

# Motion drag induced by global motion Gabor arrays

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The perceived position of stationary objects can appear shifted in space due to the presence of motion in another part of the visual field (motion drag). We investigated this phenomenon with global motion Gabor arrays. These arrays consist of randomly oriented Gabors (Gaussian windowed sinusoidal luminance modulations) whose speed is set such that the normal component of the individual Gabor's motion is consistent with a single 2D global velocity. Global motion arrays were shown to alter the perceived position of nearby stationary objects. The size of this shift was the same as that induced by arrays of Gabors uniformly oriented in the direction of global motion and drifting at the global motion speed. Both types of array were found to be robust to large changes in array density and exhibited the same time course of effect. The motion drag induced by the global motion arrays was consistent with the estimated 2D global velocity, rather than by the component of the local velocities in the global motion direction. This suggests that the motion signal that induces motion drag originates at or after a stage at which local motion signals have been integrated to produce a global motion estimate.

Keywords: motion—2D, visual cortex, middle vision

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## Introduction

### Effects of motion on perceived position

One of the most important tasks for the visual system is the localization of objects in the world. Anatomical and physiological evidence suggests that there is a functional specialization in visual cortex for processing attributes such as position, form, and motion (Zeki, 1974, 1993). This is complemented by psychophysical evidence from clinical patients showing selective deficits in the perception of visual attributes such as motion after localized damage to cortex (Zihl, von Cramon, & Mai, 1983). However, visual motion can have a pronounced effect on properties of an object such as its position (Whitney, 2002) and size (Whitaker, McGraw, & Pearson, 1999). This suggests that there are significant cortical interactions between neuronal populations coding for these object properties.

Ramachandran and Anstis (1990) showed that the boundary of a window of coherently moving random dots appears shifted in the direction of motion. De Valois and De Valois (1991) showed that the perceived position of the static envelope of a drifting Gabor is shifted in a direction normal to the drifting sine wave carrier. These effects demonstrate that the physical presence of motion can shift the perceived position of a window or aperture enclosing the motion. It is also well known that adaptation

to motion in one direction can result in a motion after-effect (MAE) in which a subsequently seen static pattern is perceived to move in the opposite direction (for a history of this phenomena, see Wade, 1994). Here motion is perceived although not physically present. A number of studies have investigated whether adaptation to motion can also produce positional after-effects.

Nishida and Johnston (1999) adapted observers to the rotation of a polar angle grating (windmill pattern grating) and subsequently presented a similar but static test grating. They were able to measure both a standard motion after-effect, in which the static pattern appeared to rotate in a direction opposite to that of the adaptor, and a spatial shift in the perceived position of the pattern, again in a direction opposite to that of the adapting motion. The after-effects had different rates of decay, the spatial shift decaying more slowly than the motion after-effect. This demonstrates that perceived motion *per se* can alter the perceived position of stationary pattern and suggests that position and motion are coded separately but interact in determining perceived position (McGraw, Whitaker, Skillen, & Chung, 2002; Snowden, 1998; Whitaker et al., 1999). The spatial shift produced after adaptation to motion occurs even when the observer is unable to report the direction of motion of the adaptor (Harp, Bressler, & Whitney, 2007; Whitney, 2005).

The perceived position of a static object is thus intimately linked to the present and past motions at the same spatial location. More surprisingly, motion signals

from spatially distinct objects can induce remote shifts in the spatial position of static objects, a phenomena we refer to here as “motion drag”. Whitney and Cavanagh (2000) presented moving gratings to observers and flashed stationary bars either side of the gratings. Although separate from the moving gratings, the bars appeared shifted in the direction of grating motion. This positional shift could be induced even when the moving grating and test objects were separated by up to 60 degrees of visual angle. However, in this experiment distance from the inducing motion was confounded with an increase in visual eccentricity. Durant and Johnston (2004) found motion drag diminished with distance from the inducing motion in a display in which the eccentricity of the target remained constant, suggesting some local influence. They also examined the time course of motion drag using a rotating bar stimulus. They found that motion drag was maximal when flashed stationary targets were presented 60 ms before the end of the rotating bar came closest to the target position.

Neurons in striate cortex are retinotopically organized, this underlies the traditionally held view that position is coded by the location of activity in a cortical map. This can be traced back to ideas such as Lotze’s (1884) theory of local signs. Effects of motion on perceived position pose a problem for intuitive explanations such as this. It seems unlikely that striate neurons with receptive fields centered on different regions of the visual field would be activated by different directions of motion from a fixed region of visual space (De Valois & De Valois, 1991). Given that primary visual cortex (V1) holds the most precise spatial representation, it has been suggested that motion-induced position shifts might be mediated by feedback from extra-striate motion areas such as area MT/V5 to V1 (Durant & Johnston, 2004; Nishida & Johnston, 1999).

A number of studies have looked at the cortical coding of the position of moving objects and the position of objects subject to motion drag. Fu, Shen, Gao, and Dan (2004) demonstrated a shift in the responsivity function of cat primary visual cortical neurons in a direction opposite to that of a moving stimulus in their receptive field. They suggest that this could cause moving stimuli to be seen as advanced relative to the static responsivity profile of a cell’s receptive field and, therefore, account for effects such as those shown by De Valois and De Valois (1991). Sundberg, Fallah, and Reynolds (2006) showed a similar effect in area V4 of the macaque monkey. In humans, Whitney et al. (2003) showed that the retinotopic BOLD response in primary visual cortex (V1) shifts in a direction opposite to that of the motion of a set of drifting Gabors. These studies suggest that an object’s motion can modulate the cortical coding of its position in low-level retinotopic areas, but that disassociations can exist between retinotopic activity and perceived position (Whitney et al., 2003). However, subsequent data have suggested an alternative view of the putative shift in the

retinotopic BOLD response in human V1 (Liu, Ashida, Smith, & Wandell, 2006). Less research has focused on the cortical coding of objects subject to motion drag, however, a recent study by Maus, Fischer, and Whitney (2009) has suggested that a physical shift in position and a position shift induced by motion drag show corresponding shifts in retinotopic activity patterns in early visual areas, including V1.

Further evidence points to the role of MT/V5 in the etiology of the motion signal that modulates perceived position in both motion-induced position shifts and motion drag. Motion-defined contours that can only be seen at a global level, by pooling and segregating local motion signals and integrating over time, also appear shifted in position (Durant & Zanker, 2009). Position shifts in luminance modulated drifting random dot fields increase with motion coherence (Mussap & Prins, 2002). Motion drag of static spatially separate flashed objects depends on the perceived motion of a bistable stimulus (Shim & Cavanagh, 2004) and can also be produced by invisible occluded object motion (Watanabe, Sato, & Shimojo, 2003).

MT/V5 is known to respond to object and pattern motion and is strongly implicated in the mediation of our phenomenal experience of motion, including global motion stimuli, which require the integration of local motion signals (Born & Bradley, 2005; Newsome & Pare, 1988; Salzman, Britten, & Newsome, 1990; Salzman, Murasugi, Britten, & Newsome, 1992). McGraw, Walsh, and Barrett (2004) looked at the effect of TMS over MT/V5 and V1 on the magnitude of position shift induced by adaptation to drifting Gabors. They found that TMS over MT/V5, but not V1, significantly reduced the magnitude of motion-induced position shift. From this, they suggest that the locus of the effect of motion on perceived position is in MT/V5 itself, rather than the result of feedback from MT/V5 down to V1. However, it remains possible that motion information from multiple levels in the visual system has an influence on perceived position. For example, anticipatory neural responses to motion have been observed at as low a level as the retina (Berry, Brivanlou, Jordan, & Meister, 1999). The focus of the present study was therefore in understanding the processing stage at which the motion signal that influences perceived position arises.

## Interaction of local motion signals

Motion processing appears to be hierarchically organized. The majority of neurons in V1 only respond to motion orthogonal to their preferred orientation (Guo et al., 2006). Since V1 receptive fields are small relative to image contours, the local motion stimulus is inherently ambiguous, a problem known as the aperture problem (Adelson & Movshon, 1982). Latter stages of processing are thought to pool these local motion signals across orientation and

space to estimate true object motion. Cortical area MT is known to play a significant role in the integration and pooling of local motion signals to estimate global motion (Newsome & Pare, 1988), although the exact nature of this pooling is still a focus of debate (Britten & Heuer, 1999; Majaj, Carandini, & Movshon, 2007). MT is also thought to play a significant role in solving the aperture problem (Born & Bradley, 2005; Movshon, Adelson, Gizzi, & Newsome, 1985; Pack & Born, 2001; Perrone & Krauzlis, 2008; Rust, Mante, Simoncelli, & Movshon, 2006; Smith, Majaj, & Movshon, 2005).

If MT has a role to play in producing motion-induced position shifts, one might expect position shifts to be induced after a stage at which local motion signals, such as those from V1, have been integrated and pooled. However, it is also possible that lower level visual areas such as V1 may have a more direct role to play in the estimation of true object motion. A subpopulation of cells in V1 show end stopping and fire preferentially for the endpoints of contours. These cells could directly signal true 2D object motion, as they are not subject to the aperture problem (Pack, Livingstone, Duffy, & Born, 2003). Other cells in V1, which are not end stopped, are modulated by the presence of contour endpoints outside of their receptive field (Guo et al., 2006). These cells could also contribute to the coding of 2D object motion. Thus a strictly hierarchical view of motion processing is likely to be a simplification of a more complex picture.

In the current study, we used global motion Gabor arrays to probe the processing stage at which motion drag is produced. Isolated Gabor patches are perceived to have a 1D motion direction orthogonal to their grating contour but are inherently ambiguous stimuli because they provide a motion signal that is consistent with an infinite family of 2D object motions (Adelson & Movshon, 1982; Movshon et al., 1985). However, an array of Gabors that drift with a speed consistent with a single 2D global motion can cohere such that the observer perceives a single rigid surface that is perceived to move in the global motion direction. Within these arrays, each Gabor element drifts with a speed that is a cosine function of the difference between the normal component orthogonal to the Gabors carrier grating and the global motion direction, multiplied by the global motion speed (Amano, Edwards, Badcock, & Nishida, 2009). Global motion Gabor arrays, therefore, provide a means by which to probe the computations underlying the spatial pooling of local motion signals to produce a global motion estimate.

A number of recent studies have investigated motion-induced position shifts using compound stimuli such as plaids and global motion Gabor arrays. For plaids, the motion-induced position shift is comparable to that produced by a Gabor oriented orthogonal to the direction of motion and is not predictable from the position shift induced by the individual or summed component gratings that make up the plaid (Hisakata & Murakami, 2009; Mather & Pavan, 2009). This suggests that the position

shift is induced after a stage at which motion information from the component gratings of the plaid, at the same spatial location, has been integrated to produce a 2D motion estimate. In contrast to plaids, global motion arrays require a set of local motion signals to be integrated across *space* in order for the array to cohere into a single surface moving in the global motion direction.

Recent evidence has shown that global motion arrays appear shifted in the global motion direction by an amount comparable to an array of uniformly oriented Gabors moving at the global motion speed (Rider, McOwan, & Johnston, 2009). In global motion arrays, there is always some local component motion in the global motion direction. To rule out the fact that it is simply this local motion that produces motion-induced position shifts, Rider et al. (2009) compared the position shift induced by standard global motion arrays with arrays that had the same component motion in the global motion direction but consisted of Gabors all oriented to be orthogonal to the global motion direction. Both types of array resulted in position shifts in the global motion direction, but the shift was greater for the standard global motion arrays. This suggests that the motion-induced position shifts can be generated by local motion signals but that this effect can be modified when these signals are consistent with a coherent 2D motion.

In the current study, we focused on motion drag. We compare the amount of motion drag induced by randomly oriented arrays, as described above, to parallel-oriented arrays where all the Gabors are oriented such that their sinusoidal carrier is orthogonal to the global motion direction. If motion drag is related to the summed influence of the component of local motions in the global motion direction, then randomly oriented arrays should induce less drag than parallel-oriented arrays. There are also reasons to think that processing mechanisms underlying the integration of local signals in each type of array may differ, which may in turn be reflected in the magnitude of motion drag produced.

A number of studies have highlighted how the relationship between the orientation and motion of local signal elements, such as drifting Gabors or drifting windowed noise, can have a large effect on how these signals are integrated (Field, Hayes, & Hess, 1993; Hess, Hayes, & Field, 2003; Ledgeway & Hess, 2002; Ledgeway, Hess, & Geisler, 2005). The integration of local orientation and motion signals underlies the perception of global motion in Gabor arrays (Amano et al., 2009), so any differences in integration between our two types of array could affect the amount of motion drag produced. Studies have shown that orientation-defined contours are easier to detect when the elements, e.g., Gabors, are oriented so that their sine wave carrier lies tangent to the contour or orthogonal to it (Ledgeway et al., 2005). Similarly motion-defined contours are easier to detect when the local motion elements drift along the contour in a single unified direction (Ledgeway & Hess, 2002). It has been suggested that the

advantage of orientation and motion alignment relative to a contour arises because of preferential cortical connectivity between neuronal populations coding for similar orientations or motions (Hess et al., 2003; Ledgeway & Hess, 2002), such as the orientation columns of V1 (Hubel & Wiesel, 1977) and motion columns of MT (Born & Bradley, 2005).

The Gabors in our arrays are placed on a rectilinear grid. Motion of the Gabors in these arrays could therefore have been seen as motion relative to a series of vertical contours or columns. If orientation and motion alignment relative to these contours are important factors in determining how motion signals interact (Ledgeway & Hess, 2002; Ledgeway et al., 2005), the parallel-oriented arrays could have a cortical processing advantage, cohere to a greater extent, and produce more motion drag compared to the randomly oriented arrays. This is because in the parallel-oriented arrays the Gabors are all oriented orthogonally to the vertical columns/contours of the array and drift at the same speed and direction along this contour. This is not the case for the randomly oriented arrays. Thus both in terms of the proportion of motion signal in the global motion direction and the interactions between local motion elements, the parallel-oriented arrays might be expected to produce more motion drag than the randomly oriented arrays.

## Integration versus segregation

There is an inherent tension in the visual system arising from the competing requirement to integrate and group information and to segregate it (Braddick, 1993). Integrating information is valuable as it can increase the signal-to-noise ratio and overcome problems associated with the ambiguity of local signals (Burr, Baldassi, Morrone, & Verghese, 2009). Local signals may also provide evidence that is best explained as coming from a single object or surface (Adelson & Movshon, 1982; Amano et al., 2009; Movshon et al., 1985). On the other hand, it would not pay the visual system to group disparate local signals wholesale, since they may originate from separate objects or surfaces (Braddick, 1993; Smith, Curran, & Braddick, 1999). There is therefore a balance to be struck between segregation and integration.

We investigated this balance by varying the density of our Gabor arrays. As density decreases, the evidence may favor the segregation of the arrays into local groups or single elements rather than the integration of local signals into a single rigidly moving surface (Braddick, 1993). On average, reducing density will result in a proportional decrease in the amount of local signal moving in the global motion direction across both types of array. If the magnitude of motion drag were simply proportional to the amount of local signal moving in the global motion direction, reducing the density of the arrays would reduce the amount of motion drag monotonically by the same rate

in both types of array. However, the coherence of the Gabor arrays into a single rigid moving surface (Amano et al., 2009) may override any local influences.

We may therefore expect a differential effect of reduced density on the two types of array. Specifically, in the parallel-oriented arrays local groups of elements, even single elements, will move in the global motion direction at the global motion speed. This is not the case for the randomly oriented arrays. Here perception of motion in the global motion direction and at the global motion speed will depend on the tendency to treat local groups or single elements as arising from a single rigid surface, or multiple smaller surfaces. Although it is theoretically possible to correctly estimate global motion from as few as two array elements, using strategies such as the intersection of constraints (Adelson & Movshon, 1982; Amano et al., 2009; Movshon et al., 1985), other strategies might be adopted. A reduction in density might therefore increase segregation and reduce motion drag more in the randomly oriented arrays.

In summary, the present study sought to investigate the stage at which the motion signal that produces motion drag arises, specifically whether the motion signal is based on local motion or whether it arises after a stage at which local motion signals have been integrated to produce a global motion estimate. We investigated this with two types of global motion array, parallel-oriented arrays and randomly oriented arrays. Both types of array are consistent with the same global motion, but they are comprised of different local motion signals. If motion drag is produced by lower level local motion information prior to the stage at which a global motion estimate is made the parallel-oriented arrays should produce a greater level of motion drag. This is because they have more local signal in the global motion direction compared to the randomly oriented arrays. Furthermore, if it is predominantly the local component motions in the global motion direction that is inducing the motion drag, global motion arrays should produce the same magnitude of motion drag as arrays that have the same component motion in the global motion direction but whose Gabors are uniformly oriented orthogonal to this direction. Additionally, the parallel-oriented arrays may have a cortical processing advantage and be less susceptible to a reduction in array density compared to randomly oriented arrays.

## General methods

Stimuli were displayed on gamma corrected 20" CRT monitor (Mitsubishi Diamond Plus 230SB) with a 1024 by 864 resolution and refresh rate of 85 Hz. The stimuli were rendered online in Matlab using the Psychophysics toolbox extensions (Brainard, 1997; Pelli, 1997). Observers were positioned in a chin and headrest such that the

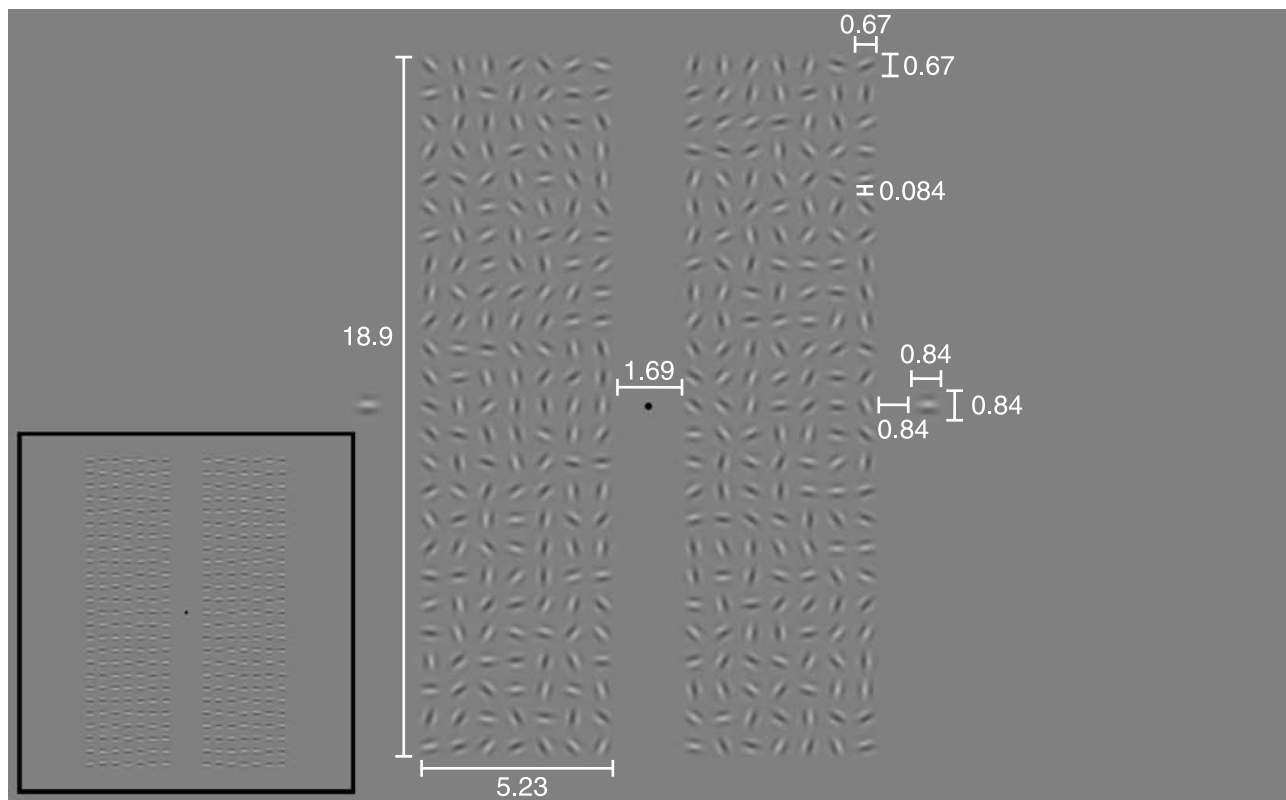


Figure 1. Diagram showing the types and dimensions of the stimuli. The main panel (A) shows an example of a full “randomly oriented array” and the inset panel (B) shows a full “parallel-oriented array”. Both types of array had the same dimensions, all of which are shown in degrees. We varied array density of the arrays from (A) a full array to (C) a most sparse array. Full arrays had 350 Gabors in total, 175 in each array. The sparsest arrays had 150 Gabors in total, 75 in each array.

viewing distance to the screen was 80 cm and a projection from the cyclopean eye intersected normal to the midpoint of the monitor screen. At this distance, the screen spanned approximately 28 by 21 degrees of visual angle. The spatial geometry of the monitor was set such that the display pixels were square.

Stimuli were two vertically oriented  $25 \times 7$  dynamic Gabor arrays, a Gabor being defined as a sinusoidal luminance modulation windowed by a Gaussian. The dimensions of the arrays can be seen in Figure 1A. Each array Gabor had a spatial frequency of 2.96 cycles per degree and a contrast of 40%. There were two types of array, randomly oriented arrays where the Gabors took a random angle between  $\pm 90$  degrees of the global motion direction (Figure 1A) and parallel-oriented arrays where the Gabors were all oriented such that the sinusoidal carrier was orthogonal to the global motion direction (Figure 1B). The phase of each array Gabor was randomized on a trial-by-trial basis.

The arrays drifted with a speed consistent with a 2D velocity of 1.35 degrees per second. In the consistent arrays, all the Gabors drifted at this speed whereas in the global arrays the drift speed for an individual Gabor was a cosine function of the difference between the normal component of the Gabor and the global motion direction multiplied by the 2D drift velocity (Amano et al., 2009).

Both array types therefore had the same global velocity but different local velocity and orientation signals. In the randomly oriented arrays, the local orientation and velocity signals in the array differed, whereas in the parallel-oriented arrays the local orientation and velocity signals were the same. The arrays could either drift globally left-up right-down or left-down right-up.

In the experiments described below, observers judged the relative vertical position of two flashed test Gabors, these had the same contrast as the Gabors in the arrays but were slightly larger and had a spatial frequency of 2.37 cycles per degree (Figure 1A). The phase of the test Gabors was randomized on each trial, but within a trial both test Gabors had the same phase. The standard deviation of the Gabors Gaussian envelope was one fifth of their dimensions; this was equivalent to 0.14 degree for the array Gabors and 0.17 for the test Gabors. Throughout the experiments, a black 0.21-degree fixation point was present at the midpoint of the screen.

## Experiment 1

Experiment 1 investigated whether motion drag in Gabor arrays is induced by the local motion signals

present in the arrays or after a stage at which local signals have been integrated to produce a global motion estimate. As such, we compared the level of motion drag induced by randomly oriented arrays and parallel-oriented arrays. Both types of array are consistent with the same global motion direction but are composed of different local motion signals. Specifically, the randomly oriented arrays have fewer local motion signals moving in the global motion direction compared to the parallel-oriented arrays in which all local motion signals are moving in the global motion direction. We also investigated the effects of reducing array density, as this could influence the extent to which the arrays cohere and produce motion drag, as discussed above.

## Methods

There were two types of array (randomly oriented versus parallel oriented), two motion direction types (either left-up right-down or left-down right-up), and five levels of array density (350, 300, 250, 200, and 150 Gabors in total, evenly split between the two arrays, i.e., 175, 150, 125, 100, and 75 in each array, respectively). This resulted in a total of 20 blocks. [Figures 1A](#) and [1C](#) show examples of the full and most sparse configuration for the randomly oriented arrays. Experimental blocks were completed in a randomized order for each observer. In total, there were five observers, one of the authors PS and four additional observers who were experienced psychophysical observers but were naive to the purposes of the experiment.

The arrays drifted for a period of 2.5 s in one of the two directions. Half a second before the end of this presentation, the two test Gabors were flashed 0.84 degree either side of the arrays for two video frames, which gave a test stimulus duration of 23 ms ([Figure 1A](#)). The test Gabors had a vertical offset from one another relative to fixation. We determined the magnitude of this offset at which the two test Gabors appeared vertically aligned with one another using the method of constant stimuli. There were 7 vertical offsets (the values of which depended on the observer and the motion direction); each was presented 20 times in a randomized order within a block. Observers judged which Gabor was higher relative to fixation. Their response was recorded with a key press.

Cumulative Gaussian functions were fitted to observers' responses for each condition and the point of subjective equality (PSE) and 95% confidence intervals around this value were determined in Matlab using the `psignifit` software package (Wichmann & Hill, 2001a, 2001b). The PSE represents the vertical offset at which the test Gabors were seen as vertically aligned with one another.

## Results

We measure the apparent spatial displacement of the flashed Gabors. Sample data and psychometric functions can be seen in [Figure 2](#).

[Figure 3](#) shows the PSE data for each observer. Direction of motion had a significant effect on the direction of motion drag across observers ( $F(1, 4) = 38.52$ ,  $p < 0.01$ ). For arrays drifting left-up and right-down, the test Gabors needed to be vertically offset such that the left test Gabor was lower than fixation and the right test Gabor higher than fixation (a positive PSE) to cancel the illusory positional offset. The converse was true for arrays drifting left-down right-up. All observers showed this effect, albeit by a smaller amount in subject HG. There is some inter-subject variability in the position of the data on the ordinate axis. For example, the PSEs of observer HH are all positive or approximately zero. This simply reflects an observer-specific standing bias in the judgement of vertical alignment.

Both types of array were equally effective in generating motion drag (no significant effect of array type,  $F(1, 4) = 0.26$ ,  $p = 0.64$ ) and the magnitude of motion drag induced was unaffected by the density of local motion signals (no significant effect of Gabor number,  $F(4, 16) = 1.60$ ,  $p = 0.22$ ). There were no significant interactions indicating that the effects of direction of motion and array density were the same for both types of array. The overall effect across observers can be more clearly seen when the relative difference between the two directions of motion for each array type is plotted. [Figure 3](#) (lower right pane) shows the difference between the two directions of motion for each array type averaged across observers. Plotting the differences in this way serves to remove criterion effects for perceived vertical alignment. From this plot, it is clear that both types of array produced the same amount of relative motion drag when described in terms of the difference between the two directions of motion. The difference was around 0.4 degree of visual angle. This was unaffected by the density of local motion signals.

## Discussion

[Experiment 1](#) demonstrated the ability of global motion arrays to produce motion drag. The amount of motion drag induced by the randomly oriented arrays and the parallel-oriented arrays was identical. This suggests that motion drag is induced after a stage at which local motion signals have been integrated to produce a global motion estimate. If motion drag were induced by the local motion signals themselves, we would have expected a reduced effect with the randomly oriented arrays, these having less local motion signal in the global motion

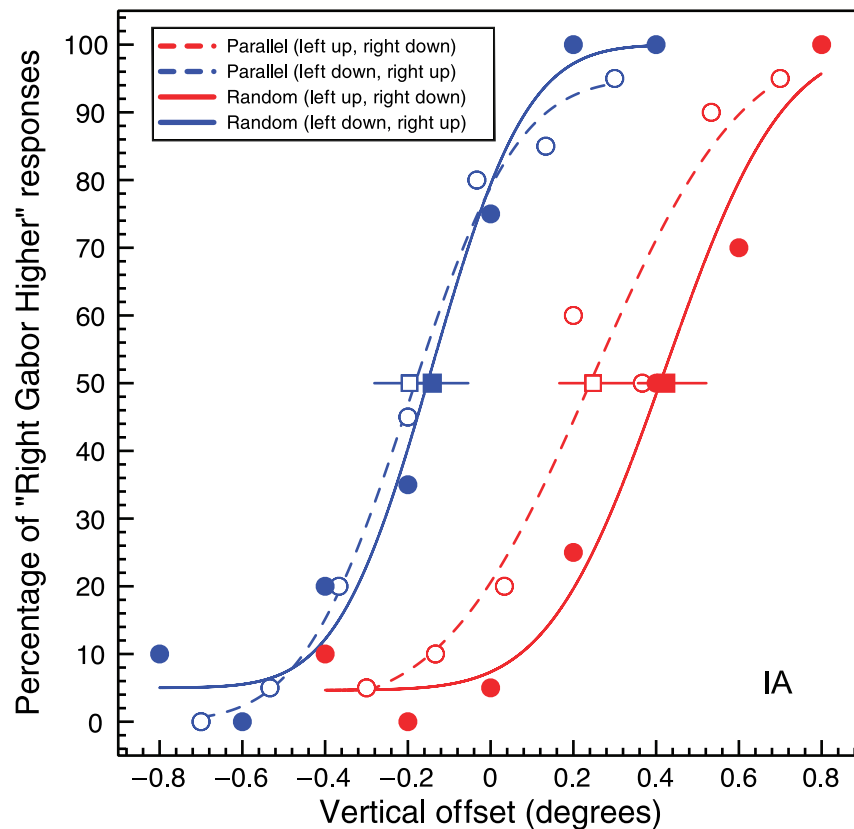


Figure 2. Sample psychometric functions for observer IA for the full array conditions. Closed circles and solid lines show the data and functions for the randomly oriented arrays. Open circles and dashed lines show the data and functions for the parallel-oriented arrays. The closed and open squares, and associated horizontal error bars, show the PSE and 95% confidence intervals from the psychometric function fits for the randomly oriented arrays and parallel-oriented arrays, respectively. All points and lines are color coded, red for array motion left-up right-down and blue for array motion left-down right-up.

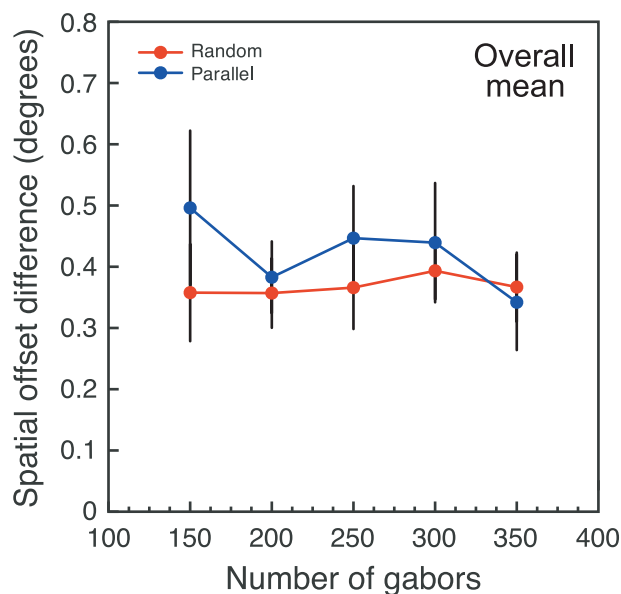
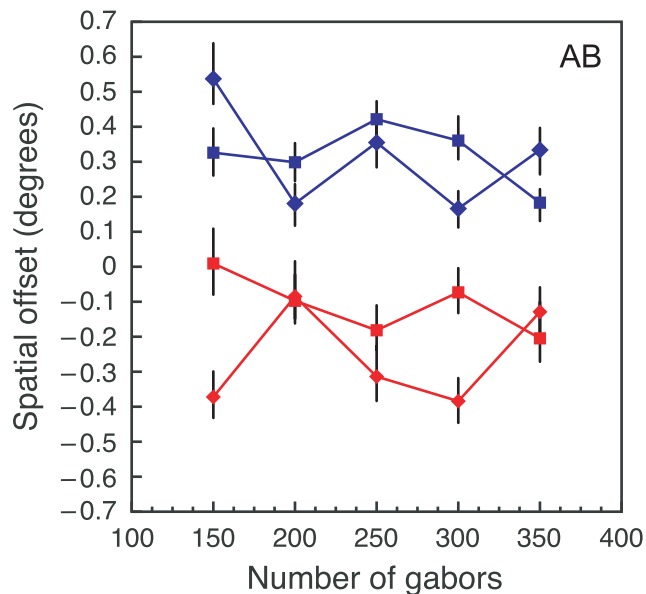
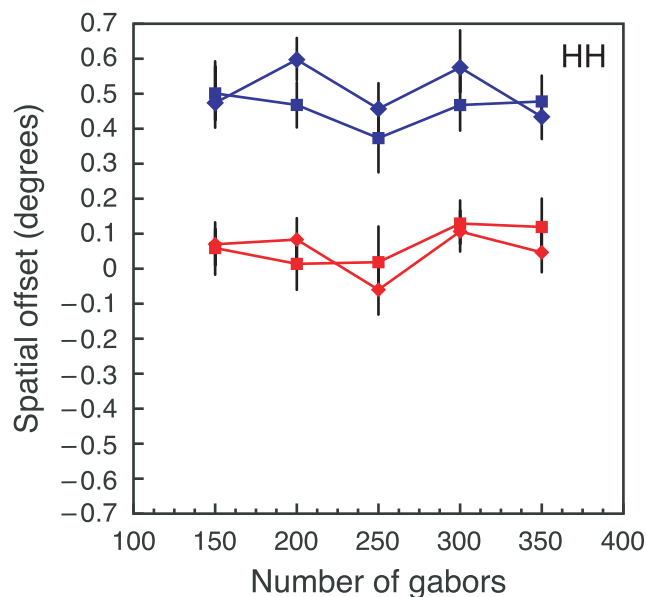
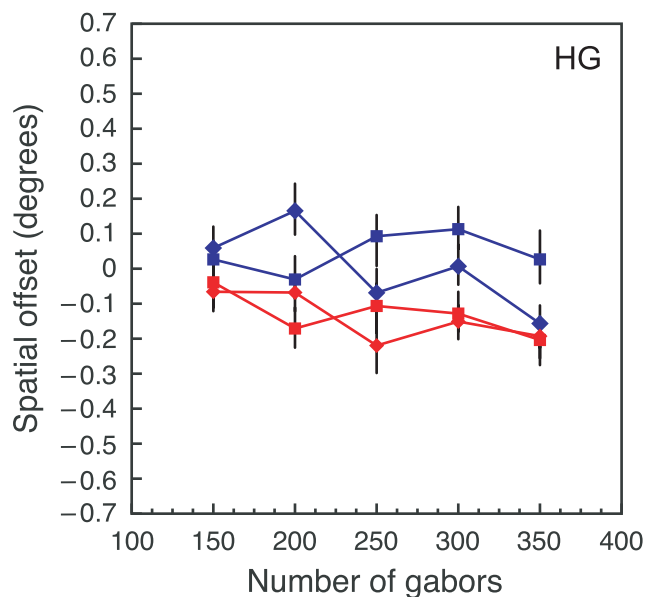
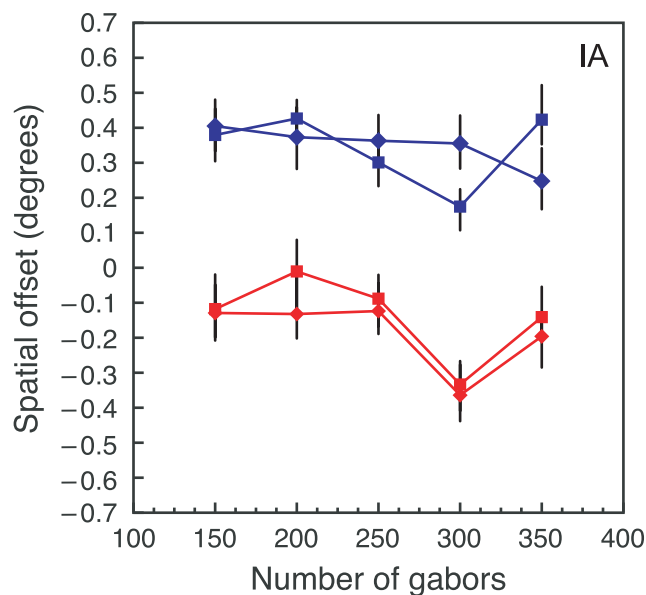
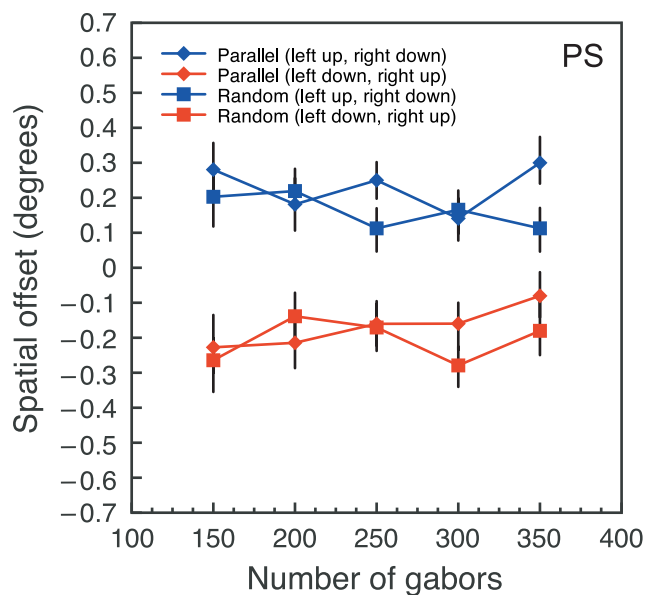
direction compared to the parallel-oriented arrays. The amount of motion drag produced in both types of array was unaffected by the density of the Gabor arrays. Thus the computations underlying global motion estimation are robust to the density of local motion signals. The data also suggest that carrier orientation and motion relative to the Gabor columns/contours was not an important factor in determining the interaction of local elements and the amount of motion drag produced.

## Experiment 2

In [Experiment 2](#), we examined the time course of the motion drag that we demonstrated in [Experiment 1](#). We investigated this using Gabor arrays that reversed in global motion direction halfway through their presentation. Previous research using gratings that reverse in direction has shown that, when probed before and after the point of reversal, motion drag is consistent with the current direction of motion and that, when probed at the point of

reversal motion, drag is consistent with the direction of motion that will be seen *after* the reversal (Whitney & Cavanagh, 2000). It is possible that randomly oriented arrays may require additional time to cohere into a single rigid moving surface compared to the parallel-oriented arrays, particularly if the local orientation and motion signals also change at the point of global motion reversal. This would be observable as a shift in the time course of motion drag such that there would be a delay in the point at which motion drag becomes consistent with the reversed direction of motion.

Figure 3. Individual and overall PSE data from [Experiment 1](#). Individual data from observers (PS, IA, HG, HH, and AB) are shown in the first five panels; here error bars show 95% confidence intervals from the psychometric function fits. The overall data are shown in the lower right panel. Here we took the absolute difference between the PSEs for each motion direction for the two types of array at each array density. This panel shows the mean of these values across observers, with error bars showing standard error of the mean.





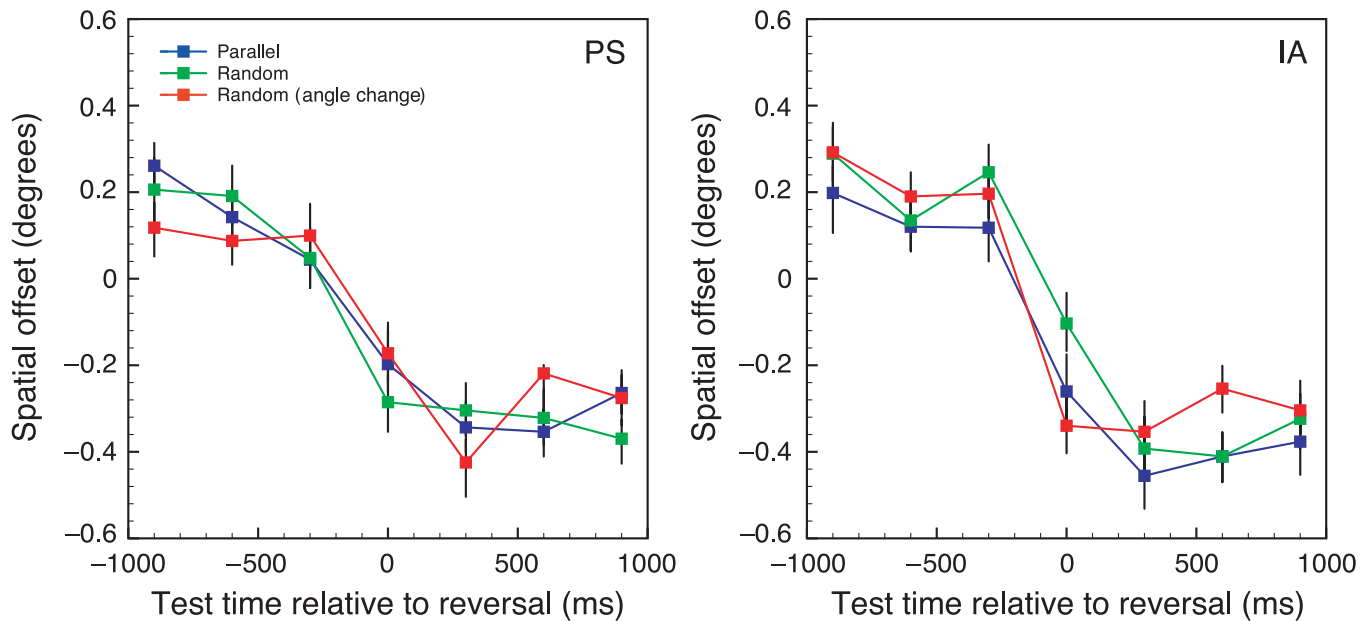


Figure 4. Individual PSE data from [Experiment 2](#) for the three types of array. Error bars show 95% confidence intervals from the psychometric function fits.

## Methods

For this experiment, we used only the full arrays with 350 Gabors in total, 175 in each in each array. The stimuli and procedures were the same as in [Experiment 1](#), with the following exceptions. The arrays now drifted for a period of 4.5 s, reversing their global motion direction halfway through the presentation. The arrays began by moving left-up right-down and then reversed direction to left-down right-up. Each direction of motion was therefore presented for 2.25 s. The test Gabors were now flashed at various points relative to the time of reversal. The time points were  $-900$ ,  $-600$ ,  $-300$ ,  $0$ ,  $300$ ,  $600$ ,  $900$  ms relative to the reversal, negative numbers being before the reversal, positive numbers after the reversal, and zero at the point of reversal.

There were three types of array: (1) parallel-oriented arrays, (2) randomly oriented arrays, and (3) randomly oriented change arrays. In the first two types of array, the drift direction of the individual Gabors reversed at the time of reversal, but the local orientation and drift rate of the Gabors remained the same. The third type of array was similar to the standard randomly oriented arrays, but at the time of reversal the individual Gabors were now assigned a new orientation and drift rate consistent with the reversed global motion direction. So for all three types of array the global motion direction reversed, but only in the randomly oriented change arrays did the local orientation and drift rates change. For all array types, the phase of the Gabors was the same before and after reversal. The observers' task was the same as in [Experiment 1](#)—to judge which of the flashed test Gabors was higher relative

to fixation. Two observers from [Experiment 1](#) took part in this experiment, IA and PS.

## Results

As in [Experiment 1](#), we fit cumulative Gaussians to the observers data and calculated the PSE and 95% confidence intervals. The data for the two observers are shown in [Figure 4](#). As can be seen in [Figure 4](#), when the Gabors were flashed before or after the point of reversal the direction of motion drag was consistent with the current global motion direction of the arrays. This gave positive PSEs for the initial left-up right-down motion direction and negative PSEs for the left-down right-up motion direction after reversal. When the test Gabors were flashed *at the point of reversal*, the direction of motion drag was consistent with the global motion direction of the arrays that the observers would see *after* the reversal point.

## Discussion

[Experiment 2](#) examined the time course of the motion drag produced by Gabor arrays. Consistent with previous research, we find that when probed before or after the reversal in direction motion drag is consistent with the current direction of motion, and that when probed at the point of reversal motion drag is consistent with the direction of motion that will be seen *after* the reversal (Whitney & Cavanagh, 2000). The time course of the effect was the same for randomly oriented arrays, parallel-

oriented arrays, and randomly oriented change arrays. For all array types, the global motion direction of the arrays reversed at the point of reversal, but only in the latter did the local orientation and motion signals change. The results suggest that the brain adopts a similar processing strategy to resolve the global motion percept in each type of array and that there is little or no lag in resolving the global motion percept upon a reversal in global motion, or a reversal in global motion with a change in the local orientation and motion signals.

## Experiment 3

Experiments 1 and 2 demonstrated that randomly oriented arrays and parallel-oriented arrays produced the same level of motion drag over a wide range of array densities, and that the time course of effect upon a reversal of global motion direction was the same, regardless of whether the local orientation and motion signals changed at the point of reversal. However, it remains possible that even the lowest density randomly oriented arrays contained enough local component motion in the global motion direction to saturate the global motion mechanism. If this were the case purely local motion could be driving the effects demonstrated in Experiments 1 and 2. To rule out this explanation, we compared the motion drag induced by parallel-oriented arrays, randomly oriented arrays, and ‘component arrays’ in which the local component motion in the global motion direction was the same as that of the randomly oriented arrays, but in which the Gabors were all oriented orthogonal to the global motion direction.

This latter type of array has the same component motion in the global motion direction as the randomly oriented arrays, but the uniform orientation of the Gabors orthogonal to the global motion direction means that the array is no longer consistent with a single 2D velocity (Adelson & Movshon, 1982; Amano et al., 2009). Thus, if it is the local component motion in the global motion direction that is driving the motion drag effect, the component arrays should produce the same amount of motion drag as the randomly oriented arrays. Conversely, if the motion signal that induces motion drag originates at or after the stage at which local motion signals have been integrated to produce a global motion estimate, the randomly oriented arrays should produce roughly the same amount of motion drag as the parallel-oriented arrays, and both of these should produce a greater level of motion drag than the component arrays.

The stability of the motion drag effect over a wide range of densities demonstrated in Experiment 1 also raises the question as to the array density at which the motion drag effect becomes apparent. In Experiment 3, we addressed these questions by investigating the motion drag induced

by parallel-oriented arrays, randomly oriented arrays, and component arrays at a range of lower array densities.

## Methods

For this experiment, there were three array densities (4, 12, and 20 Gabors in total, evenly split between the two arrays, i.e., 2, 6, and 10 Gabors in each array, respectively) and two motion direction types (either left-up right-down or left-down right-up). As discussed above, we used three types of array: (1) randomly oriented arrays, (2) parallel-oriented arrays, and (3) component arrays. The randomly oriented and parallel-oriented arrays were the same as those used previously. The component arrays were different in that the Gabors were uniformly oriented such that the sinusoidal carrier was orthogonal to the global motion direction, but they had the same local component motion in the global motion direction as the randomly oriented arrays.

To do this, we assigned each Gabor what we will call a ‘velocity orientation’,  $\alpha$ . Just as in the randomly oriented array, this angle was drawn randomly from a uniform distribution between  $\pm 90^\circ$  of the global motion direction. This angle determined the drift speed assigned to the Gabor, but not its orientation. The drift speed was given by  $G \cos^2(\theta)$ , where  $G$  is the 2D global velocity of the array and  $\theta$  is the angular difference between  $\alpha$  and the global motion direction. Thus the Gabors in the component arrays had the same local velocity components in the global motion direction as in the randomly oriented arrays but were uniformly oriented orthogonal to the global motion direction, as in the parallel-oriented arrays. As such, they were no longer consistent with a 2D object motion (Adelson & Movshon, 1982). This component condition therefore allowed us to see whether the motion drag produced by the randomly oriented arrays was due to the local velocity components in the global motion direction or the fact the local signals in the randomly oriented arrays were consistent with a 2D object motion.

In this experiment, we also measured each observer’s baseline performance in a condition with no moving array Gabors, i.e., only the flashed test Gabors were presented. This allowed us to access the magnitude of any standing biases that observers exhibit for vertical alignment of the test Gabors.

Four observers took part in this experiment; three (AB, IA, and PS) had taken part in one or both of the previous experiments, whereas DS was a naive observer who had taken part in neither of the previous experiments. All other aspects of Experiment 3 were the same as those described in the Methods section for Experiment 1.

## Results

As in Experiments 1 and 2, we fit cumulative Gaussian functions to observers data and obtained the PSE for each

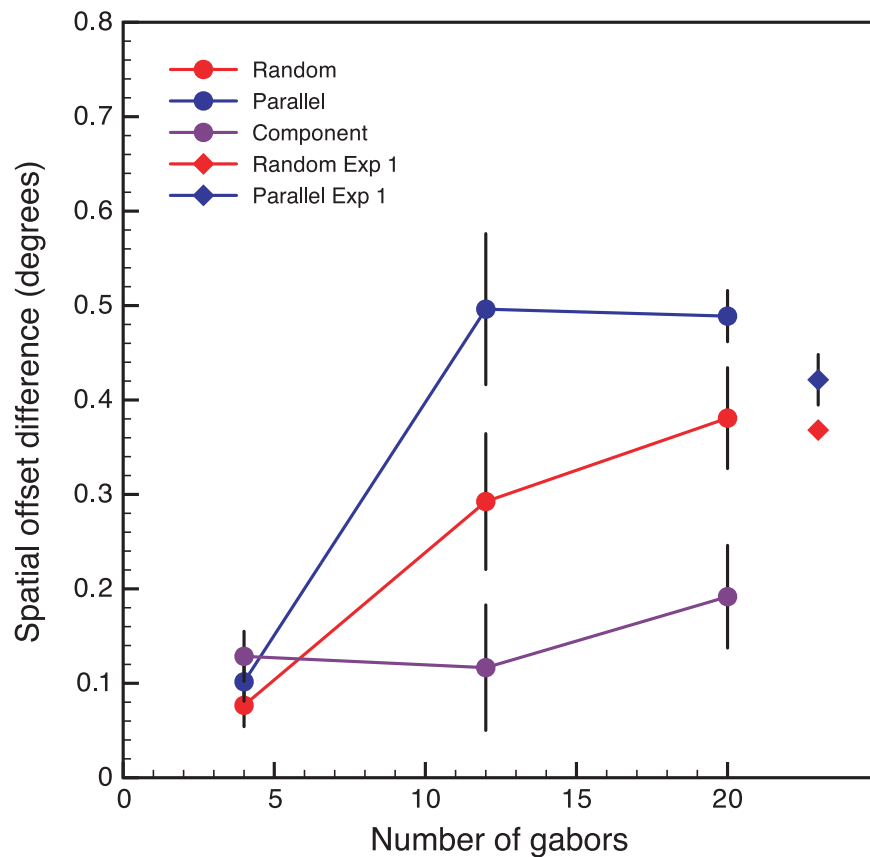


Figure 5. Overall data from [Experiment 3](#). Circular symbols show mean absolute PSE difference between the two direction motions for each type of array over our three array densities (as in the lower right panel of [Figure 3](#) for [Experiment 1](#)). The comparable values from [Experiment 1](#) are shown to the right of the graph with diamond symbols. Error bars show standard error of the mean.

condition. As expected, we found a similar effect of motion direction to that found in [Experiment 1](#). To compare the magnitude of motion drag across our three array types, we took the absolute difference of the motion drag produced in our two drift directions (left-up right-down and left-down right-up), for each observer. Small differences indicate very little motion drag, whereas large differences indicate greater motion drag. [Figure 5](#) shows the mean magnitude of this difference across observers for our three array types and three array densities. For comparison, we also plot the mean magnitude of motion drag for the parallel and random arrays from [Experiment 1](#) (as shown in lower right pane of [Figure 3](#)).

We found a significant main effect of both array type ( $F(2, 6) = 31.37, p < 0.01$ ) and number of Gabors ( $F(2, 6) = 10.34, p < 0.05$ ) and also a significant type by number interaction ( $F(4, 12) = 9.59, p < 0.01$ ). Pairwise comparisons showed that main effect of type arose because all array types differed from one another ( $p < 0.05$ ). The interaction arose because Gabor number had an effect on both parallel-oriented arrays and randomly oriented arrays, but not component arrays. For both the parallel-oriented and randomly oriented arrays, an increase in Gabor number from 4 to 12 resulted in a greater level of motion drag ( $p < 0.05$ ), whereas the effect

reached an asymptote after 12 Gabors as for both types of array an increase from 12 to 20 Gabors resulted in no significant increase in motion drag. As can be seen from [Figure 5](#), the asymptotic values for the parallel and random arrays in this experiment were similar to those found in [Experiment 1](#). With a density of 4 Gabors, all types of array produced roughly the same small magnitude of motion drag. This was close to that produced in the baseline condition with no moving array Gabors (mean  $-0.07$ , standard deviation 0.04).

## Discussion

[Experiment 3](#) investigated whether the comparable level of motion drag produced by the parallel and random arrays in [Experiment 1](#) could be explained by postulating that the parallel and random arrays, at all the densities investigated in [Experiment 1](#), contained enough component motion in the global motion direction to saturate the global motion mechanism. The results of [Experiment 3](#) suggest that this is not the case. As in [Experiment 1](#), the parallel-oriented arrays and randomly oriented arrays produced virtually the same magnitude of motion drag across all array densities. At the lowest Gabor density, the

parallel, random, and component arrays produced a similar residual level of motion drag. However, whereas the motion drag produced by the parallel and random arrays increased with increasing number of Gabors until reaching an asymptote somewhere between 12 and 20 Gabors, the component arrays remained unaffected and produced the same small magnitude of motion drag across all array densities. The asymptotic level in the parallel and random arrays was comparable to that found in [Experiment 1](#).

We can therefore conclude that the similar magnitude of motion drag produced by the parallel and random arrays was not simply due to these arrays possessing sufficient local component motion in the global motion direction to saturate the motion drag mechanism. The random and component arrays both had the same magnitude of local component motion in the global motion direction, yet the component arrays produced dramatically less motion drag. It therefore seems that it was the fact that the random arrays contained local orientation and motion signals consistent with a 2D velocity that caused them to exhibit a similar level of motion drag to that seen for the parallel arrays. This suggests that the primary motion signal driving motion drag arises at or after a stage where local motion signals have been integrated to produce a global motion estimate. The residual motion drag produced by the component arrays can be attributed to the local motion signals themselves.

## General discussion

The present study investigated the processing stage at which the motion signal that is responsible for producing motion drag arises (Whitney & Cavanagh, 2000). We used global motion Gabor arrays (Amano et al., 2009) to investigate this problem. In these arrays, local orientation and motion information needs to be integrated from the Gabors in the array in order that a global percept of a single rigidly moving object may be obtained. By manipulating the local motion signals in the array, we are able to see whether it is local motion *per se* that produces motion drag or a global motion estimate obtained by integrating the local motion signals. To do this, we compared the motion drag induced by (1) parallel-oriented arrays, in which all the Gabors are oriented such that their sinusoidal carrier is orthogonal to the global motion direction, (2) randomly oriented arrays, in which the Gabors in the array take a random orientation relative to the global motion direction but are assigned a velocity consistent with a single 2D global velocity, and (3) component arrays, which share the same local motion components in the global motion direction as the randomly oriented arrays but have their Gabors uniformly oriented orthogonal to the global motion direction, as in the parallel-oriented arrays.

The parallel-oriented arrays and randomly oriented arrays produced the same amount of motion drag, showed the same time course of effect, and were unaffected by large changes in array density. Importantly, the similarity in the magnitude of motion drag produced by these arrays was not due to the arrays having sufficient local component motion in the global motion direction to saturate the global motion mechanism. This was shown by the fact that the component arrays, which have the same local component motion in the global motion direction but are no longer consistent with a 2D velocity, produced dramatically less motion drag than either the randomly oriented or parallel-oriented arrays.

Overall, the results suggest that the brain adopts a similar processing strategy when resolving the global motion percept in both parallel-oriented arrays and randomly oriented arrays. The fact that both types of array produced the same amount of motion drag suggests that in these arrays the primary signal driving motion drag arises at or after a processing stage at which local motion signals have been integrated to produce a global motion estimate. The residual motion drag shown by the component arrays indicates that there is a small amount of motion drag directly attributable to the local motion signals themselves (for a similar result in a study investigating motion-induced position shifts, see Rider et al., 2009). The global motion mechanism showed little temporal lag in resolving the global motion percept after a change in global motion direction, even when faced with a change in local orientation and motion signals. Furthermore, we failed to observe differences between parallel and random arrays that might have been expected from previous research on interactions between local motion and orientation detectors (Ledgeway & Hess, 2002; Ledgeway et al., 2005).

Cortical area MT/V5 plays a significant role in solving the aperture problem (Born & Bradley, 2005; Huk & Heeger, 2002; Movshon et al., 1985; Pack & Born, 2001; Perrone & Krauzlis, 2008; Rust et al., 2006; Smith et al., 2005) and MT/V5 and higher areas such as MST are strongly implicated in the phenomenal experience of, and decisions related to, motion perception, including that of displays where local motion signals need to be integrated to produce a global motion percept (Born & Bradley, 2005; Celebrini & Newsome, 1994, 1995; Newsome & Pare, 1988; Salzman et al., 1990, 1992). These studies, together with the present data, therefore suggest that the motion signal that produces motion drag originates at a cortical processing stage of MT or higher. It is possible that this motion signal has direct effects on the coding of perceived position in MT/V5 (McGraw et al., 2004), or that it feeds back to lower level retinotopic areas, such as V1, where it influences the coding of perceived position (Maus et al., 2009; McGraw et al., 2004; Nishida & Johnston, 1999).

We observed that the magnitude of motion drag in the parallel and randomly oriented arrays reached an asymptote

at low Gabor densities (between 12 and 20 Gabors in total). While this seems a relatively low density, human observers clearly perceive arrays such as these to move in the global motion direction even with very few Gabor elements. Furthermore, the firing rate of neurons in macaque visual area MT that are responsive to drifting random dot stimuli has been shown to saturate at low signal strengths (Snowden, Treue, & Andersen, 1992). For example, Snowden et al. measured the effect of dot density on the response properties of V1 and MT neurons in the macaque. The response profile of neurons in both areas very rapidly increased at low dot densities before reaching an asymptote at around 7% dot density (9.2 dots per degree). It is therefore unsurprising that a relatively low global motion signal from our Gabor arrays results in an asymptotic level of motion drag. Importantly, this only occurred for the parallel and random arrays, these being the arrays that were consistent with a 2D object motion (Amano et al., 2009).

The computational rules underlying the integration of local motion signals such as those in Gabor arrays have yet to be fully understood. There are a number of candidates that include the vector average (Amano et al., 2009), the intersection of constraints (Adelson & Movshon, 1982; Amano et al., 2009; Movshon et al., 1985), and the harmonic vector average (Johnston, 2009). It is also possible that the brain uses no single strategy, instead flipping between different strategies when faced with different sense data (Amano et al., 2009). In the Gabor arrays we used, as in perception in general, there is an inherent tension between integration and segregation of local signals (Braddick, 1993). This can be seen as a contest between competing hypotheses as to how to best explain the current sense data. In the present study, we varied the density of the Gabor arrays to investigate whether a reduction in density would reduce the coherence of the Gabor arrays and encourage the segregation of local signals. Reducing density over a large range did not affect the amount of motion drag induced by both types of array. This indicates that the computational strategy the brain adopts is willing to accept, even for very sparse arrays, that the local motion signals arise from a single rigidly translating object.

## Conclusion

In the present study, we demonstrated the ability of global motion Gabor arrays to generate remote motion drag, causing the perceived position of nearby stationary objects to appear shifted in space. Both randomly oriented arrays and parallel-oriented arrays produced that same amount of motion drag. This suggests that motion drag is induced after a stage at which local orientation and motion signals have been integrated to produce a global motion

estimate. The time course of effect in both types of array was the same even when the local orientation and motion signals changed at the point of global motion reversal. Evidence points to the fact that the motion signal causing motion drag originates in MT/V5 or higher may feed back to lower level retinotopic areas such as V1 where it could alter the coding of perceived position.

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