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Position Perception: Influence of Motion With Displacement Dissociated From the Influence of Motion Alone

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Linares D, Holcombe AO. Position perception: influence of motion with displacement dissociated from the influence of motion alone. *J Neurophysiol* 100: 2472–2476, 2008. First published August 27, 2008; doi:10.1152/jn.90682.2008. When humans view a moving object, the spatial lag in perception expected from neural delays may be partially corrected by motion mechanisms biasing perceived position. The drifting-Gabor illusion seems to support this view: the perceived location of a static envelope filled with a moving pattern is shifted in the direction of motion. To test whether this shifting mechanism also extrapolates the position of moving displacing objects, we compared the perceptual position shift for drifting versus displacing Gabors when the motion is toward the fovea and when the motion is away from the fovea. For displacing Gabors, the shift was much greater for motion toward the fovea, whereas for drifting Gabors, the shift was greater for motion away from the fovea. This dissociation suggests that the illusions are caused by different mechanisms.

INTRODUCTION

The conduction time of signals in the nervous system (Schmolesky et al. 1998) delays the perception of physical events. For moving objects, this delay may yield a spatial lag in perceived position relative to actual position. However, compensation mechanisms that shift the delayed representation of the object in the direction of motion have been proposed (Berry et al. 1999; De Valois and De Valois 1991; Jancke et al. 2004; Nijhawan 1994; Sundberg et al. 2006; Witten et al. 2006; Yamagishi et al. 2001).

The drifting-Gabor illusion provides a clear demonstration of perceptual extrapolation that may compensate, at least partially, for neural delays (De Valois and De Valois 1991). In this illusion, the perceived location of a static region filled with a moving pattern is shifted in the direction of motion (Arnold et al. 2007; Bressler and Whitney 2006; Chung et al. 2007; De Valois and De Valois 1991; Pavan and Mather 2008; Ramachandran and Anstis 1990; Tsui et al. 2007). That is, although the object does not actually change location, the motion of its internal texture shifts its perceived position (Fig. 1). Possible neural correlates have been found in the visual cortex, suggesting the motion signal causes a shift of receptive field locations (Fu et al. 2004; Sundberg et al. 2006). Alternatively, other evidence suggests a role for a decrease in apparent contrast at the trailing edge of the blurred object, shifting the location of the centroid of the object (Arnold et al. 2007; Tsui et al. 2007; Whitney et al. 2003).

The drifting-Gabor illusion shows that motion alone without overall displacement can bias perceived position and raises the possibility that objects that actually move across the retina

could be extrapolated by the same mechanism. The prototypical phenomenon to study mislocalizations for displacing objects is called the “flash-lag” (for reviews, see Krekelberg and Lappe 2001; Nijhawan 2002, 2008; Schlag and Schlag-Rey 2002; Whitney 2002). In a typical experiment, subjects report the position of a moving object at the time of a flash. When the flashed object is physically aligned with the moving object, subjects perceive the moving object as being ahead of the flash (Nijhawan 1994). According to the original motion extrapolation hypothesis (Nijhawan 1994), the visual system uses the motion signal to extrapolate the position of the moving object to the “correct” location. It was argued that the flash cannot be compensated because of its unpredictability and hence it is perceived with a time delay, causing the flash-lag effect. Contrary to this explanation, it has been shown that it is the trajectory after the flash that matters (Eagleman and Sejnowski 2000; Whitney and Murakami 1998; but see Maus and Nijhawan 2006). The motion signal after the flash may shift the perceived position. Such a mechanism might provide a unified explanation of a variety of position perception effects (Eagleman and Sejnowski 2007).

The flash-lag effect is much larger for objects moving toward the fovea than for objects moving away (Kanai et al. 2004; Mateeff and Hohnsbein 1988; Mateeff et al. 1991a,b; Shi and Nijhawan 2008; van Beers et al. 2001). We hypothesized that if the perceptual extrapolation manifest in the drifting-Gabor illusion contributes to the flash-lag effect, then similar directional anisotropies should occur in both illusions. Here we measured the flash-lag effect by asking subjects to report the position of a displacing Gabor patch relative to two stationary references when the fixation point changed color. We used a color change in fixation rather than a flash presented near the moving object to avoid contamination from mislocalization of the flash (Whitney and Cavanagh 2000) which itself shows an anisotropy (Shi and Nijhawan 2008). To measure the drifting-Gabor illusion, we used a drifting Gabor for which the contrast envelope remained stationary instead of displacing. The flash-lag effect was larger for motion toward the fovea than away, whereas the drifting Gabor illusion was larger for motion away from the fovea. This suggests different mechanisms underlie the two phenomena.

METHODS

Subjects and apparatus

Two authors and two observers naïve to the goals of the experiment participated. All had normal or corrected-to-normal vision. The stim-

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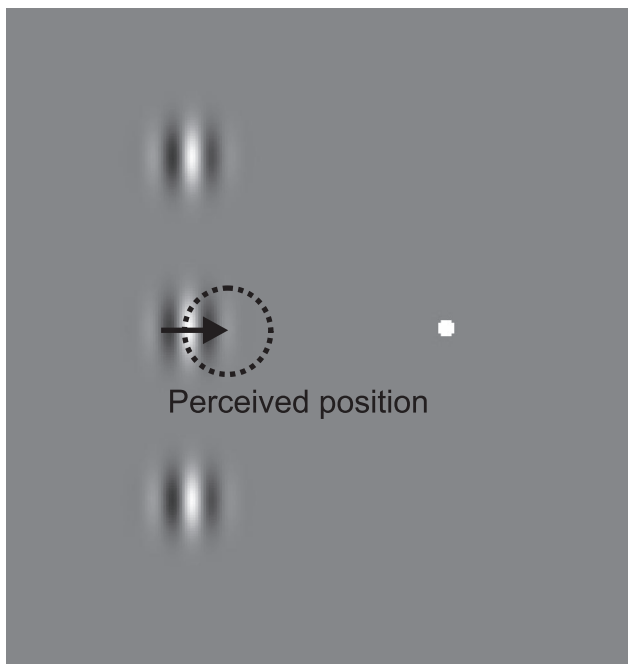


FIG. 1. Illustration of the drifting-Gabor condition. The middle patch drifted, and subjects reported its location relative to the reference patches while looking at the white circle.

uli were displayed on a 21-in CRT screen at a refresh rate of 100 Hz and were viewed from a distance of 40 cm in a dimly lit room using a chin rest.

Stimuli

A small white circle (radius: 0.2° ; luminance: 73 cd/m^2) was used as a fixation point and was always present at the center of the screen. The stimuli (Gabor patches) consisted of patches of vertical sine wave gratings (spatial frequency: 1 cycle/° , contrast close to 100%) windowed by a Gaussian envelope ($SD = 2^\circ$) displayed against a uniform gray background (luminance: 32 cd/m^2).

Procedure

We measured the perceived location of a Gabor patch (test) with respect to two static Gabor patches that served as references. The “drifting Gabor” condition and “displacing Gabor” condition differed in the nature of the motion of the test patch (see following text). Every subject conducted four sessions of the two conditions (intermixed).

Drifting Gabor condition (drifting-Gabor illusion)

In every trial, three vertically oriented Gabor patches were presented to the left or to the right of the fixation point for 2 s. The contrast of all Gabors was ramped up from zero over 500 ms at the beginning of the interval and at the end of the interval ramped back down over 500 ms. The test patch lay on the horizontal meridian. Measuring center to center of the stimuli, the reference patches were 4° above and 4° below the test, were static, both had the same phase, and this phase was determined randomly in each trial. While the contrast envelope of the test remained static throughout the trial, its internal grating drifted at 3 or 6 $^\circ/\text{s}$ directly toward or away from the fixation point (a $0^\circ/\text{s}$ speed was also used as a control). The initial phase was determined randomly in every trial. The perceived location of the test with respect to the references was measured by varying the test location using the method of constant

stimuli with nine horizontal offsets ranging from -0.8° (closer to fixation than the references) to 0.8° (farther). For *subject AH*, -1.375 to 1.375° were used. Subjects pressed the left mouse button if the test was perceived to be closer to fixation than the references and the right button if it was further. To investigate the effect of eccentricity, the test and references were sometimes presented at 6° and sometimes at 12° . Thus eccentricity, horizontal offset, speed, and also visual field (left or right) were all randomized between trials with the exception that two consecutive trials never had the same eccentricity and visual field.

Displacing Gabor condition (flash-lag illusion)

In this condition, the references were identical to the drifting Gabor condition. But rather than only the internal grating of the test drifting, the entire test patch moved as a coherent object toward or away from fixation at 3 or 6 $^\circ/\text{s}$. The spatial phase of the grating was determined randomly (and independently from the references) in every trial. The Gabor contrasts were ramped at beginning and end of the trial like in the Drifting Gabor condition. The initial horizontal distance between the target and the references was 5.25 and 10.5° for the speeds of 3 and 6 $^\circ/\text{s}$ respectively plus an additional random offset ranging from 0 to 1.25° .

The fixation point changed color to red (luminance: 13 cd/m^2 , CIE coordinates: $x = 0.62$, $y = 0.32$) when the target was at 1 of 11 possible horizontal offsets with respect to the references. The range of offsets was determined independently for each subject based on practice trials. Across subjects the most extreme values used were 2 and -3.2° .

Negative values indicate that the color change happened before the displacing Gabor reached physical alignment with the references. Subjects pressed the left mouse button if the test was perceived to be closer to fixation than the references and the right button if it was further. Like in the drifting Gabor condition, eccentricity (6 or 12°), horizontal offset, speed, and visual field were all randomized between trials with the exception that two consecutive trials never had the same eccentricity and visual field.

Data analysis

For each subject, we fitted cumulative Gaussians to the proportion of trials in which the test was seen closer to fixation as a function of its horizontal offset relative to the references.

The mean of the underlying Gaussian distribution provided the point of subjective equality. We obtained 95% confidence intervals by bootstrapping (Efron and Tibshirani 1993).

RESULTS

Figure 2 shows the spatial shifts for the flash-lag (●) and the drifting-Gabor illusion (□) for motion toward and away from the fovea. Positive values indicate errors in the direction of motion except for the static control condition (▲) for which positive values indicate that the test was perceived further away from fixation than the references. Error bars indicate the bootstrapped 95% confidence intervals.

The perceived position of the static Gabors showed little bias. For the motion conditions, however, the localization errors were in the direction of motion, replicating the drifting-Gabor and flash-lag illusions.

For all subjects the flash-lag illusion was bigger when the Gabor moved toward the fovea than when it moved away [paired $t(3) = 7.02$, $P = 0.006$]. The drifting-Gabor illusion, however, was bigger when the Gabor drifted away from the fovea than when it drifted toward it [paired $t(3) = 3.88$, $P =$

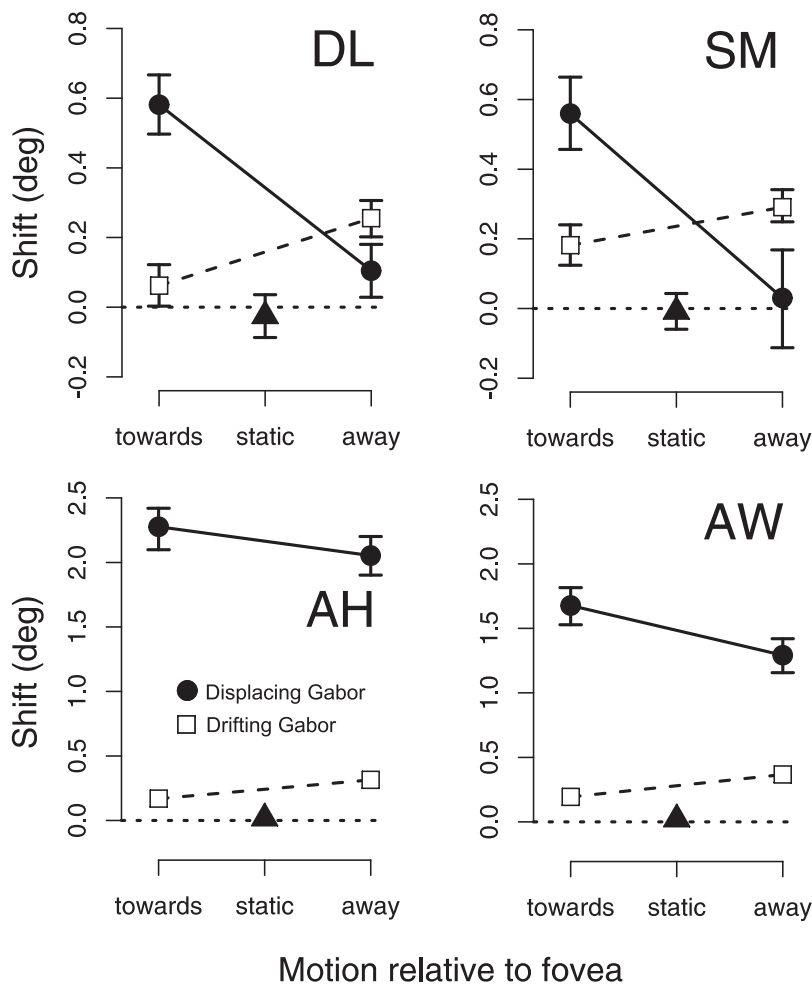


FIG. 2. Spatial shifts for the flash-lag (●) and the drifting-Gabor illusion (□) for motion toward and away from the fovea for each subject. Positive values indicate errors in the direction of motion. For the static control condition (▲), positive values indicate that the test was perceived further away from fixation than the references. Error bars (not shown when smaller than the data symbol) indicate the bootstrapped 95% confidence intervals.

0.03]. Indeed, the 95% confidence intervals for these conditions do not overlap for any subject. Moreover, Fig. 3 shows that this differential effect of motion direction on the two illusions occurs for every eccentricity and speed tested (data averaged across subjects).

The average effect of motion direction (shift for motion toward the fovea minus shift for motion away from the fovea) was 0.43° for the flash-lag effect (*DL*: 0.49° , *SM*: 0.58° , *AH*: 0.29° , *AW*: 0.38°) and -0.13° for the drifting-Gabor illusion (*DL*: -0.20° , *SM*: -0.10° , *AH*: -0.05° , *AW*: -0.18°).

For all subjects the flash-lag was larger than the drifting-Gabor illusion. The small magnitude of the drifting-Gabor illusion was quite similar across subjects (*DL*: 0.10° , *SM*: 0.16° , *AH*: 0.16° , *AW*: 0.19°), whereas big differences were observed for the flash-lag effect: two subjects (*AH*: 2.22° , *AW*: 1.49°) experienced much bigger flash-lag than the other two (*DL*: 0.34° , *SM*: 0.16°). In temporal units, these spatial shifts corresponded to 308 and 207 ms on average for the speeds of 3 and $6^\circ/s$ respectively and a directional asymmetry of 111 ms for $3^\circ/s$ and 89 ms for $6^\circ/s$.

DISCUSSION

Our results show that the tendency to localize a moving object in the direction of its motion at the time of a transient event (flash-lag effect) is larger when the object approaches the fovea than when it moves away. In contrast, when the object

remains stationary and the internal texture drifts, the spatial bias in the direction of the motion is larger for drift away from the fovea (drifting-Gabor illusion). This dissociation suggests that the flash-lag and drifting-Gabor illusions involve different mechanisms.

According to the “differential latency” theory, the flash-lag effect occurs because the neural latency for moving objects is smaller than for flashes (Purushothaman et al. 1998; Whitney and Murakami 1998). Consistent with this, Jancke and colleagues (2004), recording from neurons in cat primary visual cortex, found that the neural latency for moving objects was 16 ms smaller than that for flashes. Furthermore objects moving toward the fovea had a 4 ms smaller latency than objects moving away. However, the size of this difference between moving and flashed objects and also between objects moving toward versus objects moving away from fovea is more than one order of magnitude smaller than our behavioral data for both the directional asymmetry and the total size of the flash-lag effect. This suggests that the effects cannot be explained by differences in neural latencies in low level areas such as V1 and lower (see also Linares and López-Moliner 2007), but it could be also argued that the discrepancies are due to differences between human and cat brains.

Two previous studies reported effects of motion direction on the drifting-Gabor illusion. Kerzel and Gegenfurtner (2005)

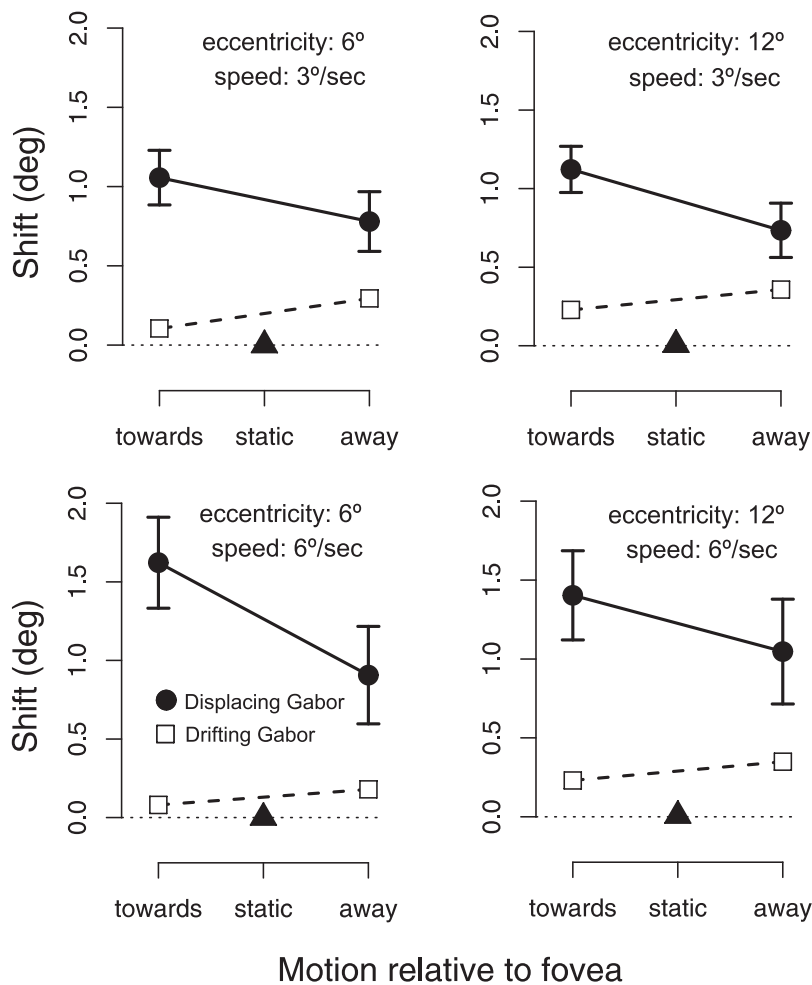


FIG. 3. Spatial shifts for the flash-lag (●) and the drifting-Gabor illusion (□) for motion toward and away from the fovea across subjects. *Top and bottom graphs* show the results for the speeds of 3 and 6°/s, respectively. *Left and right graphs* show the results for the eccentricities of 6 and 12°, respectively. Error bars (not shown when smaller than the data symbol) indicate the SE.

found the same anisotropy that we found: the spatial shift in the direction of motion was larger for motion drifting away from the fovea than for motion toward it. Yamagishi and colleagues (2001), however, found the opposite effect. Using the same stimulus parameters as Yamagishi and colleagues (eccentricity: 10°, spatial frequency: 0.5 cpd, temporal frequency: 3 and 6 Hz), we measured the drifting-Gabor illusion for *subjects DL* and *AH* but did not replicate the direction of the asymmetry they found. Again we found that the drifting-Gabor illusion was bigger for drift away from the fovea. The inconsistency is hard to explain, but may be related to the difference in task. In both the Kerzel and Gegenfurtner study and our study, stationary references were used to measure the localization of the drifting grating, whereas in the study of Yamagishi and colleagues, subjects reported the memorized location of the drifting grating relative to a ruler that was presented some time after the grating.

The effect of motion direction is large in our experiments. For the drifting-Gabor illusion, it is nearly as large (0.13°) as the average absolute size of the illusion itself (0.1525°). For the flash-lag illusion also, at least in the case of two subjects (*DL* and *SM*), the effect of motion direction is larger than the overall average position shift. The motion direction effect, then, is more than just a modulating factor, rather it is something that any theory of the flash-lag should explain.

Further constraints on theory are provided by our result that the drifting-Gabor effect was smaller than the flash-lag effect and its size was similar across subjects. The magnitude of the flash-lag effect, however, varied widely. *AH* and *AW* showed a much bigger flash-lag effect than did *DL* and *SM*. Indeed for *AH* and *AW*, the effect was ~10 times larger than the drifting-Gabor effect, which again suggests that the flash-lag is affected by a mechanism that does not manifest in the drifting-Gabor illusion. To explain the flash-lag effect, we must favor mechanisms that would both yield a flash-lag without affecting drifting Gabors and that also could vary greatly with direction of motion with respect to the fovea. Possibly attention samples the moving object after the flash (Baldo and Klein 1995; Brenner and Smeets 2001; but see Eagleman and Sejnowski 2007), by an amount of time that varies across subjects and depends on the direction the object is moving.

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REFERENCES

- Arnold DH, Thompson M, Johnston A.** Motion and position coding. *Vision Res* 47: 2403–2410, 2007.
- Baldo MVC, Klein SA.** Extrapolation or attentional shift. *Nature* 368: 565–566, 1995.
- Berry MJ, Brivanlou IH, Jordan TA, Meister M.** Anticipation of moving stimuli by the retina. *Nature* 398: 291–292, 1999.
- Brenner E, Smeets JBJ.** Motion extrapolation is not responsible for the flash-lag effect. *Vision Res* 40: 1645–1648, 2000.
- Bressler DW, Whitney D.** Second-order motion shifts perceived position. *Vision Res* 46: 1120–1128, 2006.
- Chung STL, Patel SS, Bedell HE, Yilmaz O.** Spatial and temporal properties of the illusory motion-induced position shift for drifting stimuli. *Vision Res* 47: 231–243, 2007.
- De Valois RL, De Valois KK.** Vernier acuity with stationary moving gabors. *Vision Res* 31: 1619–1626, 1991.
- Eagleman DM, Sejnowski TJ.** Motion integration and postdiction in visual awareness. *Science* 287: 2036–2038, 2000.
- Eagleman DM, Sejnowski TJ.** Motion signals bias localization judgments: a unified explanation for the flash-lag, flash-drag, flash-jump, and Frohlich illusions. *J Vis* 3: 1–12, 2007.
- Efron B, Tibshirani RJ.** *An Introduction to the Bootstrap*. New York: Chapman and Hall, 1993.
- Fu YX, Shen Y, Gao H, Dan Y.** Asymmetry in visual cortical circuits underlying motion-induced perceptual mislocalization. *Neuroscience* 24: 2165–2171, 2004.
- Jancke D, Erlhagen W, Schonher G, Dinse HR.** Shorter latencies for motion trajectories than for flashes in population responses of cat primary visual cortex. *J Physiol* 556: 971–982, 2004.
- Kanai R, Sheth BR, Shimojo S.** Stopping the motion and sleuthing the flash-lag effect: spatial uncertainty is the key to perceptual mislocalization. *Vision Res* 44: 2605–2619, 2004.
- Kerzel D, Gegenfurtner KR.** Motion-induced illusory displacement re-examined: differences between perception and action? *Exp Brain Res* 162: 191–201, 2005.
- Krekelberg B, Lappe M.** Neuronal latencies and the position of moving objects. *Trends Neurosci* 24: 335–339, 2001.
- Linares D, López-Moliner J.** Absence of flash-lag when judging global shape from local positions. *Vision Res* 47: 357–362, 2007.
- Mateeff S, Bohdanecky Z, Hohnsbein J, Ehrenstein WH, Yakimoff N.** A constant latency difference determines directional anisotropy in visual motion perception. *Vision Res* 31: 2235–2237, 1991a.
- Mateeff S, Hohnsbein J.** Perceptual latencies are shorter for motion towards the fovea than for motion away. *Vision Res* 28: 711–719, 1988.
- Mateeff S, Yakimoff N, Hohnsbein J, Ehrenstein WH, Bohdanecky Z, Radil T.** Selective directional sensitivity in visual motion perception. *Vision Res* 31: 131–138, 1991b.
- Maus GW, Nijhawan R.** Forward displacements of fading objects in motion: the role of transient signals in perceiving position. *Vision Res* 46: 4375–4381, 2006.
- Nijhawan R.** Motion extrapolation in catching. *Nature* 370: 256–257, 1994.
- Nijhawan R.** Neural delays, visual motion and the flash-lag effect. *Trends Cogn Sci* 6: 387–393, 2002.
- Nijhawan R.** Visual prediction: psychophysics and neurophysiology of compensation for time delays. *Behav Brain Sci* 31: 179–239, 2008.
- Pavan A, Mather G.** Distinct position assignment mechanisms revealed by cross-order motion. In press.
- Purushothaman G, Patel SS, Bedell HE, Ögmen H.** Moving ahead through differential visual latency. *Nature* 396: 424, 1998.
- Ramachandran VS, Anstis SM.** Illusory displacement of equiluminous kinetic edges. *Perception* 19: 611–616, 1990.
- Schmolesky MT, Wang Y, Hanes DP, Thompson KG, Leutgeb S, Schall JD.** Signal timing across the macaque visual system. *J Neurophysiol* 79: 3272–3278, 1998.
- Schlag J, Schlag-Rey M.** Through the eye slowly: delays and localization errors in the visual system. *Nat Rev Neurosci* 3: 191–200, 2002.
- Shi Z, Nijhawan R.** Behavioral significance of motion direction causes anisotropic flash-lag, flash-drag, flash-repulsion, and movement mislocalization effects. *J Vis* 8:24, 1–14, 2008.
- Sundberg KA, Fallah M, Reynolds JH.** A motion-dependent distortion of retinotopy in area V4. *Neuron* 49: 656–657, 2006.
- Tsui SY, Khoo SK, Hayes A.** The perceived position shift of a pattern that contains internal motion is accompanied by a change in the pattern's apparent size and shape. *Vision Res* 47: 402–410, 2007.
- van Beers RJ, Wolpert DM, Haggard P.** Sensorimotor integration compensates for visual localization errors during smooth pursuit eye movements. *J Neurophysiol* 85: 1914–1922, 2001.
- Whitney D.** The influence of visual motion on perceived position. *Trends Cogn Sci* 6: 211–216, 2002.
- Whitney D, Cavanagh P.** Motion distorts visual space: shifting the perceived position of remote stationary objects. *Nat Neurosci* 3: 954–959, 2000.
- Whitney D, Goltz HC, Thomas CG, Gati JS, Menon RS, Goodale MA.** Flexible retinotopy: motion-dependent position coding in the visual cortex. *Science* 302: 878–881, 2003.
- Whitney D, Murakami I.** Latency difference, not spatial extrapolation. *Nat Neurosci* 1: 656–657, 1998.
- Witten IB, Bergan JF, Knudsen EI.** Dynamic shifts in the owl's auditory space map predict moving sound location. *Nat Neurosci* 9: 1439–1445, 2006.
- Yamagishi N, Anderson SJ, Ashida H.** Evidence for dissociation between the perceptual and visuomotor systems in humans. *Proc R Soc B* 268: 973–977, 2001.