Where is the moving object now? Judgments of instantaneous position show poor temporal precision (*SD* = 70 ms)

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Humans can precisely judge relative location between two objects moving with the same speed and direction, as numerous studies have shown. However, the precision for localizing a single moving object relative to stationary references remains a neglected topic. Here, subjects reported the perceived location of a moving object at the time of a cue. The variability of the reported positions increased steeply with the speed of the object, such that the distribution of responses corresponds to the distance that the object traveled in 70 ms. This surprisingly large temporal imprecision depends little on the characteristics of the trajectory of the moving object or of the cue that indicates when to judge the position. We propose that the imprecision reflects a difficulty in identifying which position of the moving object occurs at the same time as the cue. This high-level process may involve the same low temporal resolution binding mechanism that, in other situations, pairs simultaneous features such as color and motion.

Keywords: attention, temporal vision, motion-2D, visual acuity

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Introduction

A basic function of the visual system is to localize objects in the environment. Previous research has shown that humans can be very precise in some localization tasks. For example, in Vernier tasks, a spatial offset of only a few seconds of arc is needed to detect the misalignment of two nearby objects whether they are stationary (Westheimer, 1975) or moving slowly with the same speed and direction (Westheimer & McKee, 1975). In some circumstances the spatial offset threshold increases with speed: when the speeds are high (Levi, 1996), when the objects move together in rotation (Carney, Silverstein, & Klein, 1995) or in an oblique direction (Westheimer & McKee, 1975), and when the objects are not very near each other (Bedell, Chung, & Patel, 2000; Carney et al., 1995). However, even in these situations the effect of speed on threshold is small, corresponding to the distance traveled by the objects in just a few milliseconds (Bedell et al., 2000; Carney et al., 1995; Chung, Levi, & Bedell, 1996; Levi, 1996). The high precision in these Vernier configurations may reflect access to neurons with high temporal resolution located early in the visual system (Levi, 1996). These neuron responses may signal orientation or form cues that remain stable over time due to the constant spatial offset (Klein & Levi, 1985; Wilson, 1986). This would allow later stages to represent relative location even if they do not have enough temporal resolution to follow the rapid change in position.

To act on a moving object, however, we may need to know its position relative to stationary references or to ourselves, rather than relative to another object moving with the same speed and direction. It is unknown, however, how precisely humans can judge the instantaneous position of a single moving object.

We speculated that judging the position of a moving object at a specific time would not benefit from the high temporal resolution mechanisms available for constantoffset Vernier configurations. Instead, it might suffer from the poor temporal precision that limits instantaneous pairing of some features. For example, if an object periodically alternates between two colors (red and green) and also between two directions of motion (left and right), humans cannot determine which features are present at the same time when the rate of changes is higher than 5 to 6 per second (Arnold, 2005; see also Holcombe, 2009). Nonetheless, observers report clear percepts of the individual colors and directions of motion. Similar limitations occur when binding the features of two spatially separated objects (Holcombe & Cavanagh, 2001) or pairing audiovisual signals (Fujisaki & Nishida, 2005). These tasks show that humans have difficulties

determining which values of two distinct feature dimensions are simultaneously present. A similar limitation might occur when determining the simultaneity between the position of a moving object and a change in another feature dimension (e.g., color) of another stimulus.

We elicited judgments of instantaneous position by asking subjects to report the position of a moving object at the time of a cue. We discovered that variability in positional errors across trials reflects a large (\sim 70 ms) amount of temporal variability. This is consistent with the involvement of a highlevel feature-binding process (Holcombe, 2009).

Methods

Subjects and apparatus

Two authors and two subjects naive to the purpose of the experiments participated. All had normal or correctedto-normal vision. In Experiment 4, the stimuli were displayed on a Diamond Pro 2070SB monitor at a refresh rate of 160 Hz. For the remaining experiments, stimuli were displayed on a ViewSonic G810 monitor at a refresh rate of 120 Hz. They were generated using the PsychoPy (Peirce, 2007) and VisionEgg (Straw, 2008) libraries for Python and viewed from a distance of 57 cm in a dimly lit room. The graphs in this manuscript were generated using the package ggplot2 (Wickham, 2009) for R (R Development Core 275 Team, 2008; Rao Jammalamadaka & Sengupta, 2001).

Stimuli

The basic stimulus consisted of a Gaussian blob (*SD*: 0.25° , peak luminance: 108 cd/m^2) moving at different speeds on different trials and displayed against a uniform background (luminance: 31 cd/m^2). A small white fixation circle (radius: 0.4° , luminance: 108 cd/m^2) at the center of the screen was also present. In Experiments 5 and 7, the fixation circle was near the bottom edge of the screen (horizontally centered). Subjects were told to fixate it throughout all the experiments.

Experiment 1: Color-change cue

A blob moved about the fixation point following a circular trajectory (radius: 2°). Its initial location on this trajectory was random. At a random time between 2 and 3 s from the start, the fixation mark changed color from white to red (*x*: 0.637, *y*: 0.313, luminance: 22 cd/m²) and remained red until the end of the trial. The blob continued moving for another 0.5 to 1 s (randomly varied) before disappearing. For the response phase, the blob reappeared at a random location along the circular trajectory and subjects reported the perceived position of the blob at the

time of the color change by using a mouse to move the blob about the trajectory. After they confirmed the position by pressing a mouse button, the next trial started. Five different speeds were used: 6.3, 12.6, 18.8, 25.1, and 31.4° /s (degrees of visual angle per second), which correspond to 0.5, 1, 1.5, 2, and 2.5 revolutions per second (rps). The speed and direction (clockwise or counterclockwise) were chosen randomly on each trial. For each speed, 50 measures of perceived position were collected for each subject. Subject ML was not tested in

Experiment 2: Sound cue

the fastest speed.

This experiment was identical to Experiment 1 except that a sound, instead of a color change, was used to cue the time at which the subjects had to judge the position of the blob. The sound was a 10-ms burst of white noise played through headphones (70 dB SPL). Timing of the auditory signal was confirmed using an oscilloscope ($SD \sim 3$ ms). For each speed, 50 measures of perceived position were collected for subjects DL, AH, and ML and 30 for SM.

Experiment 3: Predictable cue

Rather than reporting position at the time of a color change, subjects judged the position of the blob when a circle moving horizontally across the screen passed just above the fixation marker. At the moment of alignment, the gap between the moving circle and the fixation marker was 0.5° . The circle continued moving after reaching the fixation marker. The size and luminance of the moving circle were identical to that of the fixation point. The circle always began at the left edge of the screen at a random eccentricity between 12 and 18° and moved rightward at 6°/s. For each speed, 50 measures of perceived position were collected for each subject.

Experiment 4: Testing different eccentricities

This experiment was identical to Experiment 2, but 4 different radii $(2, 4, 6 \text{ and } 8^\circ)$ were used for the blob's circular trajectory, one of which was chosen randomly on each trial. Angular speeds ranged from 0.25 to 3.5 rps, which corresponds to linear speeds that depend on the radius, yielding a total range of 3.1 to 176.0°/s. For each radius and speed, 16 measures of perceived position were collected for DL and AH and 8 measures for ML.

Experiment 5: Linear trajectories

This experiment was similar to Experiment 1, but the blob moved horizontally from left to right or vice versa,

always in the upper visual field. The same 5 speeds as for the circular trajectories, ranging from 6.3 to 31.4°/s, were used. The trajectory was centered on the vertical midline. The blob reached the midline 1.55 s after the start of the trial and disappeared 1.55 s later for all speeds. The limited width of the screen (40 deg) cut off the beginning and ending portions of the trajectory for the three fastest speeds. The vertical distance from fixation to the trajectory also varied across trials, taking a random value of 2, 4, 8, or 16°. At a random time between 1.3 to 1.8 s from the start of the trial, the fixation mark changed color. After the blob completed the trajectory, it reappeared directly above fixation at the same vertical distance and subjects indicated the perceived position of the blob at the time of the color change by moving it horizontally along the trajectory with the mouse. For each vertical distance and speed, 46 measures were collected for DL and 40 for AH.

Experiment 6: Testing different contrasts

This experiment was identical to Experiment 2, but the blob's Michelson contrast was one of 3 values (0.05, 0.18, and 0.54) chosen randomly on each trial. For each contrast and speed, 20 measures of perceived position were collected.

Experiment 7: Judgments of constant offset

Here we used linear trajectories, as in Experiment 5, but with two blobs moving horizontally with the same speed and direction above fixation. The vertical distance between the lower blob and fixation was 2°. The vertical distance between the blobs was varied randomly across trials $(2, 4, 8, \text{ or } 16^{\circ})$. The blobs were displayed for a random duration between 2.5 and 3.5 s (for the fastest speeds, though, the sides of the screen truncated the beginning and ending of the trajectory as in Experiment 6). The contrast of the blobs was ramped up over a 500-ms period from zero to full contrast at the beginning of the trial and ramped back down to zero at the end of the trial. The horizontal spatial offset between the blobs necessary to perceive the misalignment was measured using the method of constant stimuli with seven horizontal offsets, with the maximum tested offset being the distance traveled by the object in 19 ms in the case of the 2° of vertical separation, and 144 ms in the case of the 16° of vertical separation. After the blobs disappeared, subjects reported whether the upper blob was leading or trailing the lower blob. For each vertical separation, speed, and horizontal offset, eight responses were collected.

Experiment 8: Salient, nearby cue

This experiment was identical to Experiment 1 except for the cue that determined the time at which subjects made the position judgment. Instead of a color change, two concentric rings (thickness of each: 0.25°) centered on the fixation marker and surrounding the blob's trajectory suddenly appeared. The edge closest to fixation of the inner ring was 1° eccentric, that of the outer ring was 2.75° eccentric. They remained present until the moment of the response. For each speed, 40 measures of perceived position were collected for each subject.

Experiment 9: Sensorimotor synchronization

This experiment was similar to Experiment 1, but in addition to the moving blob, a stationary bar (size: $1.4^{\circ} \times$ 0.6° , luminance: 108 cd/m²) oriented toward the fixation point and positioned more peripherally than the blob was continuously displayed. The eccentricity of the bar was the same on each trial but its angular position was chosen randomly. When the blob was aligned with the bar, the distance from the closest edge of the bar to the center of the blob was 0.8°. Subjects were asked to press a button at the moment the moving blob became aligned with the stationary bar. No feedback was provided. Subjects were instructed to not press the button the first time the blob reached the bar nor to allow more than 4.5 s to elapse before their response. Subjects practiced for a few minutes to become familiar with this criterion. For each speed, 82 measures of button-press position were collected for subjects DL and AH and 50 measures for subjects ML and SM. Subject ML was not tested in the fastest speed.

Analysis of circular data

The reported positions were coded as angles between -180° and 180° where 0° indicates that the reported position coincided with the position of the blob at the time signaled by the cue (or the position of alignment in the sensorimotor synchronization experiment, Experiment 9) and positive values indicate biases in the direction of motion (or late button presses in Experiment 9). Because -180° and 180° correspond to the same position, we analyzed the data using circular statistics. For each subject and speed, a von Mises distribution was fitted to the distribution of angles:

$$\frac{e^{\kappa\cos(x-\mu)}}{2\pi I_0},\tag{1}$$

where μ is the mean direction, κ is the concentration parameter (inverse of variability), and I_0 is the Bessel function of order 0. We obtained the 95% confidence intervals (CI) for μ and κ by bootstrapping using the "CircStats" (v. 0.2-3) package for R (R Development Core Team, 2008; Rao Jammalamadaka & Sengupta, 2001). The biases in localization (mean of reported positions) indicated in the figures correspond to the multiplication of μ and its CI by the radius in degrees of visual angle. For variability, rather than reporting κ in our results and figures we obtained the more familiar standard deviation measure by simulating Gaussian distributions with different standard deviations, wrapping them (for example, a 200° angle was recoded as -160° for example) and calculating κ for each one. The standard deviation and its CI that we report correspond to the values of the distributions that best matched the calculated values for κ and its CI.

Data analysis for linear trajectories

We calculated the mean and the standard deviation of the reported positions. To obtain the 95% CIs, we took the 2.5 and 97.5 percentiles of the distribution of standard deviations of 500 bootstrap samples.

Data analysis for the judgments of constant offset experiment

For each subject, speed, and vertical separation, we fitted cumulative Gaussians to the proportion of trials in which the upper blob was perceived ahead of the lower blob as a function of the horizontal spatial offset. As a measure of variability we report the standard deviation of the underlying Gaussian distribution. The 95% CI was obtained from the 2.5 and 97.5 percentiles of the distribution of standard deviations of 500 bootstrap samples.

Pairwise comparisons between conditions

To compare the spatial and temporal variability parameters of the variability model (see Equation 2 in the Results section) between two conditions we generated 500 bootstrapped samples for each condition by sampling from the data with replacement. For each pair of bootstrapped samples, we calculated the difference between parameters. The 95% CIs were taken from the corresponding 2.5 and 97.5 percentiles of the upper and lower limits of the distribution of differences. A parameter was considered to be different for two conditions if the CI did not include zero.

Results

Poor temporal precision independent of the cue signaling the position judgment

Subjects viewed a blob orbiting in a circular trajectory about a fixation point (Experiment 1, details given above,

Figure 1A; demo at http://www.dlinares.org/Site/imprecision. html). At a random time, the fixation mark changed color from white to red and at the end of the trial subjects reported the perceived location of the blob at the time of the color change. To characterize precision, we plot variability-the standard deviation of the reported positions in degrees of visual angle (see Methods section)-against blob speed (Figure 1A). The error bars indicate the 95% confidence intervals (CIs). Variability increases approximately linearly with speed. The rate of change of the variability in degrees as a function of speed in degrees per second provides an estimate of the variability in time units. As detailed below, the temporal variability for most subjects is not far from 70 ms, meaning that the standard deviation of position reports for each speed corresponds to the distance the object travels in 70 ms.

Apart from temporal variability, any realistic model of precision in position reports should also include a spatial variability parameter, as the visual system does not have perfect precision even when localizing stationary objects. Hence, we modeled total variability (standard deviation) as

$$\sqrt{\sigma_x^2 + (speed \cdot \sigma_t)^2},\tag{2}$$

where σ_x is the spatial variability and σ_t is the temporal variability. The best fit and the 95% CI (gray shadows, calculated by bootstrapping) are plotted in Figure 1A (the fastest speed was not included in the fit; see the end of this section). The estimates of spatial variability (σ_x) in degrees of visual angle and temporal variability (σ_t) in milliseconds are indicated inset in each panel. Spatial variability was very small (mean across subjects: 0.14°; mean CI across subjects: 0-0.41°) indicating that the main source of variability was temporal. The quality of the fits was excellent (mean r^2 across subjects: 0.94). The mean temporal variability across subjects was 75 ms (mean CI across subjects: 60-86 ms), which is more than ten times worse than the precision for judgments of relative location (Bedell et al., 2000; Carney et al., 1995; Chung et al., 1996; Levi, 1996). Neglecting the small spatial variability involved, the 75 ms figure means that one standard deviation of the distribution of the positions reported across trials occupies a 75-ms swath of the blob's trajectory.

When a sound instead of a color change signaled the position judgment (Experiment 2, Figure 1B), we found similar temporal variability (mean: 71 ms; CI: 56–82 ms). Only one subject (AH) showed a significant precision improvement from Experiment 1 (95% CI). As auditory temporal resolution exceeds visual temporal resolution in some tasks (Recanzone, 2003), the lack of a reduction in temporal variability suggests that any imprecision in the perception of the cue is not the main source of variability in the position judgment.

To investigate whether the unpredictable onset time of the cue was contributing to the measured variability, in

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Figure 1. Standard deviation of reported positions as a function of the speed for (A) Experiment 1, (B) Experiment 2, and (C) Experiment 3. Points for which the distribution of positions was not significantly different from a uniform distribution are plotted in gray. The standard deviation for the fastest speed is not included in the curve fit (see the Results section). The error bars indicate the 95% CI. Numbers inset at top left are the spatial and temporal variability parameters of the fitted model (Equation 2), respectively. The gray shading shows the 95% CI for the fit.

Experiment 3 we used a predictable cue (Figure 1C). The cue was a small circle moving from left to right across the screen, passing just above the fixation mark. The task was to report the position of the blob moving in the circular trajectory at the time that the circle was directly above fixation. Again, imprecision corresponded to high temporal variability (mean: 81 ms; CI: 65–95 ms). For all subjects, it was not significantly different from the temporal variability found in Experiments 1 and 2 (95% CI). The temporal imprecision is apparently not caused by the unpredictability of the cue signaling the position judgment.

Interestingly, this large temporal imprecision predicts that when the blob is orbiting fast enough, reported positions should be so spread around the circle that the histogram of positions should be indistinguishable from a uniform distribution. Indeed, according to a Rayleigh test (p < 0.05), for some subjects the distribution of positions for the fastest speed (31.4°/s, 2.5 rps) was not significantly different from uniform (gray points in Figure 1). In contrast, the slower speeds produced differences from the uniform distribution that were highly significant. Therefore, because data from 2.5 rps were largely noise, we excluded them and all data from higher angular speeds when estimating variability parameters in all experiments.

For 2.5 rps, not only were position reports near chance, but also some participants reported that they were not able to access the instantaneous position of the blob but nonetheless, they had a clear percept of the blob and its direction. Indeed, with a similar stimulus Verstraten, Cavanagh, and Labianca (2000) reported that subjects could discriminate clockwise from counterclockwise motion at speeds up to 25 rps, which is about ten times larger than our fastest speeds. The reader can experience the difficulty in the position judgment, which is the main point of this paper, in the following demonstration: http://www.dlinares.org/Site/imprecision.html.

Biases in reported positions relative to the motion direction

Figure 2 shows the bias or mean position of each subject's responses for each of Experiments 1, 2, and 3.



Figure 2. Mean positions as a function of speed for (A) Experiment 1, (B) Experiment 2, and (C) Experiment 3. Points for which the distribution of positions was not significantly different from a uniform distribution are plotted in gray. The mean position for the fastest speed is not included in the curve fit (see the Results section). The error bars indicate the 95% CI. Numbers inset at top left indicate the intercept and slope of the linear fit. The gray shading shows the 95% CI for the fit.

Positive values indicate mislocalization in the direction of motion. To summarize the data, we fit lines to the effect of speed on mean position (excluding the fastest speed because sometimes those data were not distinguishable from a uniform distribution, see above). The gray shadows show the 95% CI based on *t*-statistics. The intercept in degrees of visual angle and the slope in milliseconds are indicated in the top left corner of each graph. For the color-change cue experiment, all subjects except SM mislocalized the blob in the direction of motion (Figure 2A), consistent with the flash-lag illusion (Nijhawan, 1994). For most speeds in the two other experiments, participants either had no biases or localized the blob in the opposite direction of motion. The dependence of the bias on the type of cue, although not emphasized in the literature, is consistent with previous findings. For example, with an auditory cue signaling the position judgment, localization opposite to the direction of motion (flash-lead effect) has been found (Hine, White, & Chappell, 2003; Mateeff, Bohdanecky, Hohnsbein, Ehrenstein, & Yakimoff, 1991). With respect to the inconsistency of the biases across subjects, our results are also in agreement with previous studies (e.g., Linares & Holcombe, 2008). However, the preceding and succeeding sections show that the precision

of position reports is fairly independent of the cue signaling the position judgment and very consistent across subjects.

Temporal imprecision is relatively independent of low-level visual properties of the moving object

To show that temporal imprecision is not specific to the 2° eccentricity used so far, we repeated Experiment 2 using different radii (Experiment 4, Figure 3), which also allowed us to test a very large range of linear speeds (3.1–176°/s). Spatial variability was small but tended to increase with eccentricity, which is consistent with poorer spatial resolution for peripheral vision. Spatial variability was smaller for 2° relative to 4, 6, and 8° for DL (95% CI). For AH, it was smaller for 2° relative to 8° and for 4° relative to 8° (95% CI). For ML, it was smaller for 2° relative to both 4° and 6° (95% CI). Consistent with large temporal variability, we found again that the distribution of responses for the fastest angular speeds (≥ 2.5 rps) was often not significantly different from a uniform distribution (empty circles in Figure 3). Temporal variability was large (mean: 60 ms;

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Figure 3. Standard deviation of reported positions for Experiment 4. Points for which the distribution of positions was not significantly different from a uniform distribution are plotted as empty circles. The standard deviation for speeds faster than 2.5 rps is not included in the curve fit (see the Results section). Numbers inset at top left are the spatial and temporal variability parameters of the fitted model (Equation 2).

CI: 42–71 ms) and independent of eccentricity (95% CI) except the 4° vs. 8° comparison for DL.

To test whether temporal imprecision generalizes to other trajectories, we conducted an experiment similar to Experiment 1 but using horizontal linear trajectories at different distances from fixation (Experiment 5, Figure 4A). Figure 4B shows the mean reported positions for the linear trajectories. The average position error for both observers was in the direction of motion (flash-lag effect). Temporal variability was large (mean: 69 ms; CI: 47–83 ms, Figure 4A) and significantly different from zero for each distance (95% CI). It was also fairly independent of distance from fixation—as in Brenner, van Beers, Rotman, and Smeets (2006)—although for AH it was higher for 16 relative to 2° and for DL it was higher for 8 relative to 4° (95% CI). Spatial variability (mean: 1.12°; CI: 0.80–1.38°) was significantly different from zero and larger than in Experiment 1 (95% CI). In addition for DL, spatial variability was larger for the more eccentric trajectories (it was smaller for the 2° distance than others and also smaller



Figure 4. (A) Standard deviation and (B) mean of reported positions in Experiment 5. Numbers inset at top left are the spatial and temporal variability parameters of the variability model (Equation 2) in (A) and the intercept and slope of the linear fit in (B).

for 4 relative to 16°, 95% CI) consistent with poorer spatial resolution in the periphery. The larger spatial variability for linear than for circular trajectories makes the increase in variability with speed less apparent in the graphs, especially for DL who shows less temporal variability than AH. We think that the less consistent results across observers for linear trajectories might be due to two confounding factors that do not occur in circular displays. First, there is a strong tendency to report locations close to the fovea (Brenner, Mamassian, & Smeets 2008; Brenner et al., 2006; Kanai, Sheth, & Shimojo, 2004; Linares & Holcombe, 2008; Mateeff, Bohdanecky et al., 1991; Mateeff & Hohnsbein, 1988; Mateeff, Yakimoff et al., 1991; Shi & Nijhawan, 2008; van Beers, Wolpert, & Haggard, 2001). Second, as the initial location of the blob in the linear displays is not completely random, when the cue signaling the position judgment occurred late in time relative to the onset of the trial subjects could guess that the blob should be closer to the side opposite the initial location. Differences between AH and DL in the foveal bias and in the way they used the timing of the cue to estimate likely positions of the blob might explain the differences in the results. In order to investigate variability without the effect of these biases, we mostly use circular displays in this report.

If temporal imprecision were sensitive to low-level signal quality, it might vary greatly with stimulus contrast. For instance, when judging relative position of objects moving with the same speed and direction, Levi (1996) showed that thresholds were much worse for 10% contrast than for higher contrasts. We repeated our Experiment 2 but manipulated the contrast of the moving blob (Experiment 6, Figure 5A). Temporal variability was large (mean: 61 ms; CI: 45–74 ms) but did not change significantly across our contrasts of 0.05, 0.18, and 0.54 (95% CI), which supports the idea that imprecision is not caused by low-level noise. This range of contrasts did indeed affect encoding of the signal however, as seen in the effect on the magnitude of the perceived bias (Figure 5B). The slopes of the linear fits become more negative as contrast decreases (for AH this effect reached statistical significance for the pairs of contrast 0.05-0.18 and 0.05-0.54; for DL for the pair 0.05–0.54). This finding is consistent with previous studies and may be due to longer neural latencies for lower contrasts (Arnold, Ong, & Roseboom, 2009; Lappe & Krekelberg, 1998; Purushothaman, Patel, Bedell, & Ogmen, 1998; White, Linares, & Holcombe, 2008).

High precision for judging offset of two objects moving together

Using the same stimuli as in our other experiments, we confirmed the previous findings of excellent precision in judging the relative position of two objects moving together (Experiment 7, Figure 6). While fixating, subjects viewed two blobs moving horizontally at the same



Figure 5. (A) Standard deviation and (B) mean of reported positions in Experiment 6. Numbers inset are the spatial and temporal variability parameters of the variability model (Equation 2) in (A) and the intercept and slope of the linear fit in (B).





Figure 6. Standard deviation of reported position for Experiment 7. Numbers inset at top left are the spatial and temporal variability parameters of the variability model (Equation 2). For comparison, the best fit of the model for Experiment 5 is included (dashed lines).

speed. They reported whether the upper blob was leading or trailing the lower blob, and the horizontal spatial offset between the blobs was varied randomly on each trial. We tested several vertical separations between the blobs. At the three smallest separations in this relative position experiment, temporal variability was about ten times lower than in the preceding single-object experiments (mean: 4.3 ms; CI: 0.5–7.6 ms), and for the largest separation it was three times lower (28 ms; CI: 8–37 ms). For comparison, in the same figure we replot the fits for judgments of a single object in linear motion (Experiment 5).

Salient visual transients reduce variability

A visual transient such as a flash presented near a moving object can influence the bias in position judgments, even when task-irrelevant (Chappell, Hine, Acworth, & Hardwick, 2006; Linares, López-Moliner, &



Figure 7. (A) Standard deviation and (B) mean of reported positions in Experiment 8. Numbers inset at top left are the spatial and temporal variability parameters of the variability model (Equation 2) in (A) and the intercept and slope of the linear fit in (B). For comparison, the results for Experiment 1 are included.

Johnston, 2007). Do visual transients also influence precision? The visual transient that we used-the color change at fixation-seems not to influence variability differently from the sound cue. It might be, however, that the color change is not close enough to the moving blob to affect variability. To test whether closer and more salient luminance transients can influence variability, we conducted a similar experiment to Experiment 1 but the cue signaling the time of the position judgment was the onset of two rings straddling the trajectory of the blob (Experiment 8, Figure 7). Variability was much lower (blue triangles in Figure 7A; mean: 40 ms; CI: 26–53 ms) than with the fixation color change (the corresponding results of Experiment 1 are replotted as red circles; temporal variability was significantly smaller for all subjects, 95% CI). Despite the consistent reduction of variability, the pattern of results for the bias (the flash-lag effect) was idiosyncratic: it was reduced for the rings relative to the color change cue for AH and ML, for DL it was the same, and for SM it increased (Figure 7B).

Poor precision in a sensorimotor synchronization task

The experiments described so far involved an explicit judgment of the location of a moving object at the time signaled by another external event. For a very different measure of localization, we asked subjects to synchronize a button press with the moment the moving blob aligned with a stationary reference bar (Experiment 9, Figure 8). Consistent with other sensorimotor synchronization tasks, two subjects tended to press the button before the moving blob reached the landmark (Repp, 2005). The other two subjects showed no significant bias (Figure 8B).

The variability of the positions of the blob at the time of the button press increased steeply with speed (Figure 8A). The corresponding temporal variability (mean: 57 ms; CI: 49–62 ms) was smaller than that in Experiment 1 (significantly so for all subjects except ML) but still very high relative to judgments of relative position of objects moving together. Like the results of Experiment 3, these data show that unpredictability of the time of the position judgment is not necessary for large temporal variability. One might think that variability was high because subjects did not receive feedback on their performance, but a comparable amount of temporal imprecision was found with a similar task in which subjects were informed about the error after each trial (Port, Pellizzer, & Georgopoulos, 1996). Furthermore, although this synchronization task required fine motor timing, which could be another source of noise, we found that temporal variability was not higher than in the previous tasks. Therefore, perceptual noise may



Figure 8. (A) Standard deviation and (B) mean of positions at the time of the button press in Experiment 9. Numbers inset at top left are the spatial and temporal variability parameters of the variability model (Equation 2) in (A) and the intercept and slope of the linear fit in (B). The standard deviation and mean position for the fastest speed is not included in the curve fit (see the Results section).

be the main source of variability even in this sensorimotor task, as was concluded for sensorimotor performance in a very different study investigating smooth pursuit (Osborne, Lisberger, & Bialek, 2005).

Discussion

Large temporal imprecision in judgments of instantaneous position

To measure the precision of judgments of instantaneous position, we asked subjects to report the location of an object at the time of a cue. The variability in position judgments increased steeply with the speed of the moving object, indicating about 70 ms of temporal imprecision. This surprisingly large value corresponds to about 10 cm of the trajectory of a person walking at 5 km/h.

The temporal imprecision did not depend on the sensory modality of the cue signaling the position judgment (Experiments 1 and 2) and also occurred when the time of the cue was easily predicted (Experiment 3), which suggests that it is not the temporal uncertainty in the perception of the cue that causes the large variability in the position report. The characteristics of the cue are not entirely irrelevant, however: when we used a salient visual transient (rings) presented close to the moving object, temporal uncertainty was strongly reduced (Experiment 8). Further experiments would be needed to fully understand the interaction of visual transients with moving objects.

As for the moving object itself, when we varied the quality of its low-level representation by changing its eccentricity (Experiment 4) and contrast (Experiment 6), temporal variability was slightly affected. It is therefore unlikely that the variability is caused by temporal imprecision associated with the encoding of the moving object in early stages of visual processing. Indeed, the perception of motion direction shows very high temporal resolution (Burr & Ross, 1982), probably due to detectors in early cortical areas like V1. The extraordinary precision in judgments of relative position for two objects moving with the same speed and direction (Levi, 1996) suggests that some position information is also encoded with high temporal resolution. Nevertheless, we found a large amount of temporal imprecision for localizing a single moving object at the time of a cue.

The temporal imprecision may arise in binding the moment of the cue with the corresponding moment in the trajectory of the moving object. It seems that the brain does not have a unified timeline that preattentively links together all visual events (Nishida & Johnston, in press). Instead, a high-level, temporally coarse and possibly attentional mechanism may be needed to pair visual features in many cases. This would explain why our position tasks and those that probe the binding of features like color and motion both manifest such poor temporal resolution (Holcombe, 2009). In further support of the hypothesis that the same binding mechanism mediates position reports and binding of features other than position, it has been reported that salient transients greatly affect both (Holcombe & Cavanagh, 2008; Nishida & Johnston, 2002).

We speculate that performance in a variety of tasks may be afflicted by similar levels of temporal uncertainty. One example is rapid serial visual presentation tasks where participants are asked to select an item that occurs at the same time as a cue such as a ring (Vul, Hanus, & Kanwisher, 2008; Vul, Nieuwenstein, & Kanwisher, 2008). Our analysis of the results plotted by Vul et al. indicates that the spread of responses for the first target (T1) is consistent with about 70 ms of temporal uncertainty.

The flash-lag effect

Our paradigm is similar to those used to study the flashlag effect: when a flash is presented in alignment with a moving object, subjects perceive the flash to lag the moving object (Nijhawan, 1994). Typical flash-lag displays, however, might not be ideal to study the variability in judgments of instantaneous position because both the flash and the moving object are mislocalized (Whitney & Cavanagh, 2000), and in a complicated way (Eagleman & Sejnowski, 2007; Shi & Nijhawan, 2008; Shim & Cavanagh, 2006; Yilmaz, Tripathy, Patel, & Ogmen, 2007; see also Watanabe & Yokoi, 2006, 2008). To avoid contamination from this, in our experiments the location of the cues signaling the position judgment was irrelevant for the task.

Prior to this report, it seems that only Murakami (2001a, 2001b) and Brenner et al. (2006) explicitly addressed the temporal variability involved in the flash-lag effect. From their data analyses and our reanalysis of the data from López-Moliner and Linares (2006), together with estimates made from plots in other papers, we see that temporal variability in the flash-lag effect is sometimes consistent with our finding of large temporal imprecision (Brenner et al., 2006; Murakami, 2001a; Whitney, Cavanagh, & Murakami, 2000; Whitney, Murakami, & Cavanagh, 2000) but sometimes considerably smaller (Eagleman & Sejnowski, 2000; López-Moliner & Linares, 2006; Murakami, 2001b; Nijhawan, 1994). We think that the reduced variability found in these latter studies is due to the use of a strong visual transient (the flash) displayed near the moving object (Chappell et al., 2006; Linares et al., 2007). Supporting this, we reduced variability with a cue formed by bright rings flashed close to the moving object (Experiment 8). The bias or mean error (flash-lag effect) varied dramatically across both tasks and observers, indicating that the link between bias and variability in the position judgment may be complex.

Precision of action

The poor precision to localize a moving object at the time of a cue contrasts with the excellent abilities of humans interacting with moving objects. When hitting a ball with a bat, for example, the swing can be performed at the correct instant with a precision of better than 10 ms (McLeod & Jenkins, 1991). This suggests that position judgments at the time of a cue do not directly tap the mechanisms of object localization in some sensorimotor tasks. As a first attempt to produce a more ecological task, we asked subjects to synchronize an action with the moment of alignment between the moving object and a stationary reference (Experiment 9), a task that does not require an explicit position judgment at the time of a cue. We found that although temporal variability was reduced, it was still high, which again might indicate the involvement of a low temporal resolution binding mechanism. For this task, subjects may program the button press so that its subsequent sensory consequence (e.g., sound of the button press) is perceptually bound with the moment of alignment of the object with the landmark (Aschersleben & Prinz, 1995). To do that, subjects may rely on previous sensorimotor interactions (including previous trials of our experiment) to calibrate the time of future actions. Further research is needed, however, to determine the role of high-level binding mechanisms in this task and in the sensorimotor tasks for which humans show better temporal precision (Hopkins & Kristofferson, 1980; McLeod & Jenkins, 1991).

Conclusion

Previous research has revealed a temporally coarse stage of visual processing by using periodic stimuli with two changing features (Holcombe, 2009). Here, we found evidence that this stage with low temporal resolution limits abilities to judge the instantaneous position of a moving object. Although the visual system appears to be specialized for localization—much of visual cortex is retinotopic and some judgments can be made with hyperacuity—we have demonstrated that even the simplest localization tasks are afflicted by the poor temporal resolution of high-level visual processing.

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