The visual processing of motion-defined transparency

William Curran[1,*], Paul B. Hibbard[2] and Alan Johnston[3]

[1]*School of Psychology, Queen's University Belfast, Belfast, Northern Ireland BT7 1NN, UK*
[2]*School of Psychology, University of St Andrews, South Street, St Andrews, Fife KY16 9JP, UK*
[3]*Department of Psychology & CoMPLEX, University College London, Gower Street, London WC1E 6BT, UK*

Our understanding of how the visual system processes motion transparency, the phenomenon by which multiple directions of motion are perceived to coexist in the same spatial region, has grown considerably in the past decade. There is compelling evidence that the process is driven by global-motion mechanisms. Consequently, although transparently moving surfaces are readily segmented over an extended space, the visual system cannot separate two motion signals that coexist in the same local region. A related issue is whether the visual system can detect transparently moving surfaces simultaneously or whether the component signals encounter a serial 'bottleneck' during their processing. Our initial results show that, at sufficiently short stimulus durations, observers cannot accurately detect two superimposed directions; yet they have no difficulty in detecting one pattern direction in noise, supporting the serial-bottleneck scenario. However, in a second experiment, the difference in performance between the two tasks disappears when the component patterns are segregated. This discrepancy between the processing of transparent and non-overlapping patterns may be a consequence of suppressed activity of global-motion mechanisms when the transparent surfaces are presented in the same depth plane. To test this explanation, we repeated our initial experiment while separating the motion components in depth. The marked improvement in performance leads us to conclude that transparent motion signals are represented simultaneously.

Keywords: motion perception; transparency; global motion; motion integration

1. INTRODUCTION

Visual motion detection is a hierarchical process in which the initial extraction of local motion measures is followed by a 'pooling' of these measures at a later global-processing stage (Adelson & Movshon 1982; Albright 1984; Welch 1989; Johnston *et al.* 1992; Smith *et al.* 1994). These two stages of processing have been identified as occurring in area V1 and the human homologue of macaque MT/V5, respectively (Newsome & Paré 1988; Baker *et al.* 1991; Castelo-Branco *et al.* 2002; Huk & Heeger 2002).

A full understanding of the hierarchical organization of motion processing requires an understanding of the levels of processing at which perceptual phenomena occur in addition to the identification of cortical mechanisms. For example, recent evidence suggests that direction repulsion, in which the difference between two superimposed motion directions is over-estimated, is likely to operate at the global-motion level (Benton & Curran 2003). Motion transparency, in which two moving patterns are seen to exist in the same spatial location, is another phenomenon that has invited the local versus global question.

It has been reported that V1 neurons respond equally vigorously to transparent stimuli, regardless of whether the dots in the 'transparent' stimuli are locally paired and moving in opposite directions or unpaired; yet MT neurons respond differentially to these two stimulus types (Qian & Andersen 1995; Braddick & Qian 2001). In the unpaired stimulus type, the random positioning of

limited-lifetime dots gives the appearance of two transparently moving surfaces. In the locally paired case, pairs of dots moving in two different directions that are constrained such that their paths intersect halfway through the dots' lifetime do not give rise to phenomenal transparency (Qian & Andersen 1994). Similarly, Qian & Andersen (1995) found that the activity of directionally selective cells in V1 does not reliably distinguish between transparent random dot patterns and non-transparent counterphase gratings. Taken together, these results indicate that V1 activity does not correlate well with our perceptual experience of transparent and non-transparent (paired) motion; instead, the neural correlate of phenomenal transparency begins to emerge in area V5/MT, suggesting that transparency is a global-motion operation. Interestingly, single-cell recordings of MT neural responses to transparent motion reveal that our ability to perceive motion transparency is not dependent on multiple peaks in MT neuron activity profiles; rather the overall shape of the MT population response appears to be the primary factor in determining the number of transparent motion signals perceived (Treue *et al.* 2000). The importance of higher cortical areas in motion transparency perception is supported by other psychophysical and imaging studies (McOwan & Johnston 1996; Castelo-Branco *et al.* 2002; Edwards & Greenwood 2005).

Our ability to perceive transparently moving components suggests that the visual system can register multiple vectors simultaneously in the same spatial neighbourhood. 'Performance-based' measures of transparency, in which observers have to make directional

* Author for correspondence (w.curran@qub.ac.uk).

judgments based on both components, have been applied to demonstrate that transparency involves the equivalent representation of two vectors in the same region (Braddick *et al.* 2002). However, as demonstrated by the absence of transparency in locally balanced stimuli (Qian *et al.* 1994), this co-representation of different components does not occur at a single point but, rather, occurs at a relatively coarse spatial scale. The related issue of whether transparently moving surfaces can be perceived as existing in the same depth plane has also been a focus of debate (Snowden & Verstraten 1999, 2000; Grunewald 2000; Vidnyánszky *et al.* 2002).

Our apparent inability to represent more than one motion at the same region in space raises the question of whether the visual system can detect multiple moving components *at the same point in time*. While most studies of motion transparency appear to accept this implicit assumption, few have actually tested it. There is evidence that performance deteriorates when one moves from a task requiring judgments of unidirectional stimuli to one requiring judgments of both directions in a transparent stimulus (Mather & Moulden 1983; Braddick *et al.* 2002) or of a unidirectional signal in noise (Snowden 1989). While these results do not address directly the question of whether multiple motion directions are represented simultaneously, they do hint that this may not be the case.

While there have been attempts to quantify the maximum number of transparent moving planes that can be processed by the visual system (Andersen 1989; Mulligan 1992; Edwards & Greenwood 2005), to our knowledge the issue of simultaneous processing of multiple motion has been addressed systematically in only one previous study. De Bruyn & Orban (1993) found that, when stimulus duration was sufficiently short, observers were unable to detect accurately the global directions of two superimposed optic flow patterns. Yet when instructed to attend to either one of them, ability to detect the global direction of the attended pattern was near perfect. De Bruyn & Orban argue that their results are evidence of parallel processing giving way to serial processing at some point in the motion pathway. Given the evidence for independent mechanisms specialized for processing different optic flow components (Tanaka & Saiko 1989; Duffy & Wurtz 1991; Graziano *et al.* 1994; Duffy 1998), De Bruyn & Orban propose that the 'serial bottleneck' may occur at the point of addressing these mechanisms (i.e. making them available to conscious perception).

De Bruyn & Orban's model places greater weight on the addressing of coexisting representations rather than the nature of the representations themselves. However, a number of studies have demonstrated that motion transparency may be influenced by manipulating spatial separation (De Bruyn 1998; De Bruyn & Orban 1999; Verstraten *et al.* 1994), suggesting that the model may not generalize to well-separated surfaces. Experiment 1 replicated De Bruyn & Orban's findings using translating surfaces moving transparently across each other. However, two subsequent experiments reveal that differences in performance between the dual- and single-pattern tasks either disappear or are greatly reduced when the two moving patterns are spatially segregated. While the observed difference between the segregated and non-segregated experiments might be explained in terms of different mechanisms, we will argue that a more parsimonious explanation for one's poorer ability to detect non-segregated transparent motion emanates from suppression of global-motion detectors.

2. EXPERIMENT 1: CAN TWO SUPERIMPOSED TRANSLATING PATTERNS BE DETECTED SIMULTANEOUSLY?

We investigated whether observers' performance in a transparency task, which required knowledge of both component directions, matches their performance in a single-motion task. Performance is measured by identifying the shortest stimulus duration at which both tasks can be performed reliably. If performance in both tasks breaks down at the same stimulus duration, this would strongly indicate that the two translating components are processed in parallel up to and including the level of conscious perception. If, however, performance in the two-component task breaks down at a longer duration than the single-motion task, this would suggest that transparently moving patterns are processed serially at some point.

(a) *Methods*
(i) *Observers*
Three observers, one of the authors and two naive, took part in the experiment. Two observers had corrected-to-normal acuity, and one had uncorrected normal acuity.

(ii) *Stimuli*
The stimuli were random dot kinematograms (RDKs) generated by an Apple Macintosh iMac. Each stimulus consisted of a circular patch (diameter 7.8°) with a central fixation spot viewed from 118 cm distance. There were 204 dots (each of diameter 0.1°) randomly positioned within the circular patch on the first frame of each stimulus; all dots moved at a speed of $1.4° \text{ s}^{-1}$. Dot and background luminances were 4 and 40 cd m^{-2}, respectively.

(iii) *Procedure*
Observers were tested in two conditions—an 'orthogonal-angle' condition in which they had to judge the relative directions of two transparently moving dot patterns and a 'clockwise/anticlockwise' condition in which they had to make direction judgments about one dot pattern superimposed on dynamic noise (figure 1).

In the orthogonal-angle condition, half the dots moved in one direction and the other half moved in a different direction. The direction difference between the two patterns was randomly chosen on each trial from a set of seven direction differences ranging from 66 to 114° in 8° steps. The directions were approximately aligned with two of the four cardinal directions, resulting in four possible paired alignments: upwards/rightwards; rightwards/downwards; downwards/leftwards; and leftwards/upwards. The orthogonal-angle task (Braddick *et al.* 2002) required observers to judge whether the two directions differed by more or less than 90°. To ensure that judgments were derived from the global motion of each pattern, rather than from tracking one dot, each dot took an independent random walk (Williams & Sekuler 1984). Thus, on each frame, dot directions were drawn from a direction distribution width of 32° centred on the mean global
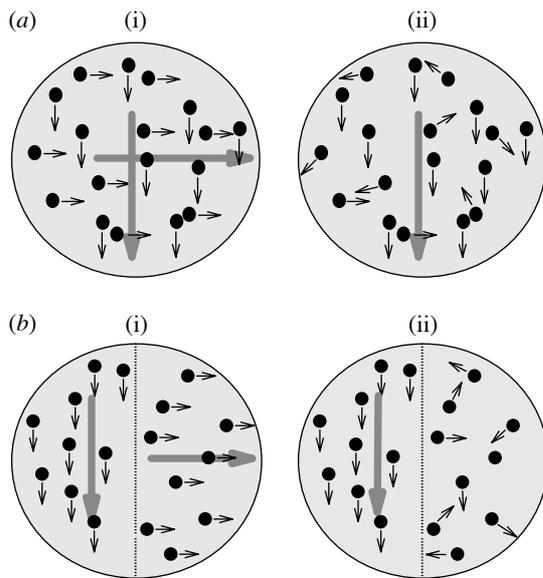
Figure 1. (*a*) Stimulus types used in (i) the orthogonal-angle condition and (ii) the clockwise/anticlockwise condition of experiment 1. In the orthogonal-angle condition, each stimulus comprised two sets of dots moving transparently across each other, and whose direction difference was taken from the range 66–114°. The two directions were approximately aligned with randomly chosen pairs of cardinal axes. Observers judged whether the direction difference was greater or less than 90°. In the clockwise/anticlockwise stimuli, half the dots moved coherently in a direction close to a randomly chosen cardinal axis and the remaining dots took random walks. The task was to judge whether the coherent dots were moving clockwise or anticlockwise relative to the nearest cardinal axis. (*b*) Stimulus configurations used in experiment 2, in which the component patterns were segregated (see text for details). Note that the dotted lines were not present in the experimental stimuli.

directions. Each stimulus presentation was followed by a 500 ms mask, in which all dots took a random walk drawn from the full 360° range. Observers were tested 50 times with each direction difference.

In the clockwise/anticlockwise task, half the dots moved in the same global direction (with a direction distribution width of 32°) and the remaining dots took 'random walks', with each dot's direction being randomly drawn from the full 360° on each frame. The mean direction of the signal dots was approximately aligned with one of the four cardinal directions and was randomly chosen on each trial from a set of seven directions ranging from 24° anticlockwise to 24° clockwise of the cardinal direction. Each stimulus was followed by a 500 ms mask. Observers judged whether the target pattern was moving clockwise or anticlockwise relative to the nearest cardinal direction. Observers were tested 50 times with each direction.

In both tasks, stimulus duration was systematically decreased until observers could no longer make reliable judgments.

We believe the two tasks to be equivalent insofar as each requires observers to make relative judgment decisions. In the case of the orthogonal-angle task, observers judge the direction of one motion stream relative to a second motion stream. In the clockwise/anticlockwise task, the judgment is of a motion stream relative to the nearest cardinal axis.

(*b*) *Results*

Figure 2 plots the results for three observers. Graphs in figure 2*a,c,e* plot performance in the orthogonal-angle task, showing that the percentage of times the direction difference between the two sets of dots was judged to be greater than 90° as a function of direction difference. Graphs in figure 2*b,d,f* plot the results of the single-motion detection task, showing percentage of clockwise judgments as a function of motion direction relative to the nearest cardinal axis. Psychometric functions were fitted to the data using a bootstrap technique (Foster & Bischof 1991). The psychometric functions plot performance across a range of stimulus durations (i.e. the time course of each stimulus prior to the noise mask appearing). We adopted the criterion that observers' responses were unreliable if the fitted psychometric function traversed less than 50% of the response scale. Take the orthogonal-angle task as an example. If the response 'greater than 90°' makes up 20% of responses for the narrowest direction difference (66°) and totals 60% of responses for the greatest direction difference (114°), then performance is deemed to have broken down because the fitted psychometric function will cross only 40% of the response scale. The duration at which observers' performance breaks down in each task is identified by the dashed line. It is apparent that all observers require longer stimulus duration to perform the orthogonal-angle task. In the case of W.C. performance breaks down at 40 ms, whereas performance in the clockwise/anticlockwise task remains reliable. The remaining two observers show a similar trend, but a more marked difference, across the two tasks. The difference in performance across the two conditions is seen in figure 3*a,c,e* which plot the standard deviations (corresponding to the 84% point on the psychometric function) from both tasks. It should be noted that poorer performance in detecting global-motion direction occurs only for relatively short stimulus durations; as stimulus duration increases, performances in both tasks converge. This is in agreement with earlier research showing that performance in a global-motion coherence task is equivalent when detecting a coherently moving pattern embedded in dynamic noise or in a second pattern moving in a direction at least 90° from the target pattern (Edwards & Nishida 1999).

On the face of it, De Bruyn & Orban's (1993) earlier work, which reported that superimposed radial and rotational moving patterns are not addressed in parallel, appears to generalize to translating patterns moving transparently across one another. We will return to this issue in experiment 3, when we consider other factors that may have contributed to the more rapid breakdown of performance in the orthogonal-angle task. The following experiment asks whether the results of experiment 1 generalize to non-overlapping, spatially segregated patterns.

3. EXPERIMENT 2: OBSERVER PERFORMANCE USING NON-OVERLAPPING DIRECTIONS

The two conditions of experiment 1 were repeated; but this time, the component patterns were spatially separated, with each pattern occupying one-half of the stimulus aperture. The form of segregation, horizontal or vertical, was randomly chosen on each trial (figure 1). It might be argued that the presence of an illusory contour in the
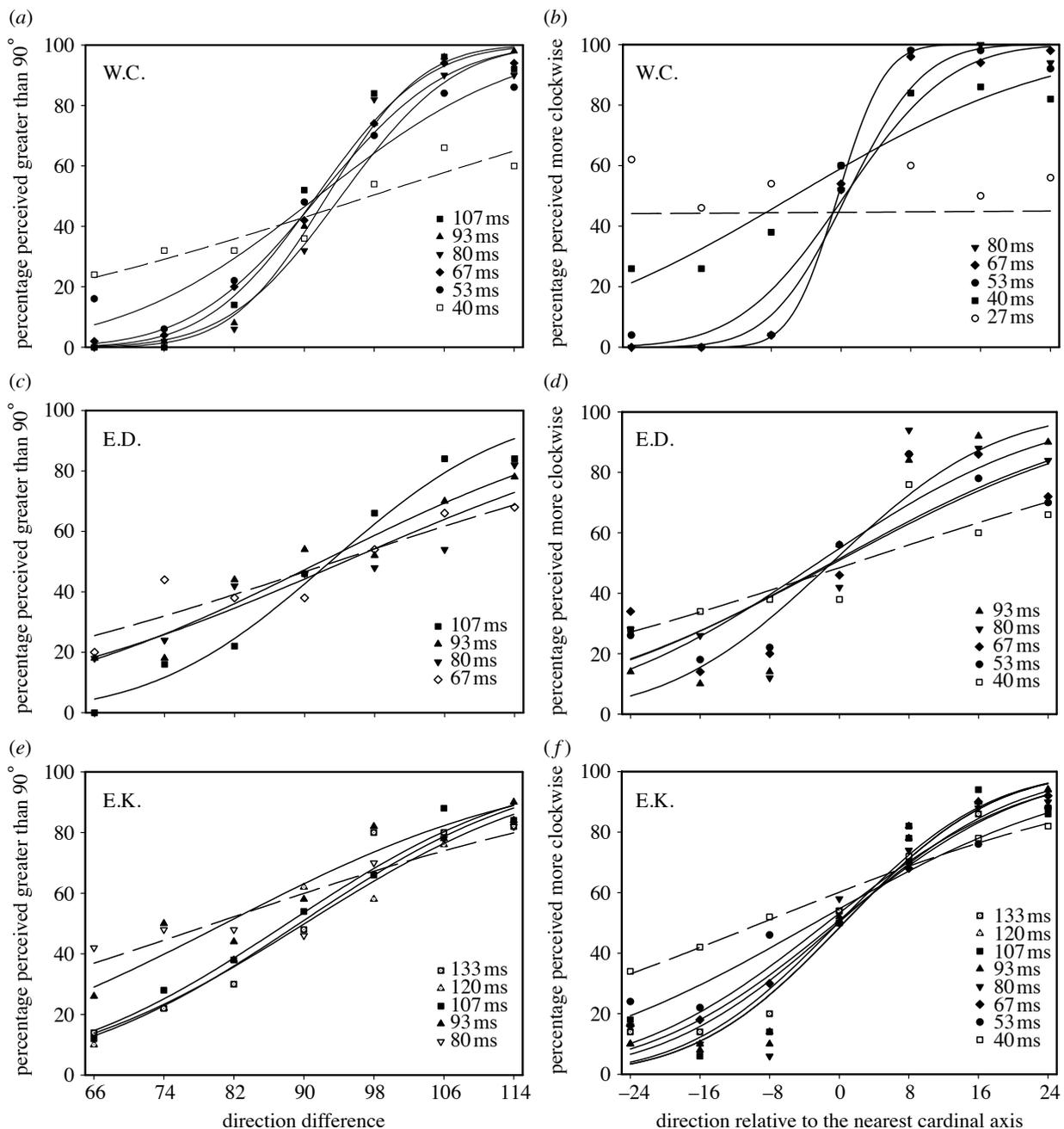
Figure 2. Results from experiment 1, showing observers' performance in (*a,c,e*) the orthogonal-angle task as a function of direction difference and (*b,d,f*) the clockwise/anticlockwise task as function of direction. Each psychometric function is derived from 350 responses. Dashed psychometric functions indicate the point at which performance breaks down.

orthogonal-angle condition (caused by dots appearing and disappearing across the midline) would result in an improved performance. While this may be true for prolonged duration stimuli, an illusory contour was not apparent in the short-duration stimuli used in this experiment. This can be attributed to a number of factors, including the relatively slow speed of the dots (1.4 deg s⁻¹), the low dot density used (5 dots deg⁻²) and the small number of frames.

(a) Results

Figure 3*b,d,f* plots the results for three observers. These data show two things. Firstly, performance has improved in both tasks. Secondly, the difference in performance observed between the two tasks in experiment 1 largely disappears when non-overlapping motion sets are substituted.

The data from experiment 2 suggest that non-overlapping components are processed in parallel. Performance in experiment 1 however may reflect visual attention switching between superimposed surfaces; alternatively, the reduction in performance may be due to a degraded transparency. We consider a number of factors that may contribute to degraded transparency.

The stimuli used in the transparent task of experiment 1 would have contained random occurrences of locally paired dots, which result in reduced firing of MT neurons (Qian & Andersen 1994). However, this is unlikely to explain the poorer performance in the orthogonal-angle task, simply because one would expect performance in the single-pattern task to be similarly affected. A more plausible explanation for the poorer performance in the orthogonal-angle task of experiment 1 is the reduced
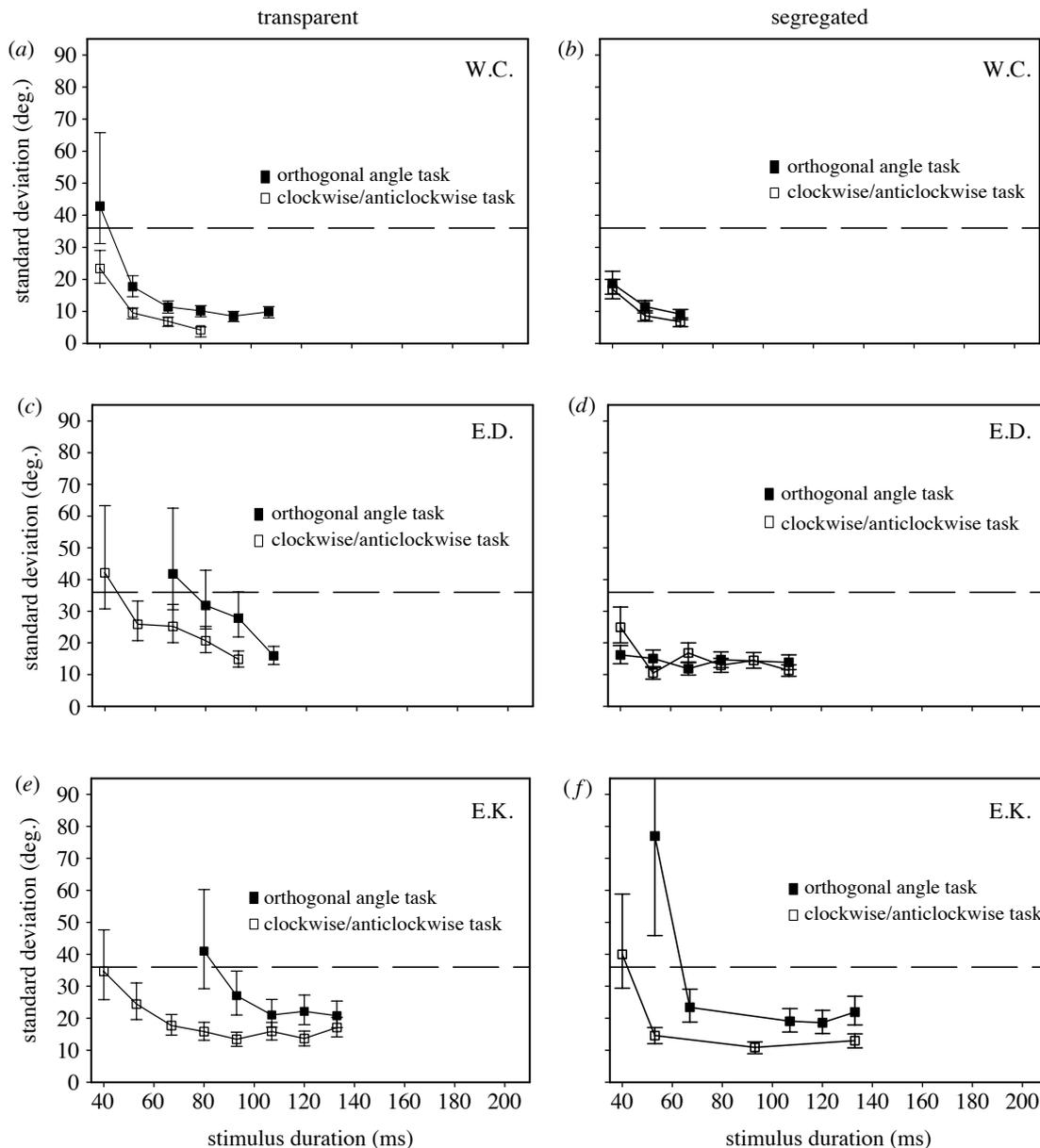
Figure 3. Differences in performance between the orthogonal-angle and clockwise/anticlockwise tasks (*a,c,e*) become indistinguishable for two of the three observers (*b,d*), and considerably reduced for the third (*f*), following the segregation of the two component patterns in experiment 2. The dashed horizontal line identifies where performance breaks down.

response of MT cells to their preferred direction when it is presented as one of the two transparent patterns (Snowden & Verstraten 1999). Bradley *et al.* (1995) report that this suppression of MT cells is reduced when the patterns have different binocular disparities. In a similar vein, Hibbard & Bradshaw (1999) found that, when positioned in the same depth plane, the motion coherence thresholds for detecting transparent patterns are higher than coherence thresholds for a single pattern. However, they found that this threshold difference disappears when the transparent patterns are assigned different disparities.

Thus, it is feasible that the poorer performance in the orthogonal-angle task of experiment 1 is a consequence of inhibitory interactions between direction-sensitive MT neurons tuned to the same disparity. If this is the case, one would expect performance to improve in the orthogonal-angle task when the two patterns are assigned different disparities.

4. EXPERIMENT 3: TRANSPARENT PATTERNS SEPARATED IN DEPTH

(a) *Methods*

(i) *Observers*

Three observers, one of the authors and two naive, took part in the experiment.

(ii) *Stimuli*

The stimuli were generated by a PC computer and displayed on a 19″ monitor. Stimuli were presented using a modified Wheatstone stereoscope so that the binocular disparity of each dot could be controlled. The viewing distance was 83.7 cm, and the stereoscope mirrors were carefully aligned so that vergence was appropriate for this distance. Each stimulus consisted of a circular patch, with a central fixation cross and nonius lines. The diameter of the patch was 7.8°. The 260 dots (each a square of width 4.2 arc min) were randomly positioned within the circular patch on the first frame of each
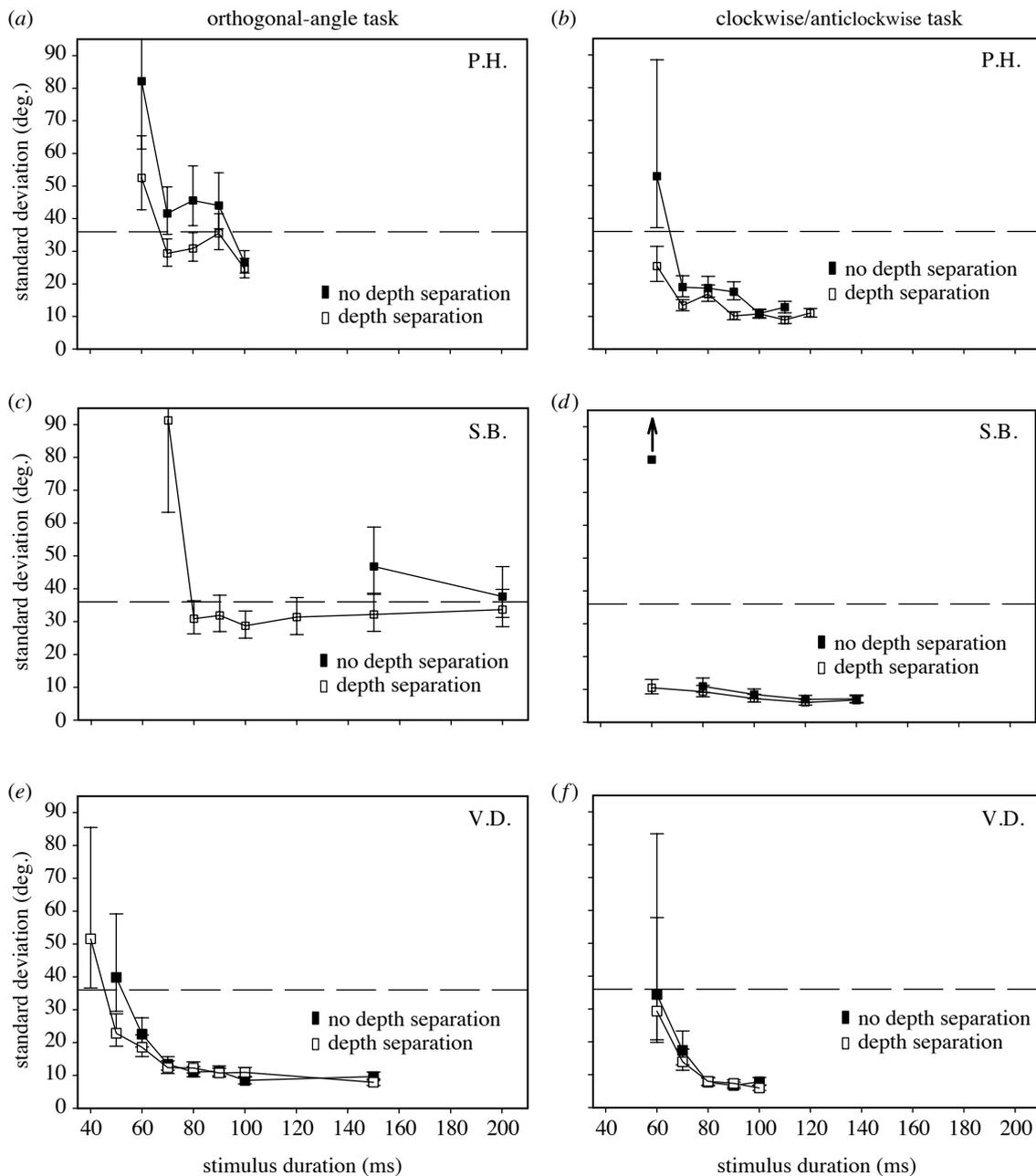
Figure 4. Performance in (a,c,e) the orthogonal-angle task and (b,d,f) the clockwise/anticlockwise tasks when the two patterns are presented with the same binocular disparity or are separated in depth. The data show a marked improvement in the orthogonal-angle task, but only a slight improvement in the clockwise/anticlockwise task, following depth separation. Arrow in (d) indicates that the associated datum point is outside the range of the graph.

stimulus, giving a dot density of 5.4 dots deg^{-2}. Each dot moved at a speed of $1.4°\,s^{-1}$. Dot and background luminances were 103.7 and 0.3 cd m^{-2}, respectively.

(iii) *Procedure*

Observers were again tested with the orthogonal-angle and clockwise/anticlockwise tasks. The one difference was that, in each case, the two motion sets were presented with different binocular disparities. For the transparent pattern stimuli, one pattern was presented with a crossed disparity of 4.2 arc min and the other with an uncrossed disparity of the same magnitude. For the clockwise/anticlockwise task, the signal dots were presented with a crossed disparity of 4.2 arc min and the noise dots were presented with an uncrossed disparity of 4.2 arc min. The target pattern therefore appeared in front of the noise dots. The

disparities used (8.4 arc min relative disparity between the two planes) are similar to those found to produce the greatest effect in previous psychophysical studies (Hibbard *et al.* 1999; Hibbard & Bradshaw 1999; Snowden & Rossiter 1999; Greenwood & Edwards 2006). The two tasks were also performed with all the dots presented with zero disparity (a replication of experiment 1).

(b) **Results**

Figure 4 plots results from the orthogonal-angle task (a,c,e) and clockwise/anticlockwise tasks (b,d,f). The first thing to note about the orthogonal-angle data is that observers' performance is similar across the two disparity conditions when stimulus duration is sufficiently prolonged. However, as stimulus duration decreases, performance deteriorates more rapidly in the zero disparity

condition than in the different-disparities condition. In other words, when performance breaks down in the zero disparity condition, it is restored simply by separating the motion components in depth. Thus, introducing a depth separation facilitates the extraction of transparent patterns. Just as introducing a depth separation between the two patterns improved performance in the orthogonal-judgment task, figure 4b,d,f reveals a similar (although less pronounced) improvement in the clockwise/anticlockwise task.

Separating the two surfaces in depth led to a marked improvement in the orthogonal-angle task and, to a lesser extent, in the clockwise/anticlockwise task. This suggests that the poorer performance in the orthogonal-angle task of experiment 1 may be due to 'degraded transparency', brought about by inhibitory interactions between directionally selective neurons tuned to the same disparity. Indeed, observers in experiment 3 reported that the transparent surfaces appeared less clear when they were assigned the same binocular disparity. It should be noted however that the introduction of a depth separation in experiment 3 does not abolish observers' relatively better performance in the clockwise/anticlockwise task. The standard deviation plots of figure 4 show that, although it results in a more marked improvement in performance of the orthogonal-angle task, introducing a depth separation does not completely null observers' superior performance in the single-motion task. Reasons for this sustained difference are considered in §5.

5. DISCUSSION

De Bruyn & Orban (1993) identified a stimulus duration at which observers can make accurate direction judgments of one, but not two, optic flow patterns in a transparent display. This was interpreted as evidence that, at some point in the motion pathway, the processing of transparent motion encounters a serial-processing stage. They proposed that this serial bottleneck occurs at the point of 'addressing' the output of mechanisms that independently process different optic flow patterns. Results from our first experiment appear to suggest that different directions of overlapping translating movement are also processed by independent neural mechanisms whose outputs are not simultaneously available to conscious perception.

Interestingly, the difference in performance between the tasks in experiment 1 was abolished when the component patterns were segregated into different hemifields (experiment 2). One might explain this by arguing that mechanisms sensitive to translating patterns are accessed serially when the patterns are superimposed, but can be accessed in parallel when they are non-overlapping. Thus, it could be argued that our data do not challenge De Bruyn & Orban's description of a serial bottleneck in the processing of transparently moving patterns, but rather indicate that their model does not generalize to spatially segregated patterns. From De Bruyn & Orban's perspective, our poorer ability to detect two superimposed moving patterns at the same location is a consequence of the visual system addressing optic flow mechanisms in a serial manner. If this were so, then our data suggest that switching from one mechanism to another would necessarily have to be rapid (dozens, rather than hundreds, of milliseconds). However, the recent finding that it takes between 300 and 600 ms for observers to switch attention between two transparent rotating patterns (Valdes-Sosa, *et al.* 2000) seriously undermines this explanation.

An alternative explanation is that both stimulus types activate the same mechanisms but, in the case of transparency, the presence of two moving patterns in the same location results in a suppression of activity in the relevant mechanisms. This explanation is in line with reports that, when presented with transparent stimuli, MT neural activity is suppressed. Experiment 3 tested this proposal by assigning a different disparity to each dot surface, a manipulation that ameliorates such response suppression of MT neurons (Bradley *et al.* 1995).

The results from experiment 3 reveal an improvement in performance for both tasks when the superimposed patterns are separated in depth. This improvement is particularly marked in the orthogonal-angle task; thus, introducing depth separation results in a substantial narrowing of the difference in performance between the two tasks. While performance was still superior in the single-motion task following this manipulation, it is worth noting that some residual suppression of MT neural activity persists following depth separation (Bradley *et al.* 1995). Suppression of MT neural activity caused by movement in the anti-preferred direction drops from an average of 40% with no disparity separation to 10–20% with separation. In other words, with a superimposed pattern moving in the anti-preferred direction, and no disparity separation, neural response to the preferred direction is 60% of what it would be with just motion in the preferred direction. With a disparity separation, it is 80–90% of the uninhibited neural response. We would argue that this residual suppression accounts for the continued, albeit smaller, difference found between the orthogonal-angle and single-motion tasks when the two dot sets were separated in depth.

We conclude that the relatively poorer ability to detect moving transparent patterns, as opposed to a single pattern in noise, may be accounted for by appealing to mutually inhibitory interactions exerted by direction-selective neural mechanisms. Given the evidence that transparently moving patterns are encoded at a global level, it is likely that the inhibitory interactions underlying our observers' poorer performance in the transparent patterns' task occurs at or beyond the motion-integration stage. Our finding that this disruption is largely ameliorated when the two patterns are placed in different depth planes is strong evidence that transparently moving patterns are processed in parallel.

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NOTICE OF CORRECTION

Figure 3 and caption are now presented in the correct form.

8 February 2007