Motion extrapolation into the blind spot: Research report

Article (Unspecified)

Motion Extrapolation Into the Blind Spot

Gerrit W. Maus and Romi Nijhawan

Psychological Science 2008 19: 1087
DOI: 10.1111/j.1467-9280.2008.02205.x

Research Report

Motion Extrapolation Into the Blind Spot

Gerrit W. Maus and Romi Nijhawan

University of Sussex

ABSTRACT—*The flash-lag effect, in which a moving object is perceived ahead of a colocalized flash, has led to keen empirical and theoretical debates. To test the proposal that a predictive mechanism overcomes neural delays in vision by shifting objects spatially, we asked observers to judge the final position of a bar moving into the retinal blind spot. The bar was perceived to disappear in positions well inside the unstimulated area. Given that photoreceptors are absent in the blind spot, the perceived shift must be based on the history of the moving object. Such predictive overshoots are suppressed when a moving object disappears abruptly from the retina, triggering retinal transient signals. No such transient-driven suppression occurs when the object disappears by virtue of moving into the blind spot. The extrapolated position of the moving bar revealed in this manner provides converging support for visual prediction.*

Objects moving across the visual field constantly change their position over time. Neural responses to moving stimuli are delayed, and persist for a significant duration after stimulation ceases. The delay in the neural response should cause a moving object to be seen in a position lagging its physical position, and response persistence should cause the moving object to appear smeared. However, moving objects appear less smeared than expected (Burr, 1980), and the instantaneous perceived position of a moving object is shifted forward in the direction of motion, as illustrated in a class of visual phenomena, most prominently in the flash-lag effect (Nijhawan, 1994). If a brief flash is presented in alignment with a moving object, then the object is seen to be ahead of the flash. Several theories have been brought forward to explain this forward shift (reviewed in Krekelberg & Lappe, 2001; Nijhawan, 2002). Temporal integration theories state that the visual system samples positions of a moving object over an extended period of time and produces an average position, possibly weighted towards more recently sampled positions (Brenner, van Beers, Rotman, & Smeets, 2006; Krekelberg & Lappe, 2000; Roulston, Self, & Zeki, 2006). The postdiction account additionally assumes that a flash resets this integration process and uses mainly positions from after the flash to produce the averaged output (Eagleman & Sejnowski, 2000). More recently, the same authors argued for a slightly different account, proposing that motion signals from after the flash bias the localization of objects towards the direction of motion (Eagleman & Sejnowski, 2007). Alternatively, motion extrapolation posits that the visual system uses motion information from the previous trajectory to predict the moving object's position, thus compensating for neural processing delays in the visual pathway (Nijhawan, 1994, 2008).

One particular observation concerning the flash-lag effect has been used to argue against the visual prediction model: When the moving object disappears (Eagleman & Sejnowski, 2000) or reverses direction (Whitney & Murakami, 1998) at the time of the flash, it does not perceptually overshoot the point of disappearance or reversal. Generally, the final position of abruptly disappearing moving objects is perceived accurately when observers keep steady fixation (Kerzel, 2000). This absence of a predictive overshoot has been a major difficulty for the motion extrapolation account. However, abrupt offsets and direction changes of moving objects elicit retinal transient signals (Schwartz, Taylor, Fisher, Harris, & Berry, 2007), which carry precise positional information. We argue that these signals can suppress the visibility of an extrapolated object representation and thus facilitate accurate localization of the object's final position despite predictive mechanisms (Maus & Nijhawan, 2006, in press; Nijhawan, 2002, 2008). When a moving object disappears from view without eliciting a retinal transient signal, it should be seen to disappear in an extrapolated position. For example, when a moving object gradually decreases in luminance contrast, it disappears from view in positions beyond its detection threshold (Maus & Nijhawan, 2006). The object is seen in positions where luminance contrast alone is insufficient to produce a percept. Here we present converging evidence for extrapolation in the absence of transient signals by showing

Address correspondence to Gerrit Maus, Psychology Department, University of Sussex, Falmer, Brighton BN1 9QH, United Kingdom, e-mail: G.W.Maus@sussex.ac.uk.

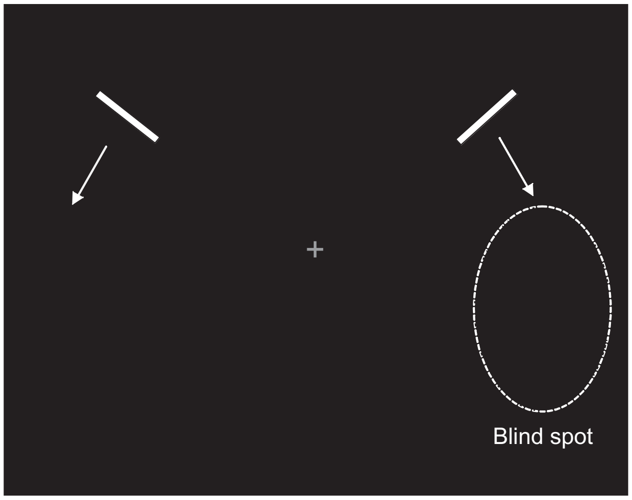

Fig. 1. Illustration of the stimulus used in the offset condition.

motion extrapolation into the retinal blind spot. This finding cannot be readily explained by a temporal integration mechanism or by a retrospective position bias based on motion signals.

Observers judged the last visible position of a bar moving into the blind spot in relation to the last visible position of a second bar that was abruptly switched off. In monocular viewing, one bar, which was ipsilateral to the viewing eye, moved into the blind spot. A comparison bar on the contralateral side of the viewing eye was presented in mirror-image positions of the first bar and was switched off near the mirror image of the blind spot border (see Fig. 1). Observers performed a temporal-order-judgment task, indicating which bar they perceived as disappearing first. Because the two bars occupied exactly mirrored positions, the point of subjective simultaneity for the disappearances also gave the last-seen position of the bar on the blind-spot side. In an additional condition, one bar started moving inside the blind spot, while the other bar abruptly started moving over intact retina. The task for observers was to indicate which bar they saw first.

In contrast to an object disappearing in full view of photoreceptors, an object moving into the blind spot does not elicit a transient retinal off-signal carrying precise position information. Therefore, we predict that if the perceived position of the object is extrapolated during continuous motion, then it should be seen as disappearing in a position shifted forward past the blind-spot boundary into the blind area. Temporal integration and postdiction would predict the object to perceptually disappear at (or slightly before) the blind-spot boundary, because positions cannot be sampled from unstimulated retinal areas.

METHOD

Participants

Five observers, including author G.M., participated. The remaining 4 observers were naive to the hypotheses. All observers had normal or corrected-to-normal vision.

Apparatus and Stimuli

Stimuli were presented on a 21-in. CRT monitor (Formac Elektronik GmbH, Blankenfeld, Germany) at 100-Hz vertical refresh rate using MATLAB and the Psychophysics Toolbox extensions (Brainard, 1997; Pelli, 1997). Observers sat 56 cm from the screen with their heads rested on a chin rest. Both eyes were tested monocularly in succession; an eye patch prevented stimulation of the opposite eye.

The stimulus consisted of moving white bars ($2.0^\circ \times 0.1^\circ$ visual angle) on a black background (Fig. 1). In all conditions, the bars were exact mirror images of each other and moved on circular trajectories around the fixation point at 15° eccentricity. The angular velocity was $61.3^\circ\ s^{-1}$ (tangential velocity = $16^\circ\ s^{-1}$). In the stimulus-offset condition, both bars started moving at an angle of 45° from the vertical axis either in the upper or the lower visual field. The bar ipsilateral to the viewing eye moved into the blind spot, while the contralateral bar was switched off abruptly. In the stimulus-onset condition, one bar started moving in the center of the blind spot, whereas the contralateral bar started moving at positions near the mirrored blind-spot boundary. Both bars were switched off when they reached the 45° position.

The task for observers was to indicate with a key press which bar they saw disappearing or appearing first. The positions of offsets and onsets of the contralateral bar were manipulated systematically in a method of constant stimuli. In the stimulus-offset condition, the contralateral bar was switched off in one of seven possible positions between 40 ms before to 200 ms after the ipsilateral bar crossed the blind-spot boundary in steps of 40 ms (i.e., between -2.4° and 12.2° from the position of the mirrored blind-spot boundary in steps of $\sim 2.4^\circ$). For the stimulus-onset condition, the contralateral bar was switched on in positions ranging from 120 ms before to 120 ms after the ipsilateral bar crossed the blind-spot boundary (i.e., approximately $\pm 7.3^\circ$). In pilot experiments, these positions of constant stimuli were determined to be ideal for the fitting of psychometric functions. Because the two bars always occupied exactly mirrored positions, the temporal-order tasks in the stimulus-offset and -onset conditions effectively also measured the last visible position of the bar disappearing in the blind spot and the first visible position of the moving bar appearing from within the blind spot, respectively.

Measurement of Blind Spots

Before the experiment, the experimenter estimated the extent of observers' blind spots for each eye by slowly moving a small crosshair mouse pointer from different directions into the blind area. The observer indicated when they saw the pointer disappear. The experimental software recorded these positions and calculated the area of the blind spot (see Table 1). Note that moving the mouse pointer into the blind spot resulted in slightly smaller estimates for the blind area (Incze, 1928). Next, the accuracy of the measurement was verified by presenting single

TABLE 1

Results of Blind-Spot Measurements for the 5 Observers

		Centroid		Diameter (°)		
Observer	Eye	x	y	Horizontal	Vertical	Area
N.Z.	Left	14.44	−1.36	4.35	6.31	19.55
	Right	15.17	−0.23	4.62	7.65	23.17
G.M.	Left	14.92	−1.36	4.96	6.04	21.09
	Right	15.09	−0.70	4.77	5.43	17.74
Z.W.	Left	14.64	0.45	4.42	5.16	16.06
	Right	14.40	−0.62	4.27	5.00	13.05
C.J.	Left	15.55	−2.65	4.73	7.65	25.69
	Right	15.70	−0.62	4.85	5.73	20.84
R.H.	Left	14.76	−2.20	4.35	7.50	25.93
	Right	14.67	−0.22	4.81	6.00	20.86
Mean		14.93	−0.95	4.61	6.25	20.40
SEM		0.14	0.30	0.08	0.32	1.28

Note. Coordinates of the centroid of the polygonal area of the blind spot are listed in degrees of visual angle from the central fixation cross. Area is given in degrees squared.

static frames from the motion sequence, where the bar was just inside the measured blind area. Observers judged whether the bar was visible. If the bar was still visible, it was moved further into the blind spot by one or more frames until it was no longer visible. This bar position entirely within the blind spot was defined as the blind-spot boundary (position 0 in Fig. 2). Although this measurement cannot be regarded as highly accurate, it was sufficient for our purpose, as we used it merely to set the positions of constant stimuli and in the analysis compared the offset and onset conditions.

Procedure and Analysis

The experiment consisted of one block of trials of the stimulus-offset and -onset conditions for each eye. Stimulus presentation in the upper and lower visual field was randomized within each block. All blocks consisted of 140 trials, 2 (upper or lower) visual fields × 7 (offset or onset) positions × 10 trial repetitions; in total, there were 280 trials for each viewing eye. The order of blocks was counterbalanced across observers. Independent psychometric functions were fitted to each observer's responses at four separate blind-spot boundaries: the upper and lower boundary for the blind spot of the left eye and the upper and lower boundary for the blind spot of the right eye. For 2 blind-spot boundaries (out of a total of 20 examined), fitting psychometric functions was not possible due to inaccurate measurements of the blind-spot area. These measurements were excluded from further analysis. Points of subjective simultaneity and perceived posi-

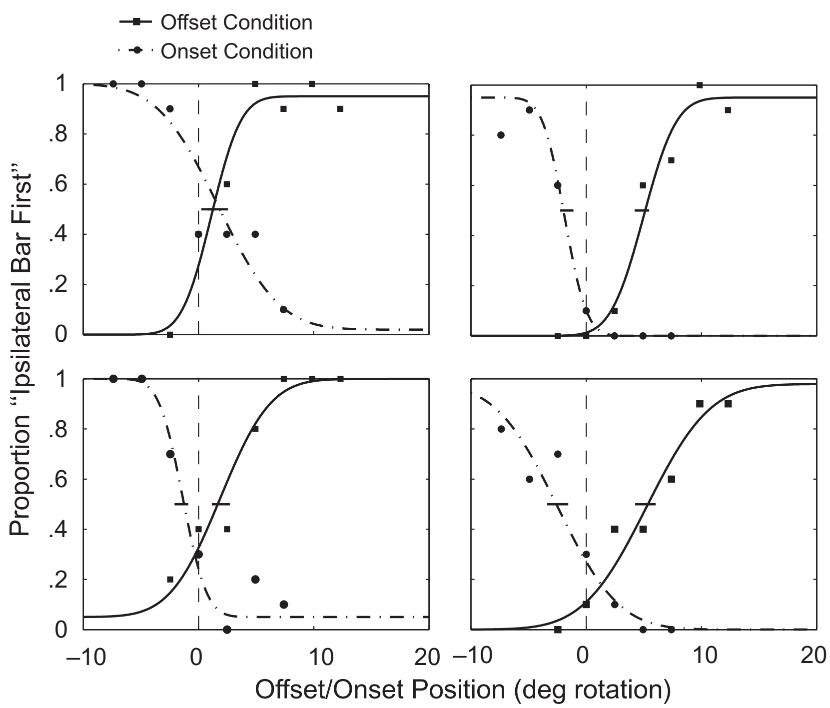

Fig. 2. Psychometric functions for 1 typical naive observer (N.Z.). The four panels represent the four blind-spot boundaries at which the experimental task was performed: at the upper and lower border of both left and right blind spots. The x-axis denotes the position of the abrupt offset or onset of the contralateral bar in degrees rotation (0 is at the blind-spot boundary, indicated by the dashed vertical lines; positive numbers are positions inside the blind spot). The y-axis denotes the proportion of responses indicating that the offset or onset was perceived on the side of the blind spot first. Horizontal lines represent 95% confidence intervals for points of subjective simultaneity of the fit.

tions for stimulus offsets and onsets were calculated from the 50% threshold points of psychometric functions.

RESULTS AND DISCUSSION

Psychometric functions for 1 naive observer are shown in Figure 2, and average perceived first and final positions for all observers are shown in Figure 3. All observers perceived the bar moving into the blind spot as shifted well into the blind area. The average forward displacement from the blind-spot boundary was 3.1° rotational angle, $SEM = 0.5°$, one-sample t test $t(17) = 6.17$, $p < .001$, $r = .83$, on the circular trajectory of the bar, equivalent to approximately 51 ms ($SEM = 8.3$ ms) or 0.81° visual angle ($SEM = 0.13°$). The bar moving out of the blind spot was reliably detected at the same time as the bar on the contralateral side started moving, with on average no displacement, 0.0°, $SEM = 0.6°$, one-sample t test $t(17) = 0.04$, $p = .965$, $r = .01$. The crucial comparison is between the different motion directions. The last perceived position of the disappearing bar and the first seen position of the appearing bar were significantly different from each other, paired-samples t test $t(17) = 3.94$, $p = .001$, $r = .69$.

The null result in the stimulus-onset condition does not imply that observers perceived the bar starting right at the blind-spot boundary, or at the true position of the stimulus onset. Both bars are likely to be perceived as shifted forward from their true positions due to the Fröhlich effect (Fröhlich, 1923; Kirschfeld & Kammer, 1999). Interestingly, the null result indicates that a bar appearing from within the blind spot is perceived no differently than a bar abruptly appearing over intact retina. However, the bar disappearing from view in the blind spot is perceived as shifted forward relative to the bar with an abrupt offset.

In contrast to previous experiments investigating the perceived final position of a fading visual object (Maus & Nijhawan, 2006), in the present experiments there was no subthreshold stimulation that could explain the forward shift by lowered

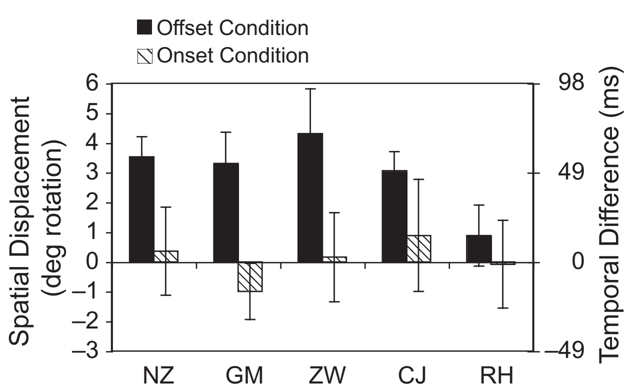

Fig. 3. Mean displacements of offset and onset positions from the blind-spot boundary within each of the 5 observers. Positive numbers denote forward displacements in the direction of motion. Values are given in both degrees of rotation and milliseconds (±1 *SEM*).

thresholds along the anticipated trajectory (Jancke, Erlhagen, Schoner, & Dinse, 2004). Furthermore, our findings cannot be explained by a temporal integration mechanism because there is no bottom-up input from within the blind spot. Likewise, the perceived position cannot be shifted forward by later motion signals acquired from after the object passed the blind-spot boundary (Eagleman & Sejnowski, 2007).

Could a filling-in process at the blind spot be involved in the visibility of the bar in unstimulated blind areas? Perceptual filling in occurs only if two opposite blind-spot edges are stimulated (Ramachandran, 1992; Walls, 1954). Using functional brain-imaging methods, it has recently been shown that early visual areas maintain a veridical retinotopic map in the vicinity of the blind spot, which is evidence against a passive spread of activity as the mechanism for filling in (Awater, Kerlin, Evans, & Tong, 2005). This result indicates that the integration of filled-in positions is not the cause of our findings.

The present findings show that the perceived position of moving objects is shifted forward based on information from the past trajectory. The visual system predicts the position of a moving object to overcome neural processing delays inherent in the visual pathway (Nijhawan, 1994, 2008). In the case of contradicting bottom-up input, for example, when an abrupt stimulus offset is registered by the retina, this prediction is corrected or masked from visibility, and the new bottom-up information is integrated with the percept (Maus & Nijhawan, in press; Nijhawan, 2002, 2008). When such a signal is absent, as in the case of motion terminating in the blind spot or gradually decreasing below stimulation threshold (Maus & Nijhawan, 2006), the extrapolated position is perceived as the final position of the motion trajectory. Similar results should hold for other acquired or natural scotomata, like the blue scotoma in the fovea (Magnussen, Spillmann, Sturzel, & Werner, 2004; Wilmer & Wright, 1945). In the more common case of binocular viewing, however, the transient would be registered in the opposite eye, and the final position of a moving object will be accurately localized.

To date, few studies involving motion across the blind spot have been reported. When a moving object deviates from a straight trajectory, the deviation can be grossly overestimated. This error is even larger when the direction change occurs in the blind spot (Tripathy & Barrett, 2006). In these experiments, the object motion was sufficiently fast to be perceived as continuous through the blind spot. Consistent with the results of the present study, motion was perceived to continue straight through the blind spot, and only afterwards perceived to change direction from its original trajectory. Another study showed that a singleton feature in a sequence of bars in apparent motion (e.g., a long bar among short bars) can be mislocalized in the direction of motion (Cai & Schlag, 2001). This forward mislocalization also occurs in the blind spot. When a single long bar among a sequence of short bars was presented just before the blind area, it was perceived to lie within the blind spot (Cai & Cavanagh, 2002). In this study, the motion continued after the blind spot, and the authors argued for path interpolation as a mechanism for creating the illusory percept. We claim that both of these findings (Cai & Cavanagh, 2002; Tripathy & Barrett, 2006) can be explained by a spatial extrapolation mechanism that relies on the past trajectory of a moving object to predict its current position.

REFERENCES

Awater, H., Kerlin, J.R., Evans, K.K., & Tong, F. (2005). Cortical representation of space around the blind spot. *Journal of Neurophysiology*, *94*, 3314–3324.

Brainard, D.H. (1997). The Psychophysics Toolbox. *Spatial Vision*, *10*, 433–436.

Brenner, E., van Beers, R.J., Rotman, G., & Smeets, J.B.J. (2006). The role of uncertainty in the systematic spatial mislocalization of moving objects. *Journal of Experimental Psychology: Human Perception and Performance*, *32*, 811–825.

Burr, D. (1980). Motion smear. *Nature*, *284*, 164–165.

Cai, R., & Schlag, J. (2001). A new form of illusory conjunction between color and shape. *Journal of Vision*, *1*(3), Abstract 127. Retrieved September 15, 2007, from http://journalofvision.org/1/3/127/

Cai, R.H., & Cavanagh, P. (2002). Motion interpolation of a unique feature into stimulus gaps and blind spots. *Journal of Vision*, *2*(7), Abstract 30. Retrieved September 15, 2007, from http://journalofvision.org/2/7/30/

Eagleman, D.M., & Sejnowski, T.J. (2000). Motion integration and postdiction in visual awareness. *Science*, *287*, 2036–2038.

Eagleman, D.M., & Sejnowski, T.J. (2007). Motion signals bias localization judgements: A unified explanation for the flash-lag, flash-drag, flash-jump, and Frohlich illusions. *Journal of Vision*, *7*, 3.

Fröhlich, F.W. (1923). Über die Messung der Empfindungszeit. *Zeitschrift für Sinnesphysiologie*, *54*, 58–78.

Incze, A. (1928). Über die richtige Bestimmung des blinden Flecks. *Archiv für Augenheilkunde*, *99*, 670–677.

Jancke, D., Erlhagen, W., Schoner, G., & Dinse, H. (2004). Shorter latencies for motion trajectories than for flashes in population responses of cat primary visual cortex. *Journal of Physiology*, *556*, 971–982.

Kerzel, D. (2000). Eye movements and visible persistence explain the mislocalization of the final position of a moving target. *Vision Research*, *40*, 3703–3715.

Kirschfeld, K., & Kammer, T. (1999). The Fröhlich effect: A consequence of the interaction of visual focal attention and metacontrast. *Vision Research*, *39*, 3702–3709.

Krekelberg, B., & Lappe, M. (2000). A model of the perceived relative positions of moving objects based upon a slow averaging process. *Vision Research*, *40*, 201–215.

Krekelberg, B., & Lappe, M. (2001). Neuronal latencies and the position of moving objects. *Trends in Neurosciences*, *24*, 335–339.

Magnussen, S., Spillmann, L., Sturzel, F., & Werner, J.S. (2004). Unveiling the foveal blue scotoma through an afterimage. *Vision Research*, *44*, 377–383.

Maus, G.W., & Nijhawan, R. (2006). Forward displacements of fading objects in motion: The role of transient signals in perceiving position. *Vision Research*, *46*, 4375–4381.

Maus, G.W., & Nijhawan, R. (in press). Going, going, gone: Localizing abrupt offsets of moving objects. *Journal of Experimental Psychology: Human Perception and Performance*.

Nijhawan, R. (1994). Motion extrapolation in catching. *Nature*, *370*, 256–257.

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

Nijhawan, R. (2008). Visual prediction: Psychophysics and neurophysiology of compensation for time delays. *Behavioural and Brain Sciences*, *31*, 179–198.

Pelli, D.G. (1997). The VideoToolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision*, *10*, 437–442.

Ramachandran, V.S. (1992). Blind spots. *Scientific American*, *266*, 44–49.

Roulston, B.W., Self, M.W., & Zeki, S. (2006). Perceptual compression of space through position integration. *Proceedings of the Royal Society B*, *273*, 2507–2512.

Schwartz, G., Taylor, S., Fisher, C., Harris, R., & Berry, M.J. (2007). Synchronized firing among retinal ganglion cells signals motion reversal. *Neuron*, *55*, 958.

Tripathy, S.P., & Barrett, B.T. (2006). Misperceptions of trajectories of dots moving through the blind spot. *Perception*, *35*, 137–142.

Walls, G.L. (1954). The filling-in process. *American Journal of Optometry & Archives of the American Academy of Optometry*, *31*, 329–341.

Whitney, D., & Murakami, I. (1998). Latency difference, not spatial extrapolation. *Nature Neuroscience*, *1*, 656–657.

Wilmer, E.N., & Wright, W.D. (1945). Colour sensitivity of the fovea centralis. *Nature*, *156*, 119–121.

(Received 3/20/08; Revision accepted 5/23/08)