Visual motion distorts visual and motor space

Eckart Zimmermann

Psychology Department, University of Florence, Italy,
Neuroscience Institute, National Research Council,
Pisa, Italy, &
Cognitive Neurology Section, Institute of Neuroscience and
Medicine (INM-3), Research Centre Jülich, Germany

Maria Concetta Morrone

Department of Physiological Sciences,
University of Pisa, Italy, &
IRCCS Stella Maris, Calambrone, Italy

David Burr

Psychology Department, University of Florence, Italy,
Neuroscience Institute, National Research Council,
Pisa, Italy, &
Robotics and Cognitive Sciences Department,
Italian Institute of Technology, Genova, Italy

Much evidence suggests that visual motion can cause severe distortions in the perception of spatial position. In this study, we show that visual motion also distorts saccadic eye movements. Landing positions of saccades performed to objects presented in the vicinity of visual motion were biased in the direction of motion. The targeting errors for both saccades and perceptual reports were maximum during motion onset and were of very similar magnitude under the two conditions. These results suggest that visual motion affects a representation of spatial position, or spatial map, in a similar fashion for visuomotor action as for perception.

Introduction

Goodale and Milner proposed that visual information for perception and for action are processed separately through independent streams (Goodale, 2008; Goodale & Milner, 1992; Milner & Goodale, 2008): The ventral stream, projecting from the primary visual cortex to inferotemporal cortex, processes information relevant for object recognition, while the dorsal stream, projecting from the primary visual cortex to the posterior parietal cortex, processes information for action.

There is also evidence from typical subjects for the dissociation, although this is more controversial. For example, studies have demonstrated that visual illusions can influence perceptual judgments while motor responses remained accurate (Aglioti, DeSouza, & Goodale, 1995). However, this interpretation of localization differences in perception and action has been criticized on methodological and conceptual grounds (Bruno & Franz, 2009; Bruno, Knox, & de Grave, 2010; Cardoso-Leite & Gorea, 2010; Franz, Fahle, Bülthoff, & Gegenfurtner, 2001). When task demands for perceptual and motor tasks were matched, visual illusions affected both in a similar fashion

(Franz & Gegenfurtner, 2008; Franz, Gegenfurtner, Bülthoff, & Fahle, 2000; Pavani, Boscagli, Benvenuti, Rabuffetti, & Farn, 1999). Perhaps the clearest evidence for a dissociation is that during saccades, visual perception of the location of briefly presented stimuli is grossly distorted, while rapid pointing remains accurate (Burr, Morrone, & Ross, 2001).

Although form and motion are often considered independent, there are clear interactions between them (Burr, 2004). Visual motion can affect perceived position of stimuli in a variety of ways. For example, in the flash-lag effect (Nijhawan, 2002), a flashed object is perceived to lag behind a moving stimulus when both are presented at the same position. Whereas saccades executed to the perceived position of the flash in the flash-lag paradigm are veridical, landing positions of saccades performed to the moving object are offset in the direction of motion (Becker, Ansorge, & Turatto, 2009; de Sperati & Baud-Bovy, 2008). Interestingly, when the whole background was flashed, rather than single, punctate objects, saccades to the moving object were accurate. Another example of motion influencing perceived position is that a stationary window filled with moving texture is perceived shifted in the direction of its illusory motion (De Valois & De

Valois, 1991; Ramachandran & Anstis, 1990). The change in the perceived position affects both contour-element binding (Hayes, 2000) and crowding (Maus, Fischer, & Whitney, 2011). Yamagishi, Anderson, and Ashida (2001) compared stimulus localization in the presence of stimulus motion for a perceptual judgment and a visuomotor task. However, for immediate responses, they found greater errors in the visuomotor task than in the perceptual task. On reexamination of these effects, Kerzel and Gegenfurtner (2005) demonstrated that depending on the kind of motion and probe stimuli used, differences between action and perception could be replicated, reversed, or abolished.

Visual motion can also induce long-term position shifts that outlast the motion. Prolonged viewing of a drifting grating (Snowden, 1998) or rotating windmill (Nishida & Johnston, 1999) produces not only a motion aftereffect (MAE) where a subsequently presented object appears to be moving in the opposite direction of motion but also a shift in the spatial position of the object. The position shift is independent of illusory motion perception and occurs even when the test object appears to be stationary. Whitney and Cavanagh (2000) presented a sinusoidal windmill that rotated either clockwise or counterclockwise and flashed probe bars to the left or to the right of the windmill at different times relative to motion reversal. Subjects perceived the bars to be misaligned in the direction of motion, with the misalignment strongest at the time of motion reversal. Motion-induced distortions of spatial position occur even when the probe object appears as stationary, and the position shift is independent of the classical MAE (Whitney & Cavanagh, 2003). The MAE is color-selective whereas the position shift is insensitive to chromatic changes (McKeefry, Laviers, & McGraw, 2006) as well as to changes in other stimulus characteristics as velocity, relative contrast, and relative spatial frequency (McGraw, Whitaker, Skillen, & Chung, 2002). These findings suggest that the position shift occurs at higher levels of cortical processing where integration across chromatic as well as achromatic signals takes place.

Fast reaching responses are also affected by a moving stimulus, being biased in the direction of motion, suggesting that for this illusion, action follows perception (Whitney, Westwood, & Goodale, 2003). In this study, we investigated whether saccadic landing is also distorted by motion, as saccades are ballistic movements that cannot be corrected online. The results show that saccadic landing is also affected by motion, by a similar magnitude to perceptual distortions.

Methods

The subject was seated 57 cm in front of a 22″ computer monitor (Barco) with the head stabilized by a chin rest. The visible screen diagonal was 20″, resulting in a visual field of 40 deg × 30 deg. Stimuli were presented
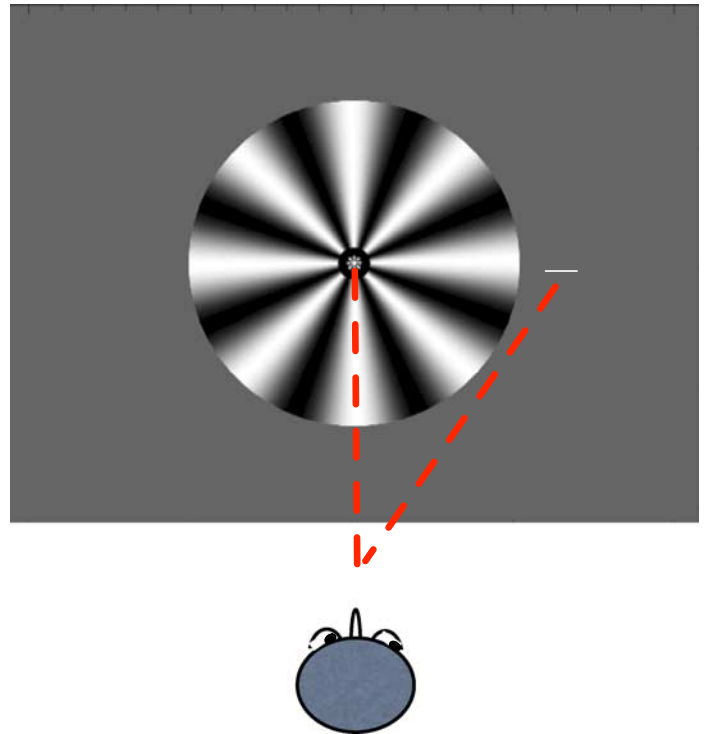
Experimental setup

Figure 1. Experimental setup. A sinusoidal windmill rotated continuously with a frequency of 1.4 Hz first clockwise then counterclockwise in the center of the screen, changing direction every 2250 ms. At different times relative to rotation reversal, a small probe bar was flashed either to the left or to the right of the windmill. Localization of the probe bar was measured in perception and saccade tasks. In the perception task, the subject had to report the vertical height of the bar relative to a bar that was presented in the middle of the windmill. In the saccade task, the subject had to perform a saccade to the perceived position of the bar.

on a gray background (luminance of 11.9 cd/m^2), on the monitor with a vertical frequency of 120 Hz at a resolution of 800 × 600 pixels (see Figure 1).

Eye movements

Eye movements were monitored by the Eyelink 2000 system (SR Research, Canada), which samples gaze positions with a frequency of 2000 Hz. Viewing was binocular, but only the dominant eye was recorded. The system detected start and end of a saccade when eye velocity exceeded or fell below 22 deg/s and acceleration was above or below 4000 deg/s^2. A radial sinusoidal windmill of 8 cycles and 7-deg radius was presented in the center of the screen and rotated continuously at 1.4 Hz, changing direction from clockwise to counterclockwise every 2250 ms. A trial consisted of a clockwise and a counterclockwise rotation phase, lasting 4500 ms in total.

The subject was instructed to direct gaze to the fixation cross in the middle of the rotating windmill. As soon as a probe bar appeared to the left or to the right of the windmill, the subject made a saccade to the perceived probe bar position. On each trial, one probe bar (1 × 0.25 deg, white color, luminance of 87.1 cd/m^2) was flashed for one frame. The probe bar was presented either to the left or to the right of the windmill, 0.5 deg from the edge. The probe bar was shown always horizontally in one of three equiprobable heights (midline, −1.5 deg, or +1.5 deg), which was randomly selected with equal probability. The probe bar was presented at one of four different times of the trial (1350 ms, 2250 ms, 3150 ms, or 4500 ms after trial onset), which was randomly selected with equal probability. After execution of the saccade, the subject directed gaze back to the fixation cross again. The next trial began when the windmill changed direction.

Perceptual localization

Perceptual localization was measured in separate sessions than the eye movement trials, with stimuli identical to those of the eye movement experiment. As before, a trial comprised 2250 ms of clockwise rotation followed by 2250 ms of counterclockwise rotation. Thresholds of perceived position were determined with a vertical vernier alignment task. The subject was instructed to fixate a white fixation point at the center of the windmill for the entire session, which also served as the reference for the vernier alignment task. A probe bar was flashed to the left or to the right of the windmill (again 0.5 deg from the

border). The subject maintained fixation at the center and indicated with the keyboard arrow buttons whether the probe was higher or lower than the fixation point. Probe bars were presented at one of seven vertical positions, from −3 deg to +3 deg, which was randomly selected with equal probability.

Results

Figure 2 shows average saccade landing positions to bars presented at motion reversal on the left (green dot) and on the right (red dots) for subjects EZ and MT. When the motion of the windmill changed from counterclockwise to clockwise direction (left panel in Figure 2), saccades to the left landed above the probes, while saccades to the right landed below the probes. The opposite bias occurred when motion of the windmill changed from clockwise to counterclockwise direction (right panel in Figure 2). Thus, the rotating windmill caused a clear bias in the direction of motion of saccadic landing.

A very similar bias was observed in perceptual localization. Figure 3 shows psychometric curves for probe bars flashed at reversal of the rotating windmill, for the same two subjects. The points of subjective equality (PSEs) of the perceived position of bars presented during the counterclockwise to clockwise transition (closed circle symbols) were clearly above the actual probe bar position, while those for bars presented during the clockwise to
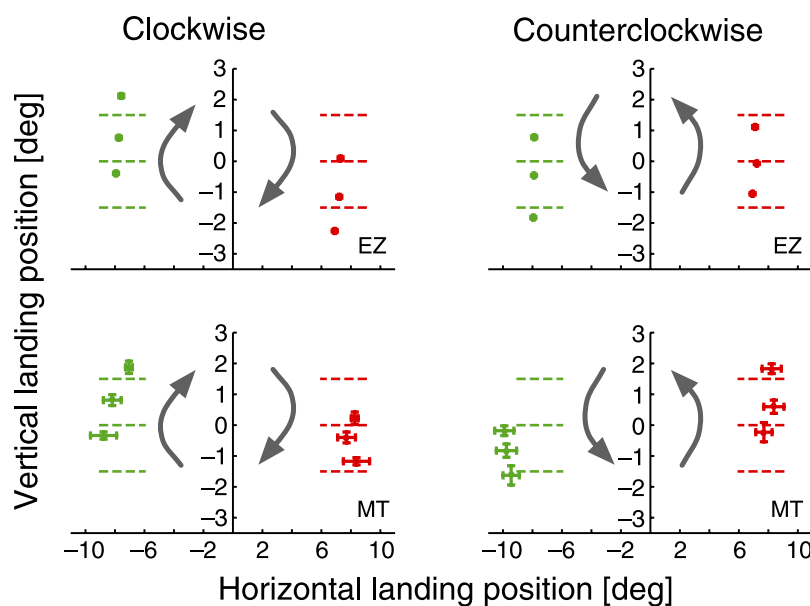

Figure 2. Average saccade landing positions for Subjects EZ and MT for probe bars presented on the left (green dots) and right (red dots) sides of the windmill. Colored bars represent standard error of sample mean of landing positions in horizontal and vertical directions. The left panel shows results for probe bars flashed at reversal to clockwise motion, while the right panel shows results for probe bars flashed at reversal to counterclockwise motion. The dashed lines indicate the three physical probe bar positions on the left and right sides.
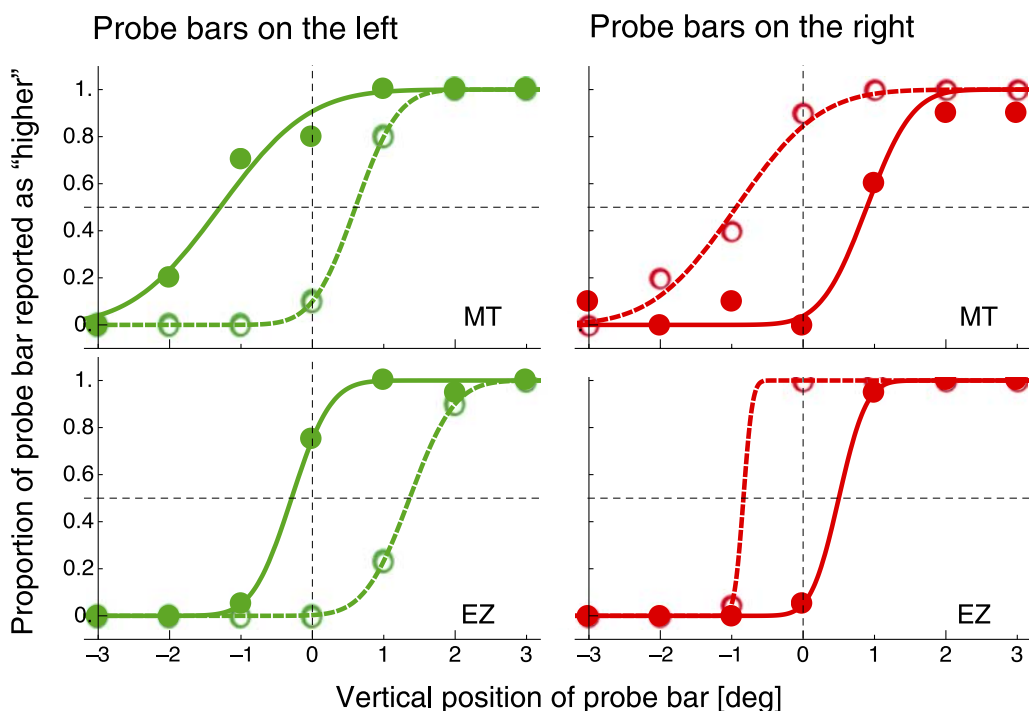
Figure 3. Results from the perceptual localization task for Subjects EZ and MT for probe bars presented on the left (green dots) and right (red dots) sides of the windmill. Closed circles represent localization data of bars flashed at reversal to clockwise motion, while open circles represent localization data of bars flashed at reversal to counterclockwise motion.

counterclockwise transition (open circle symbols) were below the probe bar position.

We analyzed the saccadic latencies, to see if the motion capture depended on latency or other variables. There was no difference between saccades executed to the left (163 ± 34 ms for EZ and 260 ± 49 ms for MT) or to the right (166 ± 33 ms for EZ and 251 ± 59 ms for MT).

In the saccade localization task, the probe bar was randomly presented in one of three different vertical positions (−1, 0, or 1 deg) to prevent saccade stereotyping. The bias for all trial times was given as the difference between average landing positions in baseline sessions with a stationary windmill and average landing positions measured in test sessions with a rotating windmill. To determine the dependency of saccade landing on saccade latency, we binned all data from both subjects into three latency groups: short (30–130 ms), medium (130–230 ms), and long latencies (230–430 ms). Figure 4A shows
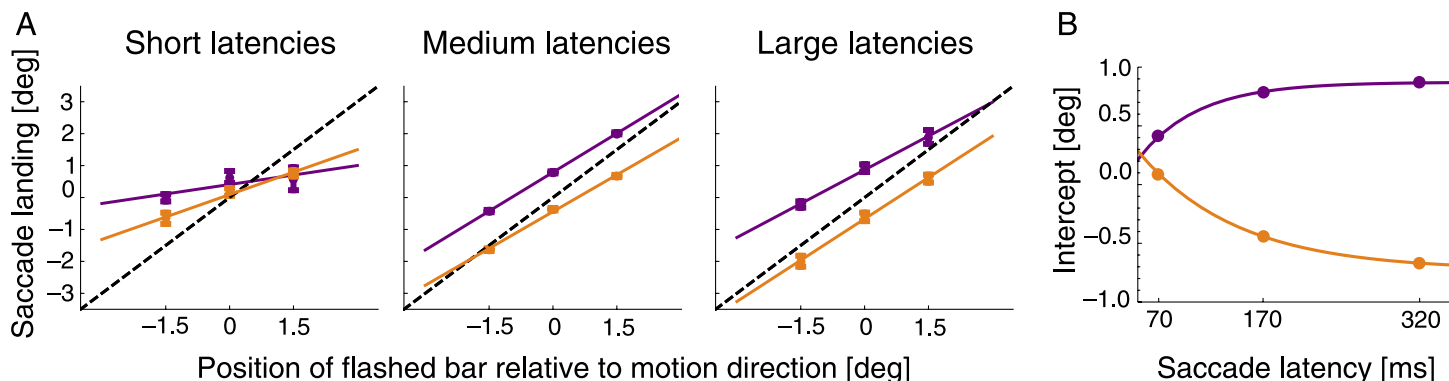

Figure 4. Average saccade landing position against target position relative to motion direction at the time of motion reversal. Saccade data are pooled across subjects and directions and split into saccades with short latencies (30–130 ms), medium latencies (130–230 ms), and long latencies (230–430 ms). Data that resulted in an upward shift in saccade landing (rightward saccades at reversal to CCW motion reversal and leftward saccades at reversal to CW motion) are shown in purple and data that resulted in a downward shift in saccade landing (leftward saccades at reversal to CCW motion and rightward saccades at reversal to CW motion) are shown in orange. An exponential fit function was fitted to the data.

average saccade landing plotted against target position for the two motion directions at the time of motion reversal. Saccade data are pooled across subjects and saccade direction. Data that resulted in an upward shift in saccade landing (rightward saccades at reversal to CCW motion reversal and leftward saccades at reversal to CW motion) are shown in purple and data that resulted in a downward shift in saccade landing (leftward saccades at reversal to CCW motion and rightward saccades at reversal to CW motion) are shown in orange. A linear fit function was fitted to the data.

The slope of the linear fit indicates how well saccade programming differentiated between the three bar positions and the intercept shows the illusion-induced bias in saccade landing. Figure 4A shows how the slope of the fits varied with latency. Saccades with short latencies (under 130 ms) showed shallow slopes, indicating a tendency for saccades to land on an averaged position rather than the actual jittered position of the bars. This tendency was much less for the medium- and long-latency saccades. Figure 4B shows the intercept of the fits against the average latency. An exponential fit function is fitted to the data. For upward (shown in purple) and downward (shown in orange) shifts in saccade latency, the size of the shift

increased with latency. The saturation for upward shift was reached with a latency of 157 ms and for downward shift with a latency of 171 ms. For this reason, saccades with a latency of less than 130 ms were excluded from the main analysis.

Figure 5 shows the perceptual localization (left panel) and the averaged saccadic localization error (right panel) as a function of time during the motion cycle and, separately, the localization for bars presented to the left (green) and right (red) sides of the windmill. The illusion was strongest at motion reversal. At reversal to clockwise motion, the perceptual effect for bars presented on the left and on the right differed by 1.2 deg for Observer EZ (bootstrap t test, $p = 0.035$) and by 1.8 for Observer MT ($p = 0.033$). The effect for bars presented at the time when the windmill changed direction to counterclockwise motion was 1.6 deg for Observer EZ (t test, $p = 0.083$) and 2 deg for Observer MT (t test, $p = 0.007$). The saccadic data are the averaged deviations for the three different landing positions. Likewise, for saccade targeting, the motion-induced bias was strongest at motion reversals. When the windmill changed to clockwise motion, the difference between leftward and rightward saccades was 1.2 deg for Observer EZ (paired t test, $p < 0.001$) and
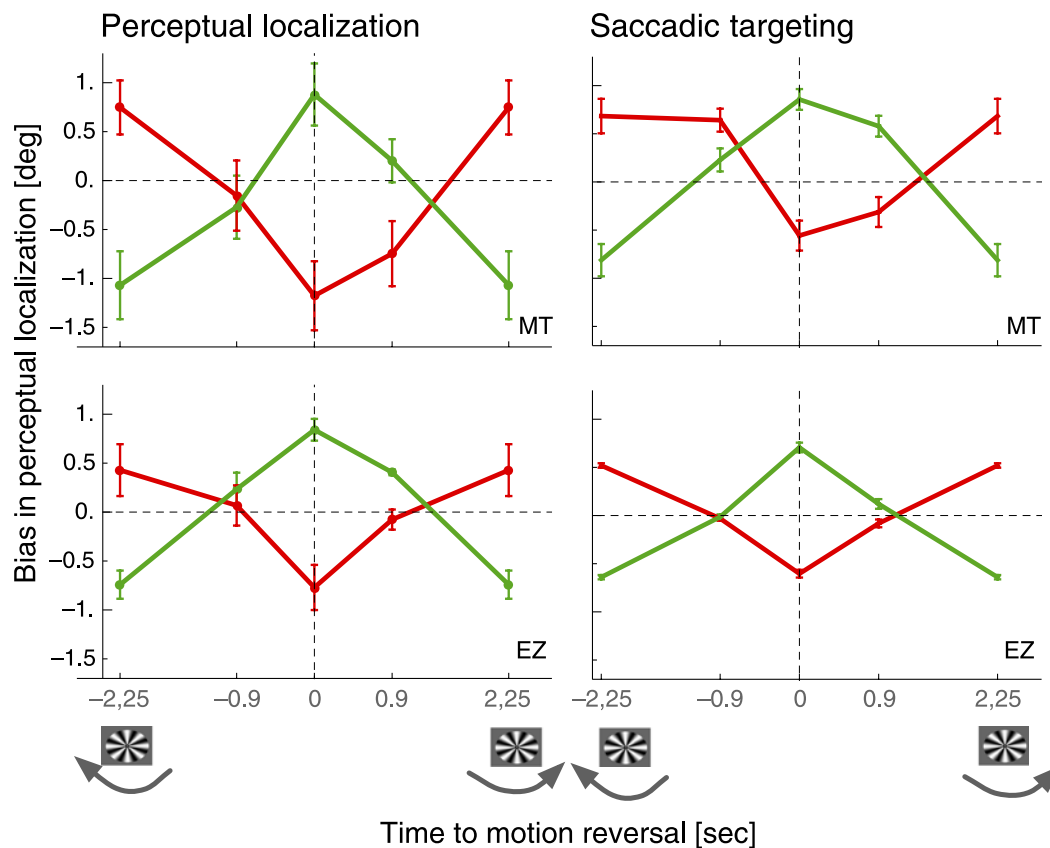

Figure 5. Average localization bias from the perception and action tasks for Subjects EZ and MT at all tested times relative to trial start. Localization of bars presented to the left of the windmill is shown in green and localization of bars presented to the right is shown in red. Error bars for the perceptual localization data are calculated by bootstrap, while error bars for saccade localization data represent standard error of sample mean.
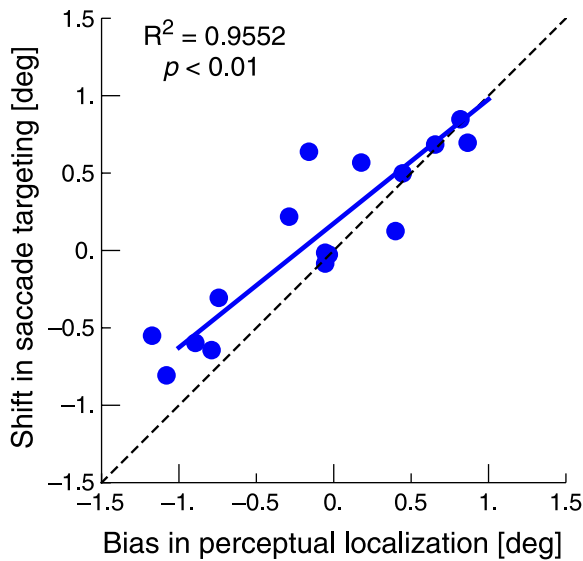
Figure 6. Orthogonal correlation between localization biases from the perception and saccade tasks. Data were fitted with the fit function $y = 0.175 + 0.8x$.

1.5 deg for Observer MT (t test, $p < 0.001$). At the time of reversal to clockwise motion, saccadic landing between leftward and rightward saccades differed by 1.3 deg for Observer EZ (t test, $p < 0.001$) and by 1.4 deg for Observer MT (t test, $p < 0.001$).

It is clear that both the saccade and perceptual localization errors follow a similar dependency on time relative to motion reversal, and the errors are of similar magnitude. In order to quantify the impact of the illusion on action and perception, we performed an orthogonal regression (that considers the error in both variables) between the perceptual and the saccade targeting bias (pooled over subjects), at the different times of the trials (see Figure 6). The correlation was clearly significant and accounted for most of the variance ($R^2 = 0.95$, $p < 0.01$). The best-fitting regression line had a slope of 0.8, showing that the saccade errors were 80% the amplitude of the perceptual errors and were thus of almost the same strength.

Discussion

Our results show that motion induces position shifts in saccadic targeting, as well as in perceptual localization. Saccades and perceptual judgments of stimuli adjacent to a moving windmill were both biased in the direction of motion, by a similar amount. The magnitude of the shifts in saccade targeting—which varied considerably with time of presentation of the stimulus in the motion cycle—correlated strongly with the magnitudes of shifts in perceptual localization. Consistent with earlier reports (Whitney & Cavanagh, 2000; Whitney et al., 2003), the bias was strongest at motion reversal.

Saccadic eye movements are ballistic in nature: Once they are initiated, visual input does not modify their performance. In the present study, saccades were exogenously triggered by a single probe bar, which requires egocentric targeting of spatial position.

While these results show that motion affects saccadic landing in a similar way to perceptual localization, it does not speak to the issue of why this error occurs at all. Is it the by-product of some mechanism, or does it confer a direct functional advantage? These issues are discussed extensively by Gomi, Abekawa, and Nishida (2006), Saijo, Murakami, Nishida, and Gomi (2005), and Whitney, Murakami, and Gomi (2010) in relation to perceptual mislocalization and manual pointing errors. Two possible mechanisms have been suggested to explain why these errors occur. The first assumes that visual motion shifts the coded location of objects (Whitney et al., 2003). The second assumes that the representation of object position remains unchanged, but visual motion induces a passive manual following response. Some evidence supported the second mechanism, showing close similarities between passive manual following responses and reflexive ocular following responses. It is however unlikely that this might explain our results, since saccades are ballistic movements whose execution cannot be perturbed once they are initiated. It would therefore seem to be more likely that the motion changes the coded locations of the objects. Perhaps the changes in spatial position serve to allow the system to compensate for the motion, allowing for the latency and duration of the saccade, so it would hit an actually moving target. Perhaps the region over which this compensatory effect operates extends past the region of actual motion. In any event, there is much evidence that space and motion are intricately interconnected, both elaborated via the dorsal stream, and this intrinsic interconnectedness causes large-field continuous motion to distort the representation of space. For whatever reason the distortion occurs, the current results show that it applies equally for saccades to brief stimuli as for identifying their position perceptually.

The effect of spatial distortion on saccades complements previous studies showing how saccades can influence space. Adaptation of saccade amplitude causes stimuli presented before saccades to be perceived shifted in the direction of adaptation (Awater, Burr, Lappe, Morrone, & Goldberg, 2005; Bahcall & Kowler, 1999; Collins, Dor-Mazars, & Lappe, 2007; Schnier, Zimmermann, & Lappe, 2010; Zimmermann & Lappe, 2009). These changes occur both for perception (measured by verbal report) and for action measured by hand pointing (Bruno & Morrone, 2007). Perception and action are also both affected, even when objects are presented during fixation, showing how saccades cause plastic changes in spatial maps (Hernandez, Levitan, Banks, & Schor, 2008; Zimmermann & Lappe, 2010). Recent studies show that the spatial maps are spatiotopic, in real-world coordinates (Zimmermann, Morrone, & Burr, 2011).

As motion in the visual field is not an infrequent event, one may expect people to be making inaccurate saccades continuously. However, it should be recalled that in our study the stimuli were flashed briefly for 10 ms, and this is quite rare in real life. We did not test the effects of motion on continuously present stimuli, but the effects may well be much reduced, as they are for perceptual localization and pointing (Whitney et al., 2003).

We found that the size of the motion-induced shift depended on saccade latency, increasing with higher latencies as de Sperati and Baud-Bovy (2008) found in a slightly different task. Saccades with latencies under 130 ms did not take into account the visual position of the flashed probe bar but tended to go to a stereotyped mean position of the three bar positions. It is thus likely that these saccades did not have sufficient time for a proper saccade planning. The maximum bias in saccade landing was found after ~160 ms.

In conclusion, the results of this study show that saccade targeting is distorted by visual motion, in much the same way as is perceptual localization. Distortions in spatial position induced by motion strongly correlated for saccade eye movements and visual perception. These results reinforce the assumption that different performance in action and perception tasks are the outcome of different reference frames for coding of object position.

Acknowledgments

Corresponding author: Eckart Zimmermann.
Email: eckartzi@gmail.com.
Address: Neuroscience Institute, National Research Council, via G. Moruzzi, 1 Località S. Cataldo, Pisa 56124, Italy.

References

Aglioti, S., DeSouza, J. F., & Goodale, M. A. (1995). Size-contrast illusions deceive the eye but not the hand. *Current Biology, 5,* 679–685.

Awater, H., Burr, D., Lappe, M., Morrone, M. C., & Goldberg, M. E. (2005). Effect of saccadic adaptation on localization of visual targets. *Journal of Neurophysiology, 93,* 3605–3614.

Bahcall, D. O., & Kowler, E. (1999). Illusory shifts in visual direction accompany adaptation of saccadic eye movements. *Nature, 400,* 864–866.

Becker, S. I., Ansorge, U., & Turatto, M. (2009). Saccades reveal that allocentric coding of the moving object causes mislocalization in the flash-lag effect. *Attention, Perception, & Psychophysics, 71,* 1313–1324.

Bruno, A., & Morrone, M. C. (2007). Influence of saccadic adaptation on spatial localization: Comparison of verbal and pointing reports. *Journal of Vision, 7*(5):16, 1–13, http://www.journalofvision.org/content/7/5/16, doi:10.1167/7.5.16. [PubMed] [Article]

Bruno, N., & Franz, V. H. (2009). When is grasping affected by the Müller–Lyer illusion? A quantitative review. *Neuropsychologia, 47,* 1421–1433.

Bruno, N., Knox, P. C., & de Grave, D. D. J. (2010). A metanalysis of the effect of the Müller–Lyer illusion on saccadic eye movements: No general support for a dissociation of perception and oculomotor action. *Vision Research, 50,* 2671–2682.

Burr, D. C. (2004). Vision: The world through picket fences. *Current Biology, 14,* 381–382.

Burr, D. C., Morrone, M. C., & Ross, J. (2001). Separate visual representations for perception and action revealed by saccadic eye movements. *Current Biology, 11,* 798–802.

Cardoso-Leite, P., & Gorea, A. (2010). On the perceptual/motor dissociation: A review of concepts, theory, experimental paradigms and data interpretations. *Seeing and Perceiving, 23,* 89–151.

Collins, T., Dor-Mazars, K., & Lappe, M. (2007). Motor space structures perceptual space: Evidence from human saccadic adaptation. *Brain Research, 1172,* 32–39.

de Sperati, C., & Baud-Bovy, G. (2008). Blind saccades: An asynchrony between seeing and looking. *Journal of Neuroscience, 28,* 4317–4321.

De Valois, R. L., & De Valois, K. K. (1991). Vernier acuity with stationary moving Gabors. *Vision Research, 31,* 1619–1626.

Franz, V. H., Fahle, M., Bülthoff, H. H., & Gegenfurtner, K. R. (2001). Effects of visual illusions on grasping. *Journal of Experimental Psychology: Human Perception & Performance, 27,* 1124–1144.

Franz, V. H., & Gegenfurtner, K. R. (2008). Grasping visual illusions: Consistent data and no dissociation. *Cognitive Neuropsychology, 25,* 920–950.

Franz, V. H., Gegenfurtner, K. R., Bülthoff, H. H., & Fahle, M. (2000). Grasping visual illusions: No evidence for a dissociation between perception and action. *Psychological Science, 11,* 20–25.

Gomi, H., Abekawa, N., & Nishida, S. (2006). Spatio-temporal tuning of rapid interactions between visual-motion analysis and reaching movement. *Journal of Neuroscience, 17,* 5301–5308.

Goodale, M. A. (2008). Action without perception in human vision. *Cognitive Neuropsychology, 25,* 891–919.

Goodale, M. A., & Milner, A. D. (1992). Separate pathways for perception and action. *Trends in Neurosciences, 15,* 20–25.

Hayes, A. (2000). Apparent position governs contour-element binding by the visual system. *Proceedings of the Royal Society of London B: Biological Sciences, 267,* 1341–1345.

Hernandez, T. D., Levitan, C. A., Banks, M. S., & Schor, C. M. (2008). How does saccade adaptation affect visual perception? *Journal of Vision, 8*(8):3, 1–16, http://www.journalofvision.org/content/8/8/3, doi:10.1167/8.8.3. [PubMed] [Article]

Kerzel, D., & Gegenfurtner, K. R. (2005). Motion-induced illusory displacement reexamined: Differences between perception and action? *Experimental Brain Research, 162,* 191–201.

Maus, G. W., Fischer, J., & Whitney, D. (2011). Perceived positions determine crowding. *PloS ONE, 6,* e19796.

McGraw, P. V., Whitaker, D., Skillen, J., & Chung, S. T. L. (2002). Motion adaptation distorts perceived visual position. *Current Biology, 12,* 2042–2047.

McKeefry, D. J., Laviers, E. G., & McGraw, P. V. (2006). The segregation and integration of colour in motion processing revealed by motion after-effects. *Proceedings of the Royal Society of London B: Biological Sciences, 273,* 91–99.

Milner, A. D., & Goodale, M. A. (2008). Two visual systems re-viewed. *Neuropsychologia, 46,* 774–785.

Nijhawan, R. (2002). Neural delays, visual motion and the flash-lag effect. *Trends in Cognitive Sciences, 6,* 387–393.

Nishida, S., & Johnston, A. (1999). Influence of motion signals on the perceived position of spatial pattern. *Nature, 397,* 610–612.

Pavani, F., Boscagli, I., Benvenuti, F., Rabuffetti, M., & Farn, A. (1999). Are perception and action affected differently by the Titchener circles illusion? *Experimental Brain Research, 127,* 95–101.

Ramachandran, V. S., & Anstis, S. M. (1990). Illusory displacement of equiluminous kinetic edges. *Perception, 19,* 611–616.

Saijo, N., Murakami, I., Nishida, S., & Gomi, H. (2005). Large-field visual motion directly induces an involuntary rapid manual following response. *Journal of Neuroscience, 18,* 4941–4951.

Schnier, F., Zimmermann, E., & Lappe, M. (2010). Adaptation and mislocalization fields for saccadic outward adaptation in humans. *Journal of Eye Movement Research, 3,* 1–18.

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

Whitney, D., & Cavanagh, P. (2000). Motion distorts visual space: Shifting the perceived position of remote stationary objects. *Nature Neuroscience, 3,* 954–959.

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

Whitney, D., Murakami, I., & Gomi, H. (2010). The utility of visual motion for goal directed reaching. In R. Nijhawan & B. Khurana (Eds.), *Space and time in perception and action* (pp. 121–145). Cambridge, England: Cambridge University Press.

Whitney, D., Westwood, D. A., & Goodale, M. A. (2003). The influence of visual motion on fast reaching movements to a stationary object. *Nature, 423,* 869–873.

Yamagishi, N., Anderson, S. J., & Ashida, H. (2001). Evidence for dissociation between the perceptual and visuomotor systems in humans. *Proceedings of the Royal Society of London B: Biological Science, 268,* 973–977.

Zimmermann, E., & Lappe, M. (2009). Mislocalization of flashed and stationary visual stimuli after adaptation of reactive and scanning saccades. *Journal of Neuroscience, 29,* 11055–11064.

Zimmermann, E., & Lappe, M. (2010). Motor signals in visual localization. *Journal of Vision, 10*(6):2, 1–11, http://www.journalofvision.org/content/10/6/2, doi:10.1167/10.6.2. [PubMed] [Article]

Zimmermann, E., Morrone, M. C., & Burr, D. (2011). Spatiotopic visual maps revealed by saccadic adaptation in humans. *Current Biology, 21,* 1380–1384.