

## Illusory speed is retained in memory during invisible motion

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**Abstract.** The brain can retain speed information in early visual short-term memory in an astonishingly precise manner. We investigated whether this (early) visual memory system is active during the extrapolation of occluded motion and whether it reflects speed misperception due to contrast and size. Experiments 1A and 2A showed that reducing target contrast or increasing its size led to an illusory speed underestimation. Experiments 1B, 2B, and 3 showed that this illusory phenomenon is reflected in the memory of speed during occluded motion, independent of the range of visible speeds, of the length of the visible trajectory or the invisible trajectory, and of the type of task. These results suggest that illusory speed is retained in memory during invisible motion.

**Keywords:** motion extrapolation, TTC, contrast, size, remembered speed.

### 1 Introduction

In the world we live in, where everything is in constant motion, we find that many objects continuously cross our visual field. At times, their trajectory becomes hidden for a brief period of time by other objects. In these circumstances, the ability to accurately judge the time of reappearance of the hidden object becomes very important. For example, to avoid an accident while driving, we have to judge, and we do it quite accurately, the time it takes for a motorbike to pass behind a still bus at a bus stop. This common skill (innate ability) brings up many interesting questions. How do we perform an estimate of occluded motion on the base of visible motion?

Previous studies have addressed this issue by using a prediction-of-motion paradigm, in which observers estimate the time to contact (TTC) using the speed information of the initiation of an object's trajectory (prior to occlusion), i.e., the time between the disappearance of a target's leading edge behind the occluder, and when it would make contact with a given point of interception. The difference between the "total response time" (total response time = TTC + duration of the visible trajectory) and the "physical arrival time" results in the "timing error."

Many studies have sought to determine which strategy is best used to estimate TTC. One idea is that people use a "cognitive clocking" strategy (DeLucia & Liddell, 1998). They compute time to contact prior to occlusion based on the rate of change in the visual angle between a moving target and its endpoint. This temporal representation can then be "counted down" during the occlusion period (Tresilian, 1995). The "cognitive clocking" model seems at odds with several findings. For example, it has been shown that moving distractors disrupt motion extrapolation performance (Lyon & Waag, 1995). Furthermore, induction of the motion aftereffect where invisible trajectory occurs systematically shifts response time (Gilden, Blake, & Hurst, 1995).

Recent studies have provided direct and indirect evidence that people use an alternative "tracking strategy" for motion extrapolation across the frontoparallel plane (de'Sperati & Deubel, 2006; Makin & Poliakoff, 2011; Makin, Poliakoff, Ackerley, & El-Deredy, 2012; Makin, Poliakoff, Chen, & Stewart, 2008). Jonikatis, Deubel, and de'Sperati (2009) claimed that observers follow the target with the spotlight of visuospatial attention while it is visible and perform a sequence of saccades that mirror the continuous extrapolated target movement. The "tracking strategy" (Makin & Poliakoff, 2011) involves using memory of the target velocity during visible motion and the shift of visuospatial attention controlled by the oculomotor system (Rizzolatti, Riggio, & Sheliga, 1994), irrespective of whether participants fixate (Huber & Krist, 2004; Peterken, Brown, & Bowman, 1991) or follow with

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a sequence of saccades (Jonikaitis, Deubel, & de'Sperati, 2009). This view is compatible with the pre-motor theory of attention, in which shifts of spatial attention are produced by sensorimotor networks that guide responses to external locations. Attention and motor planning are not distinct cognitive modules; we shift attention to a spatial location by planning an action aimed at that location, even if the planned action is never executed (Eimer, Van Velzen, Gherri, & Press, 2007). The tracking model predicts that during a visible trajectory, visual velocity signals attained by extra-retinal input are retained in short-term memory. If stored velocity information can be retrieved from short-term memory (Kaas, Weigelt, Roebroek, Kohler, & Muckli, 2010), it can remain active during occluded motion and direct overt (covert) visual attention.

In this study, we investigate how the memory of visible velocity accurately reflects the perception of speed during a visible trajectory (Kaas et al., 2010; Makin & Poliakoff). In most cases, the “timing error” of TTC is found to depend on speed (Lyon & Waag, 1995; Peterken et al., 1991; Sokolov, Ehrenstein, Pavlova, & Cavanaugh, 1997; Sokolov & Pavlova, 2003). Rosenbaum (1975) found that observers perform the task accurately at all speeds. However, several studies suggest that the relationship between visual speed and TTC is not linear. Lyon and Waag (1995) found that the lower the speed, the more difficult it is to detect when a target passes a given cue during the invisible motion. Bennett, Baures, Hecht, and Benguigui (2010) showed an overestimation of TTC during short periods of occlusion (less than 1 s) and an underestimation for long periods (greater than 1 s). Sokolov and Pavlova (2003) found that “timing error” depends on the interaction between the speed and visible trajectory.

In sum, depending on the visible velocity (either too low or too fast), on the time of occlusion, and on the length of the visible trajectory, the memory of speed during occluded motion may not always be isomorphic to the input received from the visible trajectory.

The most likely explanation is that the underlying neural mechanisms for coding velocity in part corresponds to those involved in memory of speed (Pasternak & Greenlee, 2005) and in part do not. There is evidence from both imaging (Jiang, Ding, Gold, & Powell, 2008; Lencer et al., 2004; Nagel et al., 2006; Shuwairi, Curtis, & Johnson, 2007) and primate neurophysiological data (Assad & Maunsell, 1931; Barborica & Ferrera, 2003; Ilg & Thier, 2003) of distinct regions of the cortex showing increased activity during periods of occlusion relative to full visibility. Indeed, the behavioral data associated with imaging show a difference in pursuit latency (Nagel et al., 2006) and response latency (Shuwairi et al., 2007) between occluded and un-occluded conditions. This supports the suggestion that visible and occluded motion evokes different speeds of processing.

However, psychophysical studies show that speed information is stored in an extremely precise manner in short-term memory. Speed discrimination thresholds are not impaired for the range of  $1 \pm 30$  s retention intervals (Greenlee, Lang, Mergner, & Seeger, 1995; Magnussen & Greenlee, 1992, 1999). Magnussen and Greenlee (1992) tested two velocities: 2.5 and 5 deg/s for a 2 c/deg drifting grating. Although discrimination thresholds increased at higher speeds, reference velocity did not interact with the retention interval: i.e. the Weber fraction was almost constant across retention intervals.

These results suggest that observers can use speed information stored in short-term memory precisely. Our study questions whether speed information, as modulated by target contrast and size, is stored in the early visual perceptual memory system and whether it remains active during occluded motion.

In this case, we predict that differences in perceived speed will be reflected during occluded motion, independent of the range of visible speed, of the length of the visible trajectory and occluder, and of the type of task. To our knowledge, only two studies provided indirect support for this prediction. Sokolov and Pavlova (2003) found that “timing error” depended on the interactions between speed and target size. Makin et al. (2008) showed that the current velocity of occluded motion was faster after a previous trial with a fast velocity and *vice versa*.

To establish whether perceived speed is stored in short-term memory during occluded motion, we explored whether subtle misperception of visible speed is maintained during occluded motion. We manipulated parameters that are known to produce an illusory perceived speed of a moving target. It is well known that perceived speed is affected by contrast (Thompson, 1982, 2003; Thompson, Brooks, & Hammett, 2006). Furthermore, it is well known that the perceived speed of an object is modulated by its size and by the width of the visible window where the object moves (Epstein, 1978).

We measured, as in previous works, the TTC to a visible cue (a bar). We did not compute a simple (absolute) “timing error” (Peterken et al., 1991), but rather analyzed the remembered speed: a ratio between the length of the invisible trajectory and the TTC measured only during invisible motion.

We believe that this ratio reflects a true pattern of underestimation and overestimation errors (Bennett et al., 2010; Makin et al., 2008; Sokolov & Pavlova, 2003).

## 2 Experiment 1A

We know from previous studies that high contrast stimuli appear to move faster than low-contrast stimuli (Gegenfurtner, Mayser, & Sharpe, 1999; Stone & Thompson, 1992; Thompson, 1982, 2003; Thompson et al., 2006). Thompson et al. (2006) found that underestimation of speed at low contrast occurred with grating targets of low (2 cpd) and high (8 cpd) spatial frequency. Experiment 1A was carried out to check whether the effect of contrast on perceived speed also occurred when using small circles in a continuous translational motion.

### 2.1 Method

#### 2.1.1 Participants

Six volunteers, 4 males and 2 females, aged between 23 and 25, all right handed, took part in this experiment. They all had normal or corrected-to-normal vision. We obtained informed consent from each subject at the beginning of each experiment.

#### 2.1.2 Stimuli and apparatus

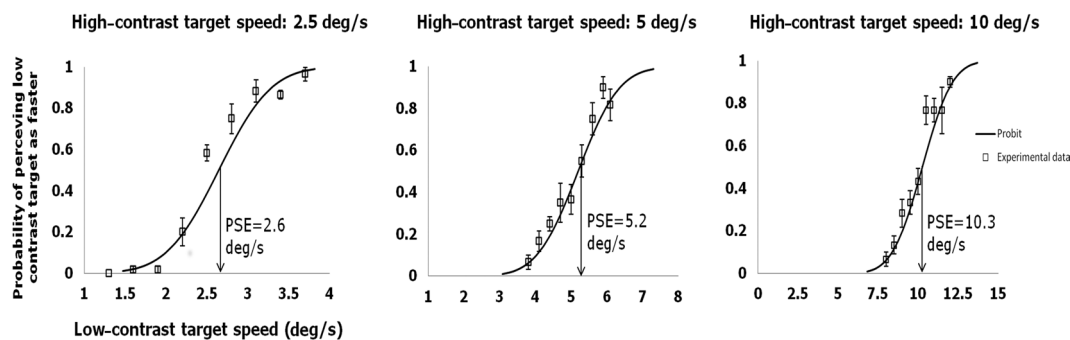
Participants sat in a dark room, 57 cm away from the display screen. Viewing was binocular. Stimuli were generated with Matlab Psychtoolbox (Brainard, 1997; Pelli, 1997) and displayed on a 19-inch CTX CRT Trinitron monitor with a refresh rate of 100 Hz. The screen resolution was 1,024 × 768 pixels. Each pixel subtended ~1.9 arcmin. The luminance of the background was 0.8 cd/m<sup>2</sup>. Stimuli were presented as small circles of 0.5 deg in diameter. The luminance of the standard stimulus (SS) was 144 cd/m<sup>2</sup> and that of the comparison stimulus (CS) was 1.1 cd/m<sup>2</sup>. Both were presented approximately at eye level. Luminance was measured using a Minolta LS-100 photometer. Each target appeared abruptly and traveled horizontally, either leftward or rightward, with equal probability. The motion trajectory was produced by presenting the target in a new position in each frame. The visible trajectory started 9 deg from the center and ended after 12 deg. The speed of high-contrast SS was fixed at 2.5, 5, or 10 deg/s; the speed of the low-contrast CS varied on nine levels: SS speed of 2.5 deg/s: 1.3, 1.6, 1.9, 2.2, 2.5, 2.8, 3.1, 3.4, 3.7 deg/s; SS speed of 5 deg/s: 3.8, 4.1, 4.4, 4.7, 5, 5.3, 5.6, 5.9, 6.1; SS speed of 10 deg/s: 8, 8.5, 9, 9.5, 10, 10.5, 11, 11.5, 12 deg/s. Stimulus duration depended on speed; it ranged from 3,243–9,230 ms, 1,967–3,157, and 1,200–1,500 ms in the low-, medium-, and high-speed conditions of the SS, respectively.

#### 2.1.3 Experimental procedure

The experiment consisted of three blocks, each devoted to one speed, preceded by 18 trials of practice (2 repetitions × 2 size × 9 speed levels). Each block consisted of a random presentation of 180 trials comprising 20 repetitions of the 9 speed levels. After 90 trials, a resting pause of 5 minutes was given. In each trial, SS and CS trajectories were randomly presented in sequence, interleaved by an interval of 500 ms. We used a 2IFC task in which the subject had to report whether the stimulus perceived was faster in the first or in the second presentation. All participants were instructed to track the moving targets and to press the appropriate key (counterbalanced between subjects) to indicate the interval with the faster target. The next trial started 1,000 ms after the subject pressed the appropriate button. No feedback was given.

## 2.2 Results

Psychometric functions (Figure 1) were fitted to the probabilities of perceiving the low-contrast target faster than the higher contrast one, as a function of the physical speed levels (Finney, 1971). We then conducted a two-tailed *t*-test to compare individual PSEs, i.e. the point of subjective equality to the point of physical equality of speed (PE). Results revealed that the PSEs were larger than PE at every speed of the SS: low ( $t_{(5)} = 2.76$ ;  $p = 0.04$ ;  $d = 1.15$ , power = 0.62); medium ( $t_{(5)} = 3.37$ ;  $p = 0.02$ ;  $d = 1.38$ , power = 0.77); and high ( $t_{(5)} = 3$ ;  $p = 0.03$ ;  $d = 1.22$ , power = 0.67). This indicates that when the circles moved at the same speed, the low-contrast ones were perceived as slower. Interestingly, the ratio between PSE and PE was constant at all speeds ( $1.04 \pm 0.01$ ), suggesting that the effect of contrast on perceived speed increased linearly with speed.



**Figure 1.** The probability of perceiving a low-contrast target faster than a high-contrast target. PSE, point of subjective equality, indicates the speed that low-contrast stimuli should have to be perceived as fast moving as the high-contrast stimuli.

### 3 Experiment 1B

Experiment 1A showed that the speed of the lowest contrast target was underestimated. The PSE–PE ratio was constant, indicating that the underestimation increased linearly with speed. Experiment 1B investigated whether the illusory speed was retained during occluded motion. If speed was retained, we predicted the low-contrast target to be “perceived” as moving slower behind the occluder with the result of an overestimation of TTC. Furthermore, we predicted a constant ratio between this stored signal and the one obtained at high contrast across visible speeds. This would be indicative of similarities between the perception of speed during visible motion and the memory of speed active during occluded motion.

#### 3.1 Method

##### 3.1.1 Participants

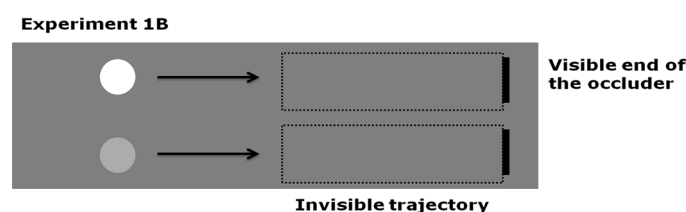
The same volunteers of Experiment 1A took part in this experiment.

##### 3.1.2 Stimuli and apparatus

The apparatus, shape, and contrast of the stimuli were the same as in Experiment 1A. The target appeared abruptly 7 deg to the left or to the right of the screen with equal probability, and the extent of the linear visible motion trajectory was always 12 deg. The speed of the stimulus was 2.5, 5, or 10 deg/s. The length of the invisible trajectory was either 4 or 12 deg. A cue, a gray bar (luminance 1.89 cd/m<sup>2</sup>, width 0.17 deg, height 1.7 deg) represented the end of the invisible trajectory (Figure 1). Stimulus duration varied from 1.6 and 9.6 s, depending on the speed and the length of the invisible trajectory.

##### 3.1.3 Experimental procedure

We used the psychophysical method of constant stimuli. The experiment consisted of six blocks, three with a low-contrast target and three with a high-contrast target. A block consisted of 120 trials randomly presented: 3 speed  $\times$  2 occluder lengths  $\times$  20 repetitions, preceded by 12 practice trials (2 repetitions  $\times$  3 speed levels  $\times$  2 occluder lengths). The observers were instructed to follow the target with their eyes until it reached the cue. They were also invited to “follow” the target with their eyes while it moved behind the occluder, and instructed to press the space bar when it reached the bar cue. The next trial started 1,000 ms after the key press. No feedback was given.



**Figure 2.** Diagrammatical representation of the events in a single trial for the high- and low-contrast conditions. The participant pressed a button at the time they thought the target should contact the visible cue (black line).

### 3.2 Results

From the  $TTC_{invisible}$  (i.e. the time of key press minus the time of target disappearance at the beginning of the invisible trajectory -  $TTC_{invisible}$ ) and the length of the invisible trajectory itself, we estimated the remembered speed:

$$\text{Remembered speed} = \text{length of the invisible trajectory} / TTC_{invisible}.$$

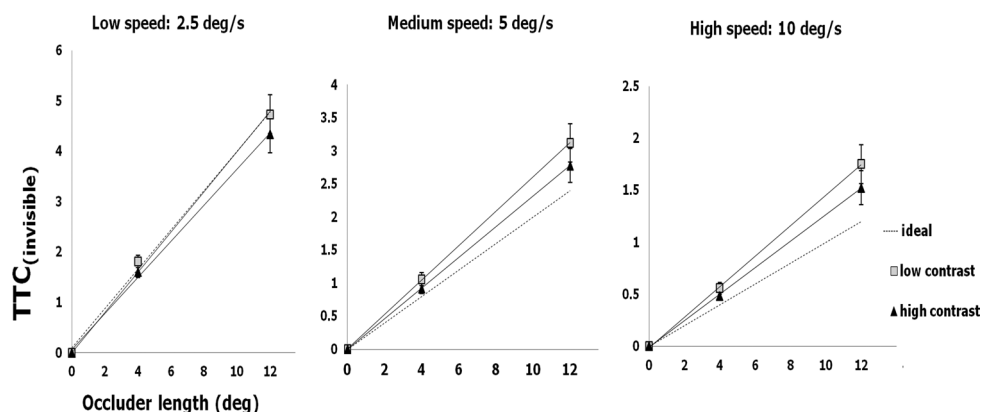
In [Figure 3](#), the oriented lines in a time–space plot reflect remembered speed (Adelson & Bergen, 1931). For each speed level, we compared remembered speed data with a two-way repeated-measures ANOVA having contrast (low vs. high) and invisible trajectory (short vs. long) as main factors. Results reveal an effect of contrast on TTC for the high ( $F_{(1,5)} = 28.02, p = 0.003$ ), medium ( $F_{(1,5)} = 27.27, p = 0.003$ ), and low speed of SS ( $F_{(1,5)} = 16.01, p = 0.01$ ). Neither the effect of the occluder length (high:  $F_{(1,5)} = 0.09, p = 0.78$ ; medium:  $F_{(1,5)} = 0.007, p = 0.94$ ; low:  $F_{(1,5)} = 4.13, p = 0.01$ ) nor the interaction contrast  $\times$  occluder length (high:  $F_{(1,5)} = 0.2, p = 0.67$ ; medium:  $F_{(1,5)} = 0.63, p = 0.46$ ; low:  $F_{(1,5)} = 1.13, p = 0.34$ ) was significant. These results indicate that target contrast modulates not only perceived speed but also remembered speed.

The ratio between the remembered speeds obtained in the high- and low-contrast conditions is constant at all speeds (low: 1.10, medium: 1.12, high: 1.12), suggesting that the effect of contrast on remembered speed increases linearly with speed. This suggests the involvement of a visual perceptual memory system that precisely retains the illusory speed during occluded motion. Interestingly, the remembered speed ratio is higher than the PSE–PE ratio obtained during visible trajectory (medium:  $t_{(5)} = 2.93, p = 0.03$ ; high:  $t_{(5)} = 3.89, p = 0.01$ ) in Experiment 1A, suggesting that an additional phenomenon may contribute to render the remembered speed illusory.

In addition, we conducted single-sample two-tailed  $t$ -tests to compare estimated TTC with actual values. The difference was significant only for the low-contrast target for both occluder lengths at the medium- (short:  $t_{(5)} = 2.65; p = 0.045, d = 1.08, \text{power} = 0.73$ ; long:  $t_{(5)} = 2.51; p = 0.05, d = 1.03, \text{power} = 0.69$ ) and high-speed conditions (short:  $t_{(5)} = 2.78; p = 0.04, d = 1.14, \text{power} = 0.77$ ; long:  $t_{(5)} = 2.96; p = 0.03, d = 1.59, \text{power} = 0.76$ ). These data indicate a true underestimation of the remembered speed with a low-contrast target.

### 4 Experiment 2A

Results of Experiment 1 show that remembered speed, which according to the “tracking model” is needed for judging TTC, retains the illusory effect of contrast on perceived speed. To further investigate whether the illusion of speed is retained in memory, we applied the “transposition principle” (Brown, 1931). According to this principle, the perceived speed of one object is modulated by its size and by the width of the visible window within which the object moves. The bigger the target size and the frame that delimits its motion, the slower is the perceived speed (Wallach, 1939). Other studies followed this seminal work (Epstein, 1978; Rock, Hill, & Fineman, 1968; Zohary & Sittig, 1993). Epstein & Cody (1980) pointed out that the crucial factor producing the illusion was the size of the target, whereas the presence of the frame was irrelevant.



**Figure 3.** The slopes of the oriented continuous lines on a time ( $TTC_{invisible}$ ) space (occluder length) plot reflect remembered speed in the low- and high-contrast conditions. The dotted line represents the ideal slope that would be obtained if remembered speed perfectly reflected physical speed.



In Experiment 2A, we varied the shape and size of the target, i.e. a flat and long rectangle versus a square 10 times taller, in order to allow targets of different sizes to reach the end of the invisible trajectory at the same time. To our knowledge, there are no studies that report the “transposition principle” when shape and size co-vary and it is worthwhile to inquire whether the transposition principle holds in these conditions. With size and shape co-varying in Experiment 2A, we evaluated the extent of the transposition principle during visible motion.

## 4.1 Method

### 4.1.1 Participants

A different group of nine participants, 2 males and 7 females, aged between 22 and 30, took part in this experiment. All participants had normal or corrected-to-normal vision.

### 4.1.2 Stimuli and apparatus

The apparatus was the same as in previous experiments. The SS (small shape) was a rectangle of 0.25 deg in height and 2.5 deg in width, and the CS was a square of 2.5 deg. Both were presented approximately at eye level, with a luminance of 144 cd/m<sup>2</sup> on a dark background (luminance 0.8 cd/m<sup>2</sup>). Each target appeared abruptly and traveled horizontally, either leftward or rightward. Frame rate and visible trajectory were as defined in Experiment 1A. The speed of the small SS was fixed at either 2.5 or 7.5 deg/s; the speed of the large CS varied according to nine levels: SS speed of 2.5 deg/s: 1.3, 1.6, 1.9, 2.2, 2.5, 2.8, 3.1, 3.4, 3.7; SS speed of 7.5 deg/s: 5.5, 6, 6.5, 7, 7.5, 8, 8.5, 9, 9.5. Stimulus duration ranged from 3,243 to 9,230 ms and 1,263 to 2,181 ms in the low- and high-speed conditions, respectively.

### 4.1.3 Experimental procedure

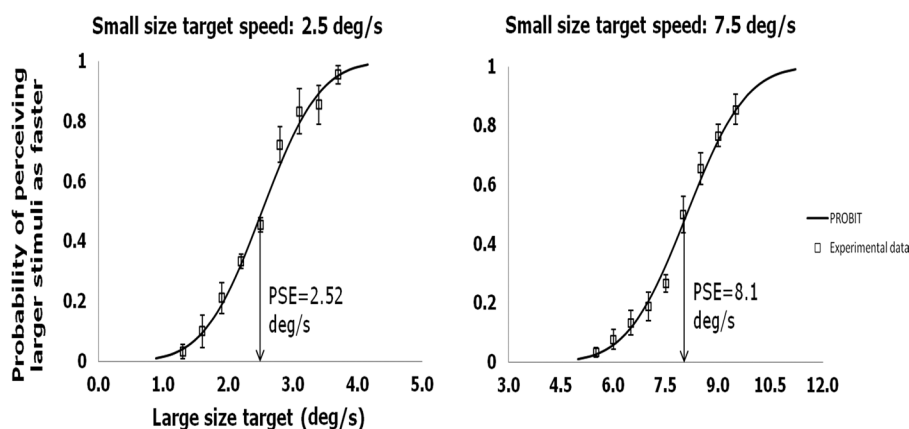
We used the same experimental procedure as in Experiment 1A.

## 4.2 Results

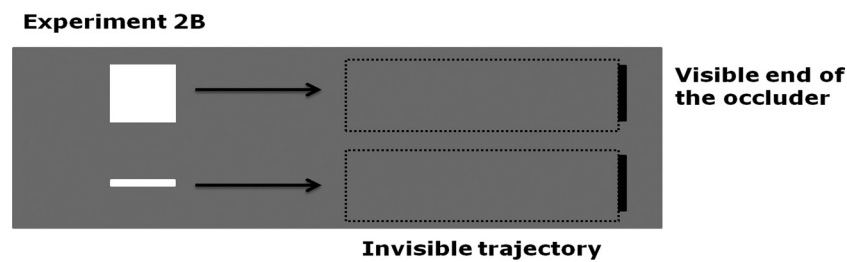
Psychometric functions (Figure 4) were fitted to the probabilities of perceiving the large shape as faster, as a function of the physical speed levels. We then conducted a two-tailed *t*-test to compare individual PSEs with PE. Results showed that the PSEs were larger than PE at high speed ( $t_{(8)} = 6.03$ ;  $p < 0.001$ ;  $d = 2$ , power = 0.93) but not at low speed ( $t_{(8)} = 0.28$ ;  $p = 0.79$ ;  $d = 0.09$ , power = 0.06). This indicates that at a speed of 7.5 deg/s, the larger shape was perceived as slower. Different from Experiment 1, a PSE–PE ratio larger than 1 was found only at the highest speed (1.08).

## 5 Experiment 2B

Experiment 2A shows that at faster and equal speeds, a larger target is perceived as slower than a target of smaller size. Experiment 2B investigated whether the illusory speed, as inferred from TTC, is retained during occluded motion. Both targets had the same width and speed, then reached the end of the occluder at the same time. However, we predicted the largest target to be “perceived” as moving



**Figure 4.** Probability of perceiving the large shape as faster than a small shape. The PSE indicates the speed that the large shape should have to be perceived as faster as the small shape.



**Figure 5.** Diagrammatical representation of the events in a single trial for the larger and smaller size conditions. The participant pressed a button at the time they thought that the target should contact the visible cue (black line).

slower behind the occluder, resulting in an overestimation of TTC. As in Experiment 2A, we predicted a remembered speed ratio  $> 1$  at highest speed. This would be indicative that a visual perceptual memory system is active during occluded motion, which precisely retains subjective visible speed.

## 5.1 Method

### 5.1.1 Participants

The same nine volunteers took part in this experiment.

### 5.1.2 Stimuli and apparatus

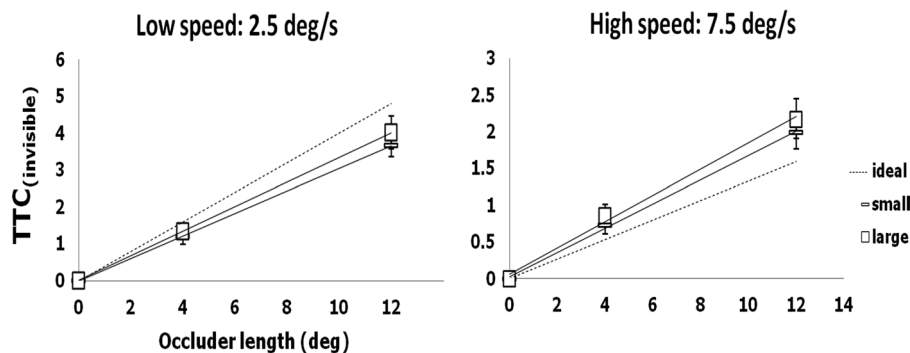
The apparatus, stimulus shapes, and luminance were identical as in the previous experiment (2A). The target appeared abruptly 7 deg to the left or to the right of the screen with equal probability, and the extent of the visible motion trajectory was always maintained at 12 deg (Figure 5). The speeds of the stimuli were either 2.5 or 7.5 deg/s. Stimulus duration was 1.6 or 4.8 s, depending on the speed and the length of the invisible trajectory: 4 or 12 deg.

### 5.1.3 Experimental procedure

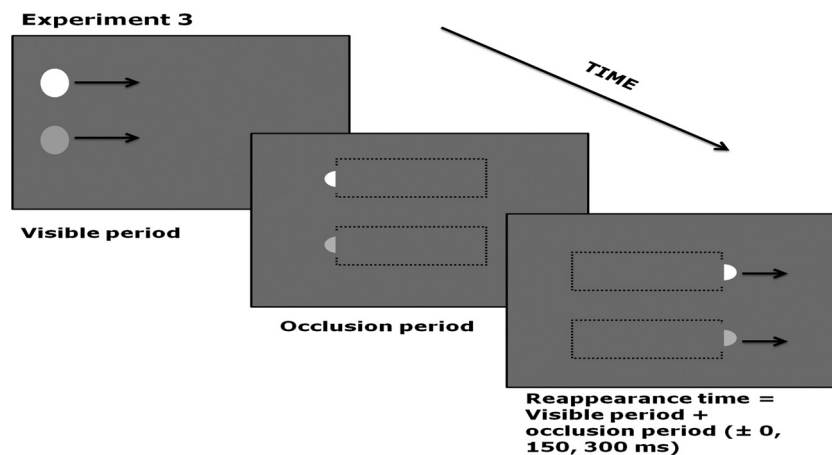
We used the psychophysical method of constant stimuli. This experiment consisted of one block of 160 trials randomly presented: 2 speed  $\times$  2 occluder lengths  $\times$  2 size of the target  $\times$  20 repetitions, preceded by 16 practice trials (2 size  $\times$  2 speed levels  $\times$  2 occluder lengths  $\times$  2 repetitions). After 80 trials, a 2-minute pause was given. The observers were instructed to follow the target with their eyes during its visible and invisible trajectory, and to press the space bar when it reached the bar cue. The succeeding trial started 1,000 ms after the subject pressed the appropriate button. No feedback was given.

## 5.2 Results

Remembered speed is represented on a time–space plot (Figure 6). Although size did not affect the PSE at low speed, results of this experiment revealed an effect of size on remembered speed for both low ( $F_{(1,8)} = 10.93$ ;  $p = 0.01$ ) and high speed ( $F_{(1,8)} = 18.14$ ,  $p = 0.003$ ) during occluded motion. Neither the effect of the occluder length ( $F_{(1,8)} = 1.29$ ,  $p = 0.29$ ;  $F_{(1,8)} = 1.99$ ,  $p = 0.19$  for low and high speed, respectively) nor that of the interaction size  $\times$  occluder was significant (low:  $F_{(1,8)} = 1.82$ ,



**Figure 6.** The slopes of the oriented continuous lines on a time (TTC<sub>invisible</sub>) space (occluder length) plot reflect remembered speed in the small and large size conditions. Dotted lines represent the ideal slope that would be obtained if remembered speed perfectly reflected physical speed.



**Figure 7.** Diagrammatical representation of the events in a single trial for the high- and low-contrast conditions. The target reappeared either at the correct time or with an error of  $\pm 150$  or  $300$  ms, assuming a constant velocity during occlusion. Participants discriminated between early and late reappearances.

$p = 0.21$ ; high:  $F_{(1,8)} = 1.61, p = 0.24$ ). This indicates that the subjective illusory speed during visible trajectory is retained during the occluded motion.

The one-sample  $t$ -test revealed that with a large target, the TTC is significantly greater than the actual one at high speed for both occluder lengths (short:  $t_{(8)} = 2.31, p = 0.05, d = 0.70, \text{power} = 0.59$ ; long:  $t_{(8)} = 2.74, p = 0.02, d = 0.80, \text{power} = 0.72$ ).

At high speed, where the transposition principle works, the remembered speed ratio (1.12) does not significantly differ from the PSE–PE ratio (1.08) obtained during visible trajectory ( $t_{(8)} = 1.61, p = 0.15$ ).

## 6 Experiment 3

Our data show an underestimation of remembered speed for the low contrast (Experiment 2A) and for the large targets (Experiment 2B), indicating that remembered speed is involved during occluded motion and reflects the perception of visible speed. It is possible that changing contrast and size/shape influences subjective perception of speed during the initial visible part of the presentation, which combined with amplitude of the visible and occluded part of the trajectory could then influence the estimation of TTC prior to target occlusion, and then countdown to contact without any need to memorize speed during occlusion. To check this possibility, we ran a third experiment in which the occlusion duration and the position of reappearance were always unpredictable, preventing any *a priori* knowledge of when or where reappearance would occur (DeLucia & Liddell, 1998; Makin & Poliakoff, 2011; Makin et al., 2008). A persistence of an effect of contrast with this paradigm would favor the hypothesis that subjects can precisely use speed information stored in short-term memory during the extrapolation of occluded motion.

### 6.1 Method

#### 6.1.1 Participants

Six volunteers, 3 males and 3 females, aged between 23 and 28, all right handed, took part in this experiment. They all had normal or corrected-to-normal vision. We obtained informed consent from each subject at the beginning of each experiment.

#### 6.1.2 Stimuli and apparatus

The apparatus was the same as in Experiment 1A. The stimuli, luminance, and diameter were the same as in Experiment 1A. The length of the invisible trajectory was 4, 8, or 12 deg. The velocity of the stimuli was always 7.5 deg/s. The visible trajectory (12 deg) started 11 deg from the center. Without altering the length of the invisible trajectory, a reappearance error of  $\pm 0, 150$ , and  $300$  ms was added (Figure 7). After the reappearance, the target ran 6 deg and then disappeared. At 300 ms after target offset, a 300-Hz pure tone alerted observers to press the response button.



### 6.1.3 Procedure

We used the psychophysical method of constant stimuli. The experiment consisted of 300 trials randomly presented: 2 contrast  $\times$  3 occluder lengths  $\times$  5 levels of reappearance errors  $\times$  10 repetitions, preceded by 30 practice trials (2 contrast  $\times$  3 occluder lengths  $\times$  5 levels of reappearance error  $\times$  1 repetition). After 180 trials, a 2-minute pause was given. The observers were instructed to press an appropriate button to indicate whether the target reappeared earlier or later, even when the target reappeared in time. Eye movements were allowed. The next trial started 500 ms after the subject pressed the appropriate button. No feedback was given.

## 6.2 Results

We conducted a  $2 \times 3 \times 5$  repeated-measures ANOVA with contrast (low vs. high), occluder length (short, medium, and long), and reappearance errors ( $-300, -150, 0, 150, 300$  ms) as main factors. Results (Figure 8) revealed a significant main effect of the contrast ( $F_{(5)} = 16.87, p = 0.009$ ) and reappearance errors ( $F_{(5)} = 9.96, p = 0.003$ ), indicating higher accuracy with low-contrast targets.

This effect confirms (Magnussen & Greenlee, 1992) that remembered speed follows Weber's law. Indeed, if remembered speed at low contrast is underestimated, this would explain why subjects are more accurate in discriminating very small reappearance errors in the low-contrast condition.

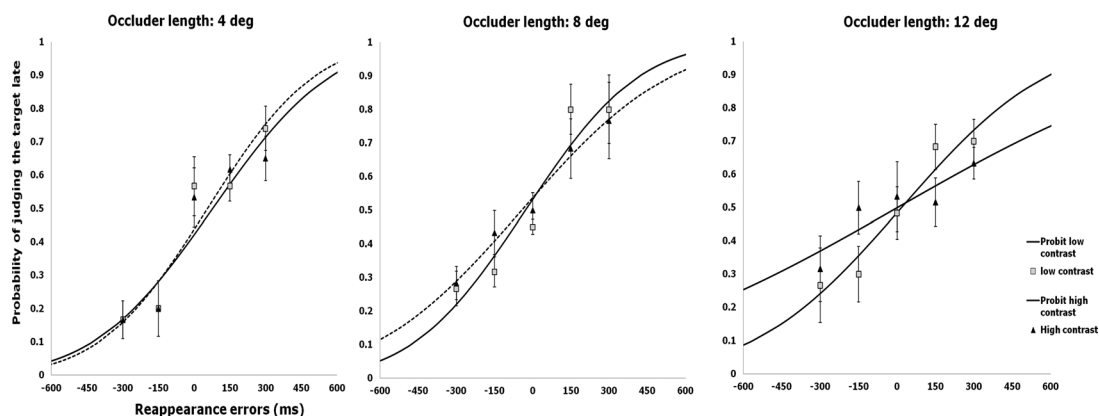
## 7 Discussion

In agreement with the literature, Experiments 1A and 2A show that speed is underestimated when the size of the target is increased or when its contrast is lowered. We did not replicate the finding (Thompson et al., 2006) that the effect of contrast inverts when the target speed is larger than either 4 deg/s (with 2-cpd target) or 2 deg/s (with a 8-cpd target). Alternatively, we found a linear relationship between the effect of contrast and speed. This may be due to the different stimulus analyzers involved: high-level shape analyzers in our stimulus conditions versus low-level spatiotemporal tuned filters in the conditions of Thompson et al. (2006). In Experiment 2A, we found an effect of large target size despite the absence of the reference frame. However, it is smaller (8%) with respect to that reported in previous studies. Epstein (1978) reported an increment of 45% in perceived velocity when the size was halved. The absence of the reference frame could explain the difference. However, Epstein and Cody (1980) showed that the frame of reference is not necessary. Compared with previous studies, we used a fixed trajectory length. This factor, together with the different shapes used (the smaller size target was a rectangle and the larger one a square), could explain the smaller illusion.

Most importantly, Experiments 1B, 2B, and 3 showed that the misperception of speed due to either contrast or size influenced remembered speed, as inferred from TTC during occluded motion.

Interestingly, results of Experiment 2B are in line with previous findings (Sokolov & Pavlova, 2003; Sokolov et al., 1997), but not with studies made in a more ecological environment (Horswill, Helman, Ardiles, & Wann, 2005).

In Experiment 3, by using a paradigm that prevents or at least discourages counting (DeLucia & Liddell, 1998; Makin & Poliakoff, 2011; Makin et al., 2008), we confirmed that contrast affects remembered speed. Results suggest that remembered speed follows Weber's Law: given that remembered



**Figure 8.** Psychometric functions of probability of judging the target late on reappearance error, for the low- and high-contrast conditions.

speed<sub>(low contrast)</sub> < remembered speed<sub>(high contrast)</sub>, a smaller  $\Delta$  remembered speed needs to be added (or subtracted) to discriminate it. Indeed, as [Figure 8](#) shows, the effect of the contrast seems greater with the longer occluder length. This may account for higher accuracy in discriminating very small reappearance errors with a low-contrast target.

The results provide support for the involvement of an early visual perceptual memory system during occluded motion. We believe that the modulation of remembered speed by contrast and size is an effect that cannot be assimilated to any of the speed effects previously described. Apart from other studies that find a dependency of TTC on the length of the occluder (Bennett et al., [2010](#); Sokolov & Pavlova, [2003](#)), we found no effect of occluder length on remembered speed, neither in Experiment 1B nor in Experiment 2B. In other words, given a fixed visible speed, the remembered speed gathered from TTC is similar, regardless of occluder length. We believe that these results are reliable because they are free from bias. Instead, previous studies used the “timing error” which is not a bias-free parameter: since speed is space over time, the same variation in remembered speed leads to a smaller “timing error” at high speed. Thus, the lower error at high speed previously found (Peterken et al., [1991](#); Sokolov & Pavlova, [2003](#)) could only be an artifact. Second, the illusory remembered speed cannot be confounded with the effect of speed on TTC (Bennett et al., [2010](#); Lyon & Waag, [1995](#); Peterken et al., [1991](#); Sokolov & Pavlova, [2003](#)). [Figures 3](#) and [6](#) disentangle these two effects. They show, as expected, that remembered speed is underestimated in both experiments at high speed, whereas at low speed, remembered speed either reflects perceived speed in a precise manner (Experiment 1B) or is overestimated (Experiment 2B). Yet, we found that the remembered speed ratio is isomorphic with the PSE–PE ratio. In Experiment 1, the two ratios are constant across speeds. In Experiment 2, the illusion is present in both perceived and remembered speeds only at high speed. Third, the illusory remembered speed cannot result from an interaction between speed and visible trajectory (Sokolov & Pavlova, [2003](#)) since the visible trajectory is fixed in all conditions.

One apparent contradiction in the results of Experiment 1 is that the value of remembered speed ratio (~1.12, Experiment 1B) is larger than that of the PSE–PE ratio (~1.04, Experiment 1A). One possible explanation is that size constancy by depth cues fails during occlusion (Dresp, Durand, & Grossberg, [2002](#); Gregory, [1963](#); Ward, Porac, Coren, & Girgus, [1977](#)). Therefore, observers judge the target as smaller than it is, and according to Thompson et al. ([2006](#)), this gives rise to a larger effect of contrast.

Consolidating our results demonstrates that visible illusory speed affects either the absolute judgment (Experiments 2A and 2B) or the discrimination (Experiment 3) of remembered speed. This suggests the involvement of an early visual memory system by either a mental imagery or a higher level velocity representation (more likely during pursuit) that retains the sensory characteristics of visible speed. Based on these findings, we are tempted to speculate that remembered speed may share processing with visual memory processes occurring at low cortical levels (Huber & Krist, [2004](#); Jonikaitis et al., [2009](#)). Indeed, Makin et al. ([2009](#)) showed a positive event-related component over occipitoparietal areas both with visible and invisible moving targets, although in the occluded condition the peak occurs 200 ms after the onset of occlusion and is not related to a target velocity. Kaas et al. ([2010](#)) showed that imagery of a motion trajectory produced a bold signal in MT/V5+.

In conclusion, our results agree that TTC estimation during occluded motion is mediated by memory and suggest that an early visual perceptual memory system closely linked to mechanisms of visual discrimination is involved (Huber & Krist, [2004](#); Jonikaitis et al., [2009](#)). This memory may share the properties of either visual imagery or mental representation and produce an internal simulation of the continuous motion of the invisible target.

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