditionally viewed as competing models, neither the IOC nor VA accounts predict that both solutions should be encoded simultaneously at short durations. While a recently proposed Bayesian model (Weiss, Simoncelli, & Adelson, 2002) does sometimes predict IOC solutions and sometimes VA solutions for type II plaids in the presence of noise, the estimates for the above patterns obtained from this model do not agree with the pre-adaptation directions we observed (Fig. 2). One model that does agree with the pre-adaptation directions is another recently published model (Bowns, 2002), the component level feature model, with the important difference that information corresponding to the IOC and VA directions is available simultaneously. The model uses oriented Gabor filters to extract component information; features are then extracted that correspond to the mean luminance values of the components. If the mean luminance values from two or more components intersect, then the motion of this common spatial position is tracked. There are groups of intersections that are displaced in both the IOC and VA directions.

Another model that predicts multiple solutions to pattern motion proposes that pattern velocity is extracted after the operation of non-linear neural processes that result in additional Fourier information (Derrington, Badcock, & Holroyd, 1992; Lu et al., 1995). For example, if the pattern is rectified (squared), new frequencies would be introduced which could provide motion information about pattern direction. For the type II patterns we have used, squaring introduces two new frequencies, one of which moves in the VA direction (Bowns, in press). If the coexisting solutions implicated in the data above were to result from a non-linear operation such as rectification producing new Fourier components, and these new components represented separate solutions, (NB. to date there has been no combination rule described for these particular models) then the effectiveness of the adapting pattern should exhibit a tuning to spatial and temporal frequency. That is, effective adaptation should only occur when the adaptor spatial and/or temporal frequency matches that of the encoded solution. On the other hand, if the multiple solutions are independent of spatial frequency and temporal frequency, as they are in the component level feature model, then the effectiveness of the adapting pattern would not be expected to show such tunings. To test this hypothesis, we took plaids with speed ratio 1:0.75 and 1:0.45 and repeated the procedure of adapting their perceived direction of motion with a sine-wave grating. We varied the adaptor's spatial frequency (temporal frequency held constant) and temporal frequency (spatial frequency constant) over broad ranges. Results are for are shown in Figs. 3A and B. It is clear that the effectiveness of the adapting pattern did not depend at all on temporal frequency (Fig. 3A), with the data being strikingly flat over a 6-octave range. For speed ratio 1:0.75 ($n = 3$, gray lines), adaptation in the VA direction resulted in a VA-to-IOC shift at all temporal frequencies, and IOC adaptation resulted in speed ratio 1:0.45 ($n = 5$, black lines) being seen to move in the VA direction at all temporal frequencies. The spatial frequency data, too, over the lowest 4-octaves, are flat and suggest that the adaptation effect is not spatially tuned (Fig. 3C). As the motion system prefers lower spatial frequencies, and given that spatial channels are on the order of 1.5-octaves wide (Pantle & Sekuler, 1968; Wilson, McFarlane, & Phillips, 1983), a 4-octave range would have been more than sufficient to reveal a spatially tuned motion mechanism if indeed it existed. Although the effectiveness of the adaptor in altering post-adaptation direction decays between 1.7 and 3.3 cpd and is not effective above this level, this probably does not constitute a spatial tuning per se. Rather, it probably reflects jointly the very slow speed of the patterns at higher spatial frequencies (required to hold temporal frequency constant), and the motion system's preference for lower spatial frequencies, meaning that the motion system was only weakly driven by these high-frequency stimuli. Overall, there is a striking absence of variation across broad ranges of spatial and temporal frequencies, suggesting that the process determining perceived direction when two directional signals coexist is not spatio-temporally tuned.

When the IOC and VA directions differ, as with type II patterns, which of them will determine perceived direction? One solution would be a winner-take-all competition between the candidate directions so that one of the directions determines perception exclusively. Another would be to add both directions according to a combination rule, such as a vector average. To shed light on these possibilities, we examined the adaptation time course of the VA-to-IOC shift (Fig. 2A) obtained with speed ratio 1:0.75, and the IOC-to-VA shift obtained with speed ratio 1:0.45 (Fig. 2B). Exposure durations ranged from 8 s down to 0.125 s, with results plotted for three subjects in Fig. 3C.

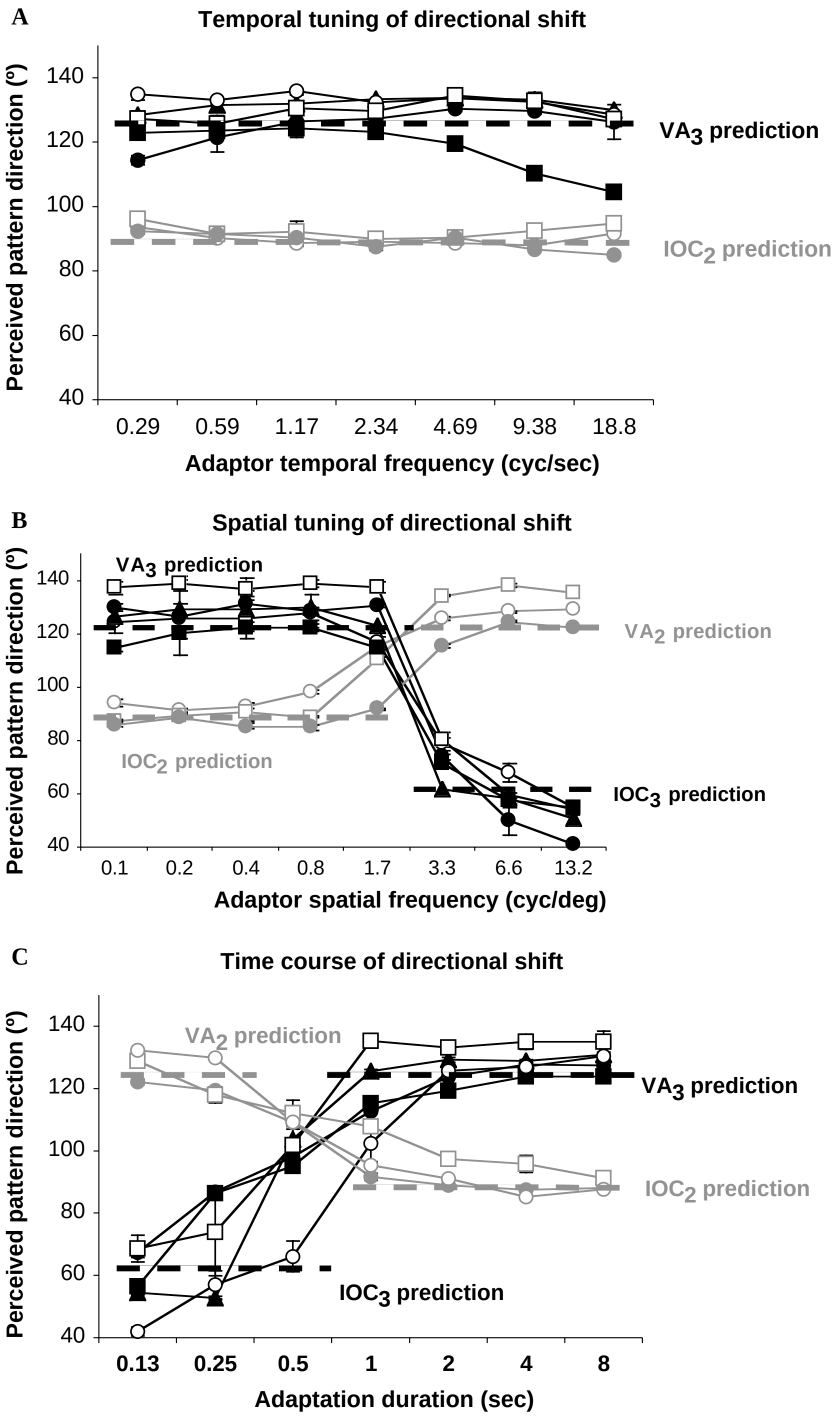

Fig. 3. Results for individual subjects showing the time course, and the spatial and temporal tunings for the large adaptation-induced directional shifts plotted in Fig. 2. (A) The effect of temporal frequency (with spatial frequency fixed) of the adaptor on the IOC-to-VA shift in speed ratio 1:0.45 ($n = 5$, black lines) and on the VA-to-IOC shift in speed ratio 1:0.75 ($n = 3$, grey lines). The functions are remarkably flat for both stimuli, showing that the directional shifts are independent of temporal frequency over a 6-octave range. (B) The effect of spatial frequency of the adaptor (with temporal frequency fixed) on the IOC-to-VA shift ($n = 5$, black lines) and on the VA-to-IOC shift ($n = 3$, grey lines). Although the functions are not flat over the full 7-ocatve range, they are flat over the lowest 4-octaves, a range large enough to suggest the adapted mechanism is not spatial frequency tuned. (C) Perceived plaid direction as a function of duration of adaptation in the IOC direction ($n = 3$, black lines) or the VA direction ($n = 3$, grey lines). In most cases, as little as 1 s of adaptation is sufficient to produce the IOC-to-VA or VA-to-IOC directional shifts. Shorter adaptations resulted in partial shifts.

Adaptation of just 1 s was generally sufficient for subjects to exhibit a complete VA-to-IOC or IOC-to-VA shift. As adaptation duration decreased below 1 s the extent of the switch reduced and intermediate directions were observed. The shortest adaptation period (0.125 s) produced little or no directional change. The adaptation time course is similar for both the IOC and VA processors. These data suggest that IOC and VA directions combine to determine perceived plaid direction and that increasingly attenuating one direction through adaptation will gradually alter the perceived pattern direction in favour of the unadapted direction. Thus, although there is an apparently catastrophic switch in direction in our first experiment (Fig. 2), this experiment suggests that the underlying mechanism is not itself catastrophic.

We also conducted a control experiment to verify that the large directional changes shown in Fig. 2 are really due to adaptation of a pattern direction and not to adaptation of component directions. For example, although adaptation in the VA direction appears to make speed ratio 1:0.75 change to the IOC direction (Fig. 2A), it might possibly still be a VA solution, but one based on components whose speed and/or direction have been altered by the adapting grating. Analogously, the apparent IOC-to-VA shift in speed ratio 1:0.45 following IOC adaptation (Fig. 2B) may actually be the IOC solution calculated from adapted components. To check this possibility, we began by measuring the perceived speed and direction of the components of speed ratio 1:0.75 and speed ratio 1:0.45, as shown in Figs. 4A and B. These measures were then repeated following adaptation in the VA direction (for speed ratio 1:0.75) or in the IOC direction (for speed ratio 1:0.45).

5. Method

Measurements of speed and direction of the plaid components were made for speed ratio 1:0.75 and speed ratio 1:0.45 before and after exposure to adaptation in the pattern direction. Direction measurements were made relative to a landmark (a small spot, 1° in diameter) lying 10° from the centre of the display and along the same line as the component being measured (i.e., either 112° or 135°). Subjects judged whether brief presentations (160 ms) of the component appeared to move along a trajectory clockwise or anticlockwise of the reference point. An adaptive staircase procedure (Quest: Watson & Pelli, 1983) was used to home in on the point of subjective alignment. The data from three Quest procedures were combined and a psychometric function fitted to the pooled data set to find the perceived direction of each component. For speed, a two-alternative forced-choice procedure was used. First, a grating was briefly played in the central viewing aperture, followed by a comparison grating played in two oval regions which flanked the central region and whose areas summed to that of the central aperture. Two flanking regions made the task easier for observers. Observers judged whether the central grating appeared to move slower or faster than the flanking grating, with the speed of the comparison grating determined by Quest. The standard stimulus was the same as in the original experiment, and the comparison stimuli were similar with the exception of the area as described above. Three data sets were pooled and fitted with a psychometric function to find the point of subjective equality of speed.

6. Results

Post-adaptation measures of direction and speed differed from pre-adaptation baselines by moderate but significant amounts, error bars in Fig. 4 indicate the standard error of the mean. Using these post-adaptation measures, new VA and IOC directions were calculated for speed ratio 1:0.75 and speed ratio 1:0.45, respectively. These are shown by the square symbols in Fig. 4C, together with the mean VA-to-IOC shift for speed ratio 1:0.75 and the mean IOC-to-VA shift for speed ratio 1:0.45 (from Fig. 2). For speed ratio 1:0.75, the VA direction based on adapted components produces a small directional shift but it is in the direction opposite our original result and so cannot account for it. For speed ratio 1:0.45, while the IOC solution from adapted components is in the same direction as our original finding, it is far too small to account for more than a fraction of the result. From these data, we conclude that the large VA-to-IOC and IOC-to-VA shifts shown in Fig. 2 really are due to adaptation of one of two possible global motion solutions.

Finally, we investigated the effect of test duration on direction judgements. It was noted above that type II plaids tend to be perceived in the VA direction during the very early phase of stimulus presentation (up to about 200 ms), before switching to the IOC direction (Yo & Wilson, 1992). Recent neurophysiological data from Pack and Born (2001) bear interestingly on this point. They found that single units in the middle temporal area of visual cortex exhibited changes in preferred direction over time that showed a similar time course to that of plaids. When first responding to the stimulus (a drifting bar), the directional preference was always orthogonal to the bar's orientation. However, by about 150 ms after stimulus onset, MT cells had progressively changed their directional preference to encode the true direction of movement (either ±45° from orthogonal). Because area MT is thought to be the site of global motion computation for plaid stimuli (Movshon et al., 1985; Rodman & Albright, 1989), the shared time courses of perceived plaid direction and of directional tunings of MT cells might indicate that a VA-to-IOC shift in type II plaids is an inevitable consequence of directional preferences for MT cells changing over the first 150 ms or so. While this suggestion is tantalising, our data (where stimulus duration was 160 ms) only partially support it in that while speed ratio 1:0.75 was perceived to move in the VA direction speed ratio 1:0.45 was reliably perceived in the IOC direction (Fig. 2). To explore how plaid directions are affected by test duration we repeated our first experiment using the same plaid stimuli but with longer (1 s) test durations. The results (Fig. 4D) show that speed ratio 1:0.75, prior to adaptation, is indeed perceived to move in the IOC direction now that the exposure duration is longer (cf. Fig. 2). Interestingly, however, if the IOC direction is then adapted by a period of exposure to a grating drifting in that direction, the perceived direction of both plaids with speed ratio 1:0.75 and 1:0.45 is shifted back to the VA direction, even at this longer test duration. Thus, type II plaids can be perceived to move steadily in the VA direction if the IOC

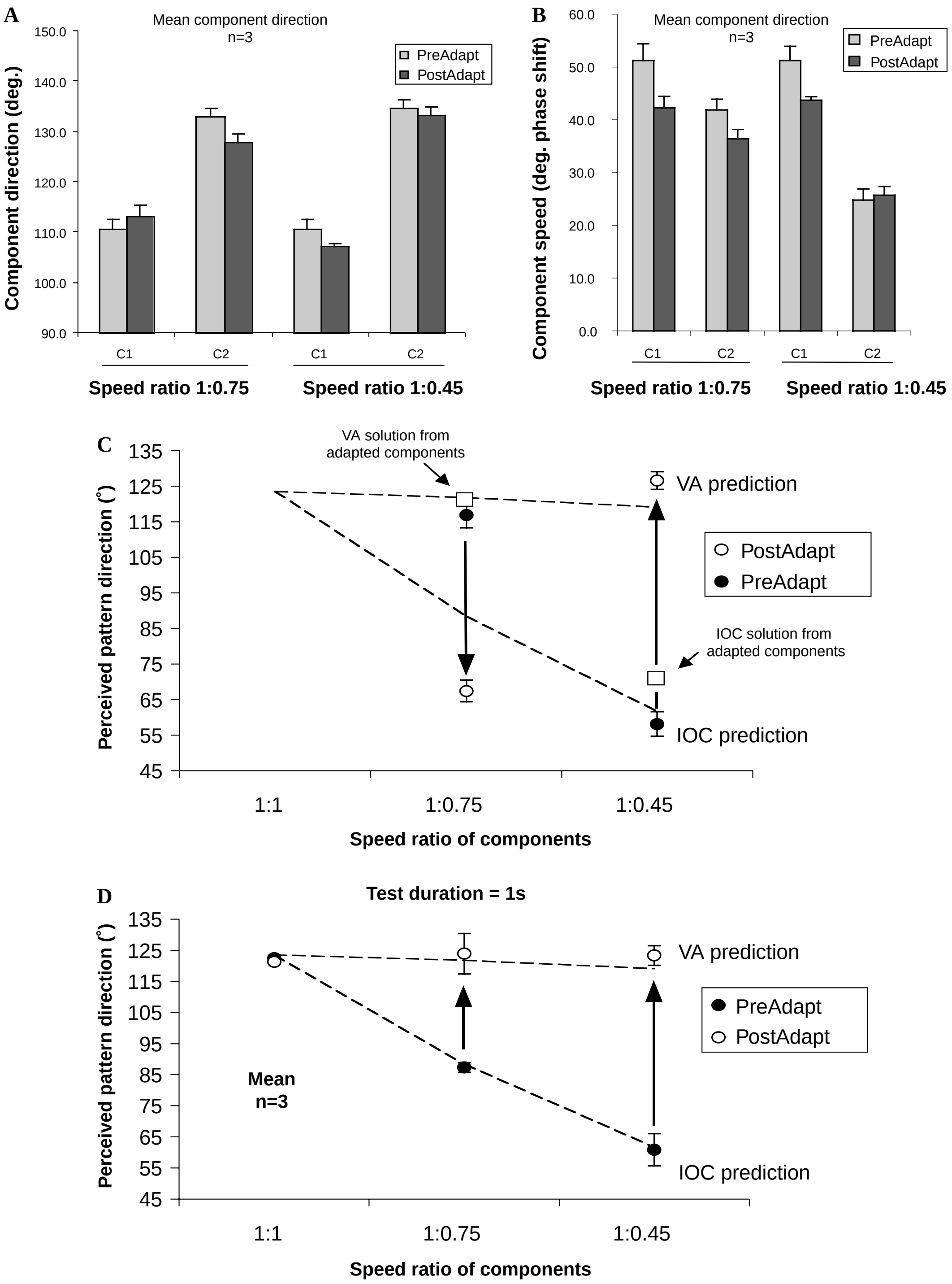

Fig. 4. (A and B) Data from three observers showing how adaptation in the plaid's pattern direction affects the perceived speed and direction of the plaid's components. For speed ratio 1:0.75, adaptation was in the VA direction (which produced the VA-to-IOC shift in Fig. 2), and for speed ratio 1:0.45, adaptation was in the IOC direction (which produced the IOC-to-VA shift in Fig. 2). Prior to adaptation, perceived component direction is veridical for both plaids and adaptation resulted in moderate shifts in perceived direction. Adaptation also produced moderate changes in perceived component speed. (C) The circles replot the mean directional shifts from one global motion solution to the other shown in Fig. 2. The squares show the directions predicted from adapted components (from A and B) without assuming a switch in global motion solution. For speed ratio 1:0.75, this produces a negligible shift in the wrong direction, and for speed ratio 1:0.45 a modest directional shift that is just a small fraction of the effect we observed. This indicates that the large directional shifts we report for plaids two and three did in fact result from a switch between competing global motion solutions. (D) Results for three subjects showing directional shifts measured with 1 s test periods. Prior to adaptation, both type II plaids were perceived to move in the IOC direction. After 10 s of IOC adaptation, post-adaptation directions for both plaids exhibited a IOC-to-VA shift (arrows). These data show that the VA direction can be a steady-state percept in a type II plaid and that adaptation-induced directional shifts are not limited to a transient initial period of up to 200 ms in which the VA direction is typically perceived.

solution is adapted, indicating that the VA direction observed in short duration type II plaids is not necessarily a transient phase, such as a default direction seen while the IOC solution is being calculated. Rather, it appears to be a viable steady-state solution that competes with the IOC solution and which can dominate perceptually provided the IOC solution is attenuated by adaptation.

Taken together, our findings provide strong evidence that both the IOC and VA solutions to pattern motion can be neurally encoded by the human visual system. In patterns where the IOC and VA solutions differ, adapting the perceived direction, whether it be IOC or VA, is sufficient to reveal the other direction. This directional shift is not due to adaptation-related changes in the speed or direction of the pattern components, nor to motion repulsion. Neither does it exhibit spatial or temporal tuning, implying that the process of selecting one of the directions to determine perceived pattern motion is not the result of early spatio-temporal filtering. These findings suggest that IOC- and VA-based solutions, often opposed in the literature as competing models, can be incorporated into a single framework. What appears to be being adapted in our study is a "late" velocity encoding system. A number of facts suggest this, (1) that adaptation is unaffected by the spatio-temporal properties of the adaptor, (2) information from apparently different source categories affect one another. For example, even if we accept that the source of the VA direction is second-order spatio-temporal information, it is still affected by the IOC direction for which there is no second-order information (see Bowns, in press for a complete description of the first and second-order information in these stimuli.). The IOC and VA directions have a similar source available in the component level feature model Bowns, 2002 but it too is a late velocity encoding system. We believe that further research directed to understanding why certain stimulus configurations appear to favour one solution over the other will provide insight into the mechanism underlying this late velocity encoding system.

Acknowledgments

L.B. was supported by a grant from the EPSRC. We thank Craig Stockdale for assistance.

References

Adelson, E. H., & Movshon, J. A. (1982). Phenomenal coherence of moving visual patterns. *Nature, 300*, 523–525.

Alais, D., Wenderoth, P., & Burke, D. (1994). The contribution of one-dimensional motion mechanisms to the perceived direction of drifting plaids and their after effects. *Vision Research, 34*, 1823–1834.

Bowns, L. (1996). Evidence for a feature tracking explanation of why type II plaids move in the vector sum direction at short durations. *Vision Research, 36*, 3685–3694.

Bowns, L. (2002). Can spatio-temporal energy models of motion predict feature motion? *Vision Research, 42*, 1671–1681.

Bowns, L. (in press). "Squaring" is better at predicting plaid motion than the vector average or IOC. *Perception.*

Derrington, A. M., Badcock, D. R., & Holroyd, S. A. (1992). Analysis of the motion of two-dimensional patterns: Evidence for a second-order process. *Vision Research, 32*, 699–707.

Huk, A. C., & Heeger, D. (2002). Pattern-motion responses in human visual cortex. *Nature Neuroscience, 5*, 72–75.

Lu, Z.-L., & Sperling, G. (1995). The functional architecture of human visual motion perception. *Vision Research, 35*, 2697–2722.

Movshon, J. A., Adelson, E. H., Gizzi, M. S., & Newsome, W. H. (1985). In C. Chagas, R. Gatass, & C. Gross (Eds.), *Pattern recognition mechanisms* (pp. 117–151). New York: Springer.

Pack, C. A., & Born, T. (2001). Temporal dynamics of a neural solution to the aperture problem in visual area MT of macaque brain. *Nature, 409*, 1040–1042.

Pantle, A., & Sekuler, R. W. (1968). Size-detecting mechanisms in human vision. *Science, 162*, 1146–1148.

Rodman, H. R., & Albright, T. D. (1989). Single-unit analysis of pattern-motion selective properties in the middle temporal visual area (MT). *Experimental Brain Research, 75*, 53–64.

Schrater, P. R., & Simoncelli, E. P. (1998). Local velocity representation: Evidence from motion adaptation. *Vision Research, 38*, 3899–3912.

Stone, L. S., Watson, A. B., & Mulligan, J. B. (1990). Effect of contrast on the perceived direction of a moving plaid. *Vision Research, 30*, 1049–1067.

Stoner, G. R., & Albright, T. D. (1992). Neural correlates of perceptual motion coherence. *Nature, 358*, 412–414.

Watson, A. B., & Pelli, D. G. (1983). QUEST: A Bayesian adaptive psychometric method. *Perception and Psychophysics, 33*, 113–120.

Weiss, Y., Simoncelli, E., & Adelson, E. H. (2002). Motion illusions as optimal percepts. *Nature Neuroscience, 5*, 598–604.

Wilson, H. R., Ferrera, V. P., & Yo, C. (1992). A psychophysically motivated model for two-dimensional motion perception. *Visual Neuroscience, 9*, 79–97.

Wilson, H. R., McFarlane, D. K., & Phillips, G. C. (1983). Spatial frequency tuning of orientation selective units estimated by oblique masking. *Visual Research, 23*, 873–882.

Yo, C., & Wilson, H. R. (1992). Perceived direction of moving two-dimensional patterns depends on duration, contrast and eccentricity. *Vision Research, 32*, 135–147.