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Estimating Time to Contact during Pursuit Eye Movements: Comparison between Geometric Model Prediction and Human Performance

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While an object is approaching a particular location, we can make an estimate of the time when the object will arrive at that location. A geometric model predicts that the estimate of time-to-contact (TTC) is greatly improved by using the rate of change of visual direction of the object when the object is moving with a slow velocity toward a point of nearest approach at a distance far from the observer. It has been shown that pursuit eye movements provide the rate of change of visual direction of an approaching object. We conducted psychophysical experiments, and compared TTC estimates during pursuit eye movements to those during fixation. We found that the differences in TTC estimates between fixation and pursuit show a qualitatively similar pattern to the geometric model prediction. However, the results also show that the magnitudes of the TTC estimation errors are greater than the theoretical values from the geometric model, indicating that the human visual system has a perceptual bias in estimating TTC. These results suggest that the human visual system estimates TTC during pursuit eye movements in a different way from the geometric model, although the effect of these eye movements on TTC estimates in human performance is qualitatively consistent with the model prediction.

Key words: time to contact, pursuit eye movements, extra retinal cue, motion in depth, visually timed action

1. Introduction

In a variety of everyday tasks it is important to judge when an approaching object will arrive at a particular location. We avoid obstacles when we drive,[1–3] we sidestep dangerous objects moving toward us,[4] and we judge the timing of interceptive acts when we catch or hit an approaching ball.[5–9] In all these tasks we make estimates of time-to-contact (TTC). Much experimental research has addressed the question of what kinds of retinal information are used to make estimates of TTC.[10–12] It has been suggested that the visual system can use changing retinal size and changing binocular disparity to estimate TTC.[13–15]

In various tasks, however, estimating TTC is often accompanied with pursuit eye movements. In cricket, for example, a batsman follows the trajectory of an approaching ball using his eye after the bounce of the ball, although he makes a predictive saccade to the place where he expects the ball to hit the ground before the ball bounces.[16] In baseball, a fielder keeps his eye on an approaching ball to catch it.[17] However, it has been shown that batters do not keep their eyes on the ball but move them to a predicted location.[18] Also, in crossing a street, a person looks at an approaching car to determine a safe time to cross.[19] These behavioral observations suggest that pursuit eye movements may play some role in estimating TTC.

How do these eye movements contribute toward estimating TTC? Based on the geometry of an object approaching with constant velocity toward a given point (Fig. 1), Lee and Young pointed out two things.[5] First, if the approaching object is not on a collision course, the rate of change of visual direction of the object (ψ in Fig. 1) is needed for an accurate estimate of TTC. Second, the rate of change of visual direction of the object is, in principle, available from extra-retinal information provided by turning the eye to track the object. Tresilian found that TTC estimates are better when the eyes track an approaching object than when they do not.[20] This suggests that extra-retinal information about pursuit eye movements provides the rate of change of visual direction of the object. However, little is known about whether the human visual system estimates TTC during

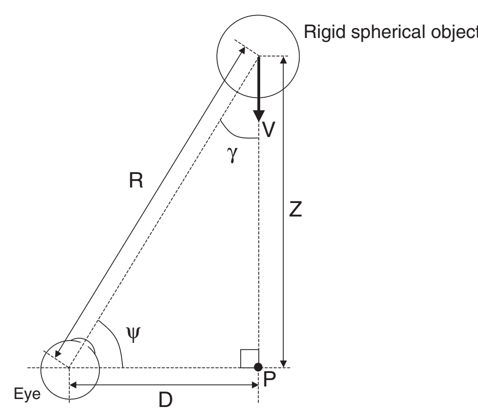

Fig. 1. Situation in which a rigid spherical object is approaching the point p with constant velocity V. The object is located at a point of distance R from the eye and distance Z from point p, and is moving along a straight path toward point p.

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pursuit eye movements in the same way as the geometric model proposed by ref. 5.

Here we used that geometric model to predict how pursuit eye movements affect TTC estimates in a variety of geometric situations. The geometric model predicted that such estimates are greatly improved by using the rate of change of visual direction of an approaching object when the object is moving with a slow velocity toward a point of nearest approach at a distance far from the observer. We tested whether pursuit eye movements cause this geometric effect using psychophysical experiments. Moreover, to assess whether the geometric model can quantitatively explain the human performance of TTC estimates during pursuits, we compared the magnitude of TTC errors between the human performance and the geometric model prediction.

2. Geometric Model Prediction

Under the situation depicted in Fig. 1, a rigid spherical object is located at a distance R from the eye and at a distance Z from point p, and it is moving at a constant velocity V along a straight path to point p. The time to contact (T_C) of the moving object at point p is given by

$$T_C = \frac{Z}{V} = \frac{\tau}{1 + (\tau\dot{\psi})^2}, \tag{1}$$

where τ is defined as $R/V\cos\gamma$ and $\dot{\psi}$ is the rate of change of visual direction of the moving object (ref. 5). Also, consider the variation with time of the approaching object's angular radius (θ). For small θ,

$$\tau = \frac{R}{V\cos\gamma} \approx \frac{\theta}{\dot{\theta}}. \tag{2}$$

Thus, τ is approximately specified by the optical looming information (ref. 5).

Now, suppose that the visual system only uses an extra-retinal signal given by pursuit eye movements in order to obtain $\dot{\psi}$ in eq. (1). Following this assumption, $\dot{\psi} \neq 0$ when observers turn the eye to track an approaching object, and $\dot{\psi} = 0$ when they do not turn the eye to keep it fixated on a location. In the former case, the visual system can in principle estimate TTC ($\tilde{T}_C$) given as follows:

$$\tilde{T}_C|_{\dot{\psi}\neq 0} = \frac{\tau}{1 + (\tau\dot{\psi})^2} = T_C. \tag{3}$$

Also, in the latter case, the visual system can in principle estimate TTC ($\tilde{T}_C$) given as follows:

$$\tilde{T}_C|_{\dot{\psi}=0} = \frac{\tau}{1 + (\tau\dot{\psi})^2} = \tau. \tag{4}$$

Subtracting the actual TTC (T_C) from eq. (3), TTC error in the eye-movement condition (E_{EM}) is given by

$$\begin{aligned} E_{EM} &= \tilde{T}_C|_{\dot{\psi}\neq 0} - T_C \\ &= T_C - T_C \\ &= 0. \end{aligned} \tag{5}$$

In the same way, subtracting the actual TTC (T_C) from eq. (4), TTC error in the fixation condition (E_{FIX}) is given by

$$\begin{aligned} E_{FIX} &= \tilde{T}_C|_{\dot{\psi}=0} - T_C \\ &= \tau - T_C \\ &= \frac{R}{V\cos\gamma} - \frac{Z}{V} \\ &= \frac{D^2}{VZ} \\ &(\because \cos\gamma = Z/R,\ R^2 = D^2 + Z^2). \end{aligned} \tag{6}$$

Alternatively, suppose that the visual system only uses the displacement of a retinal image in order to obtain $\dot{\psi}$ in eq. (1). Following this assumption, $\dot{\psi} = 0$ when observers turn the eye to precisely track an approaching object, and $\dot{\psi} \neq 0$ when they do not turn the eye to keep it fixated on a location. We find that TTC errors in the eye-movement (E_{EM}) and fixation (E_{FIX}) conditions are given by

$$E_{FIX} = \tilde{T}_C|_{\dot{\psi}\neq 0} - T_C = T_C - T_C = 0, \tag{7}$$

$$E_{EM} = \tilde{T}_C|_{\dot{\psi}=0} - T_C = \tau - T_C = \frac{D^2}{VZ}. \tag{8}$$

The relationship between E_{EM} and E_{FIX} is found to be the opposite compared with the assumption when the extra-retinal signal is used to obtain $\dot{\psi}$.

In summary, if the visual system uses extra-retinal information to obtain the rate of change of visual direction of an approaching object ($\dot{\psi}$), TTC errors in the eye-movement and fixation conditions should be consistent with the geometric model predictions formulated by eqs. (5) and (6), respectively. Alternatively, if the visual system uses retinal information to obtain $\dot{\psi}$, TTC errors in the eye-movement and fixation conditions should be consistent with the geometric model prediction formulated by eqs. (7) and (8), respectively. Figure 2 shows the geometric model prediction for $Z = 38$ and 26 m. In the figure, TTC errors in the case of $\dot{\psi} = 0$ increase with distance to nearest approach, whereas TTC errors in the case of $\dot{\psi} \neq 0$ do not.

3. Experiment 1

We simulated a rigid spherical object moving on the ground at a constant velocity along a straight path. The simulated object was presented on a CRT display. We manipulated a variety of simulated geometric parameters represented in Figs. 3(a) and 3(b): object diameter, object velocity, distance to nearest point, and traveling distance. We measured TTC judgments when pursuing the object by the eye or keeping the eye at the fixation point.

3.1 Methods

3.1.1 Apparatus

Observers sat in a totally dark booth and viewed visual stimuli monocularly. The observer's head was fixed by a combination of a chin rest and a forehead rest. The visual stimuli were presented on a CRT display with a refresh rate of 75 Hz. The display subtended 39 deg in height and 51 deg in width when viewed from 40 cm away, and was controlled by a computer (Apple PowerMac G3). All surfaces surrounding the display were covered by black cloth or black paper.

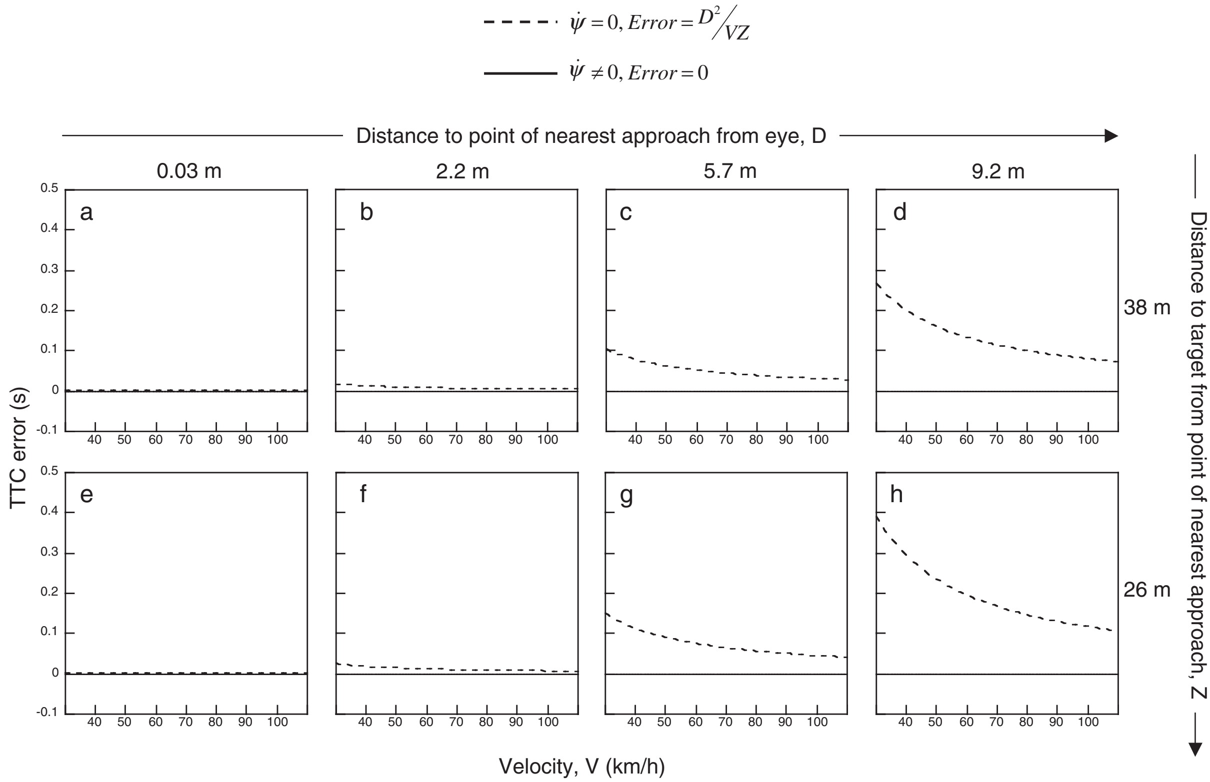

Fig. 2. Model prediction. Errors in time-to-contact are plotted as a function of velocity (V) for a variety of geometric parameters. Each column represents a different distance to the point of nearest approach from the eye (D). Each row represents a different distance to an approaching object from the point of nearest approach (Z). The dashed and solid lines represent errors in time-to-contact calculated by eqs. (5) and (6) [or eqs. (8) and (7)], respectively. Equations (5) and (6) correspond to the conditions of $\dot{\psi} \neq 0$ and $\dot{\psi} = 0$, respectively. In the $\dot{\psi} \neq 0$ condition, error in time-to-contact is constant across the distance to nearest approach, but, in the $\dot{\psi} = 0$ condition, it varies with change in this distance.

3.1.2 Stimuli

Visual stimuli were created by simulating a rigid spherical object moving on the ground at a constant velocity along a straight path toward a point of nearest approach to the eye. Figures 3(a) and 3(b) represent the top and side views of the simulated situation, respectively. A sensation of approaching motion in depth was created by change in size of the object. The simulated object disappeared after traveling 12 or 24 m from the starting point. The point of nearest approach was located at a point some distance away from the observer's right eye. The spherical object was rendered using anti-aliasing and geometric perspective projection from the right eye. Figure 3(c) represents the trajectory of the spherical object and the change in size of its image in the display. The spherical object consisted of a white disk (50 cd/m^2) on a black background as shown in Fig. 3(c). We manipulated the geometric parameters represented in Figs. 3(a) and 3(b). The simulated object diameter was varied over values of 0.75, 1.5, 1.8, and 2.5 m, and the velocity was varied over values of 40, 60, 80, and 100 km/h. The simulated distance to the point of nearest approach from the eye was varied over values of 0.03, 2.2, 5.7, and 9.2 m. The simulated traveling distance to the center of the target from the starting point was varied over values of 12 and 24 m. Thus, the simulated distance to the center of the target from the point of nearest approach was varied over values of 38 and 26 m [see Fig. 3(a)]. In the eye-movement condition, the simulated sphere was only presented in the display, while in the fixation condition the simulated sphere and a fixation cross (1×1 deg) were both shown, the latter 3 deg below the center of the display.

3.1.3 Procedure

During an experimental run, an observer was instructed either to pursue the center of the simulated approaching sphere by pursuit eye movements or to keep his eyes on the fixation-cross. The motion trajectory of the simulated sphere was initiated when the observer pressed a button, and then continued to press the button. After the target had disappeared, the observer released his finger from the button at the time the target arrived at the subjective frontal plane making contact with his forehead. The time from first pressing the button to releasing it was recorded in the computer. TTC error was calculated by subtracting the actual TTC from that recorded time. We did not measure eye movements.

An experimental run consisted of 48 trials (4 target diameters $\times$ 4 points of nearest approach $\times$ 3 repetitions). Four velocities, two traveling distances, and two experimental conditions (i.e., eye-movement or fixation) were

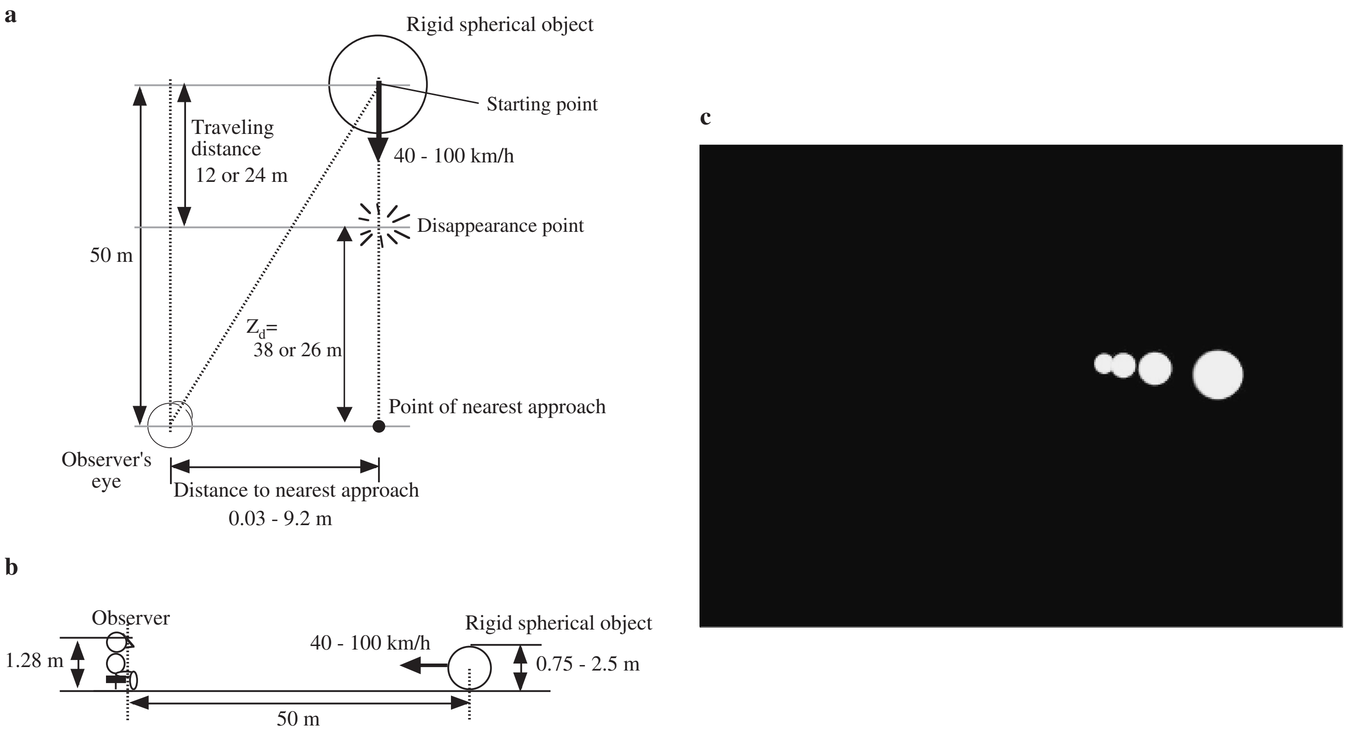

Fig. 3. Simulated situation and visual stimuli. Visual stimuli were created by simulating a rigid spherical object (diameter between 0.75 and 2.5 m) moving on the ground at a constant velocity (between 40 and 100 km/h) along a straight path toward the point of nearest approach. When the simulated sphere traveled 12 or 24 m from the starting point and arrived at the disappearance point, the sphere was removed from the display. (a) Top view of the simulated situation. (b) Side view of the simulated situation. (c) Motion trajectory and looming created by simulating spherical object motion. The spherical object was rendered using anti-aliasing and geometric perspective projections from the right eye, and was a white disk on a black background in the display.

randomly interleaved on an experimental run. Each observer performed 16 experimental runs.

3.1.4 *Observers*

Five observers participated in experiment 1. Each had normal or corrected to normal visual acuity. Age ranged from 22 to 31 years. Four of them were naïve with respect to the purpose of this study, the fifth was one of the authors.

3.2 *Results and discussion*

Figure 4 shows the mean TTC estimation errors for the five observers as a function of velocity. Solid and open symbols represent the eye-movement and fixation conditions, respectively. Each configuration of the symbols represents a different size of the sphere. Each column shows the TTC estimation errors for a different distance to nearest approach, and each row shows the TTC estimation errors for a different traveling distance. In Fig. 4, the TTC estimation errors show a similar pattern to those predicted by eqs. (5) and (6), not eqs. (7) and (8), for all of the target diameters and the traveling distances (see Fig. 2).

An analysis of variance (ANOVA) was conducted using four distances to nearest approach and four target diameters for each condition of eye state for each traveling distance. For the traveling distance of 12 m (distance from a point of nearest approach: 38 m), the TTC estimation errors in the fixation condition increased as the distance to nearest approach increased ($F(3,48) = 6.631$, $p < 0.001$). The TTC estimation errors varied with target diameter ($F(3,48) = 8.720$, $p < 0.0005$), but there was no significant interaction between distance to nearest approach and target diameter ($F(9,48) = 0.324$, $p = 0.963$ ns). The TTC estimation errors in the eye-movement condition did not depend on the changes in the distance to nearest approach ($F(3,48) = 1.920$, $p = 0.139$ ns). These errors varied with target diameter ($F(3,48) = 6.180$, $p < 0.005$), but again there was no significant interaction between distance to nearest approach and target diameter ($F(9,48) = 0.518$, $p = 0.854$ ns). For the traveling distance of 24 m (distance from point of nearest approach: 26 m), the TTC estimation errors in the fixation condition significantly varied with distance to nearest approach and target diameter ($F(3,48) = 5.669$, $p < 0.005$ and $F(3,48) = 14.088$, $p < 0.0001$, respectively), but there was no significant interaction between distance to nearest approach and target diameter ($F(9,48) = 0.328$, $p = 0.961$ ns). The TTC estimation errors in the eye-movement condition did not significantly vary with distance to nearest approach ($F(3,48) = 0.539$, $p = 0.658$ ns), but did significantly vary with target diameter ($F(3,48) = 5.849$, $p < 0.005$). Again, there was no significant interaction between distance to nearest approach and target diameter ($F(9,48) = 0.408$,

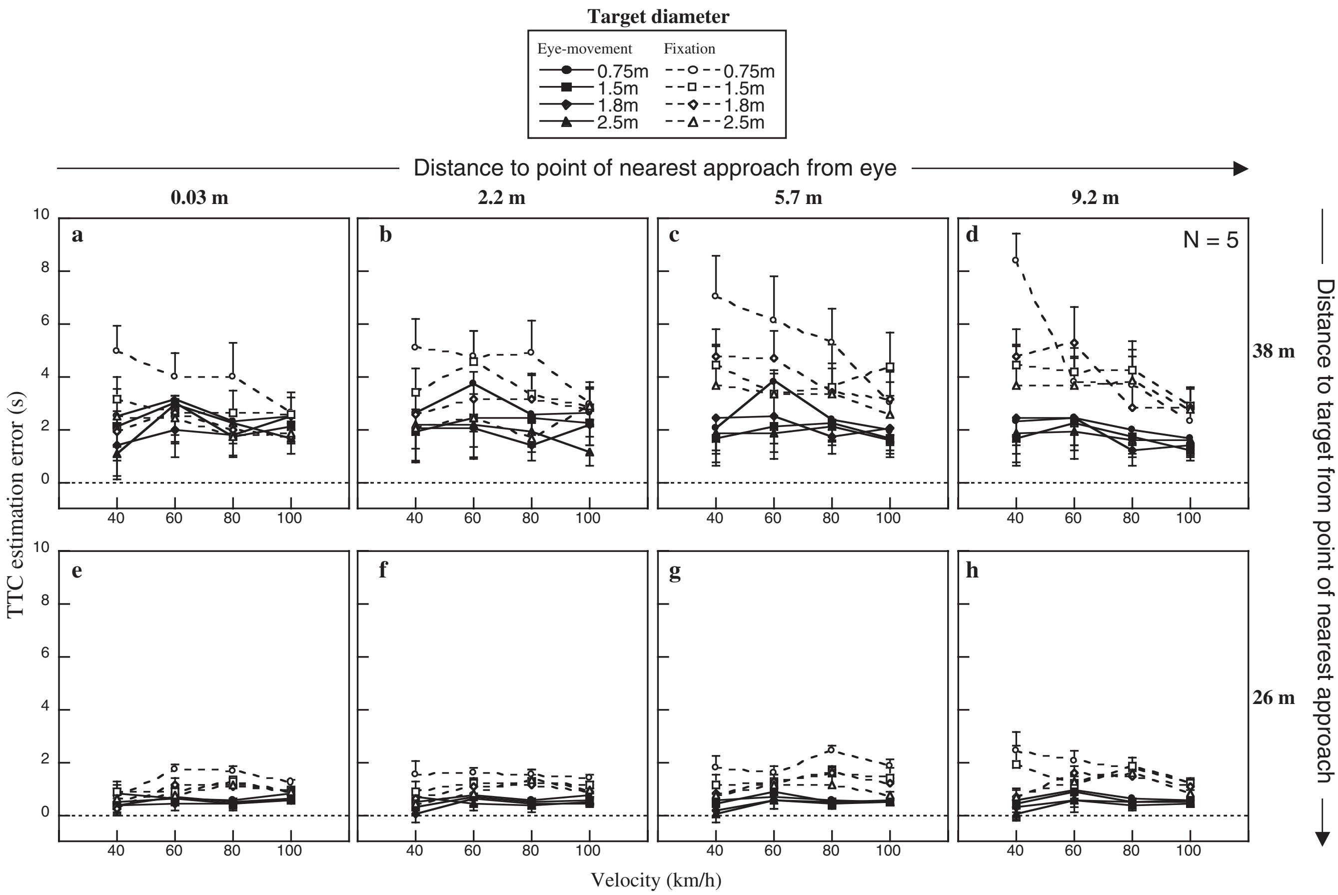

Fig. 4. Results of experiment 1. The mean errors in time-to-contact of five observers are plotted as a function of velocity. The solid and open symbols represent the eye-movement and fixation conditions, respectively. The configuration of the symbols represents target diameter. The arrangement of the graphs is the same as Fig. 2. The data show a similar pattern to the prediction of eqs. (5) and (6) (see Fig. 2). Error bars are standard errors.

$p = 0.925$ ns). The statistical analysis indicates that the trends in the experimental data are consistent with the prediction given by eqs. (5) and (6). This suggests that the human visual system uses extra-retinal information provided by pursuit eye movements to obtain the rate of change of visual direction of an approaching object.

There was also a significant effect of the sphere size on TTC estimation; the TTC estimation errors tended to be slightly smaller for the larger spheres. This size effect is consistent with the results reported by other studies.[21–23] We could attribute this size effect to the reliability of looming information, because it has been shown that larger spheres provide more reliable looming information.[24]

In Fig. 4, the observers have overestimated TTC considerably in the case that the simulated distance to the disappearance point of the sphere from the point of nearest approach (Z_d) was 38 m [see Fig. 3(a)], compared with the case of the distance Z_d of 26 m. In the case of the distance Z_d of 38 m, the observers seemed to considerably underestimate the sphere velocity. This is because the change of the retinal size of the sphere was much smaller in the case of the distance Z_d of 38 m than the case of the distance Z_d of 26 m. The observers might therefore have had the impression that the simulated sphere was moving more slowly in the distance Z_d of 38 m, resulting in the large overestimation of TTC judgments.

Although the size-changes of the simulated sphere were very large in the case of the distance Z_d of 26 m, TTC estimates were overestimated more than the theoretical values from the geometric model as follows: (i) TTC estimation errors in the eye-movement condition were positive values, not zero. (ii) Most of TTC estimation errors in the fixation condition were greater than 0.5 s [Figs. 4(e)–4(h)]. However, the geometric model predicted TTC estimation errors of zero in the case of $\dot{\psi} \neq 0$ and less than 0.5 s in the case of $\dot{\psi} = 0$ [Figs. 2(e)–2(h)]. This might be due to the method used in experiment 1, in which the observer pressed and released a button to make an estimate of TTC, resulting in an effect of motor delay on that estimate. This might have caused the overestimation of TTC even though the large size-change of the sphere provided sufficient looming information. In experiment 2, we tested this possibility.

4. Experiment 2

To test whether the use of a button to make an estimate of TTC could account for the overestimation of TTC in experiment 1, we adopted the method developed by Gray and Regan.[14,25] In their method, a brief auditory click was generated at the designated time of contact some time after the approaching sphere had disappeared. The observer's task was to indicate whether this click occurred before or after the approaching sphere would have arrived at the eye. This method removes any effect of motor delay on TTC estimates. If the use of a button to make an estimate of TTC produces TTC overestimates, adopting the method of Gray and Regan should remove any effect of motor delay on these estimates, resulting in the elimination of TTC overestimates from the human performance.

4.1 Methods

4.1.1 Apparatus

An observer sat in a totally dark booth and viewed visual stimuli monocularly. The observer's head was fixed with a combination of a chin rest and a forehead rest. The visual stimuli were presented on a CRT display with a refresh rate of 80 Hz. The display subtended 43 deg in height and 54 deg in width when viewed from 38 cm away, and was controlled by a visual stimulus generator (Cambridge Research Systems, ViSaGe).

4.1.2 Stimuli

Visual stimuli were the same as experiment 1 except for the following: The simulated object diameter was 2.0 m. The simulated traveling distance was 10 m. The simulated distance from the starting point to the point of nearest approach was 35 m [see Fig. 3(a)]. In experiment 2, there were two geometric conditions. In the first condition, the simulated distance-to-nearest-approach was varied over values of 3.0, 4.5, 6.0, and 7.5 m with the simulated object velocity of 40 km/h. In the second condition, the simulated object velocity was varied over values of 35, 40, 45, and 50 km/h with the simulated distance-to-nearest-approach of 7.5 m. These geometric parameters provided sufficient looming information for the approaching object.

4.1.3 Procedure

During an experimental run, observers were instructed either to pursue the center of the simulated approaching sphere or to keep their eyes at the fixation-cross. The motion trajectory of the simulated sphere was initiated when the observer pressed a button. Some time after the simulated sphere had disappeared, a brief auditory click was generated. The observer's task was to indicate whether the click occurred before or after the simulated approaching sphere would have passed through the right side of the observer's forehead. The timing of the auditory click was varied from trial to trial using a staircase method.[26] The mid-run estimates[26] provided estimates of a 50% probability that the observer would judge that the simulated approaching sphere would pass before the auditory click. In the first condition, four staircases corresponding to four values of the simulated distance-to-nearest-approach (3.0, 4.5, 6.0, and 7.5 m) were randomly interleaved. In the second condition, four staircases corresponding to four values of the simulated velocity of the sphere (35, 40, 45, and 50 km/h) were randomly interleaved. Thus, observers could not anticipate trial-to-trial variations in the timing of the auditory click. We did not measure eye movements.

An experimental run consisted of 100 trials (4 distances or 4 velocities $\times$ 25 times). An experimental run for the eye-movement condition was separate from that for the fixation condition. Each observer performed 20 experimental runs.

4.1.4 Observers

Three observers participated in experiment 2. Each had normal or corrected to normal visual acuity. Age ranged from 22 to 33 years. Two of them were naïve with respect to psychophysical experiments, the other observer was one of the authors.

4.2 Results and discussion

In the first condition, we varied the simulated distance-to-nearest-approach over values of 3.0, 4.5, 6.0, and 7.5 m with the simulated object velocity of 40 km/h. Figure 5(a) shows the mean TTC estimation errors (that is, the difference between the estimated and calculated TTC) for the three observers as a function of distance-to-nearest-approach. Solid and open squares represent the eye-movement and fixation conditions, respectively. Thick solid and thick dashed lines represent the geometric model predictions of $\dot{\psi} \neq 0$ and $\dot{\psi} = 0$, respectively [see eqs. (5) and (6)]. In Fig. 5(a), TTC estimation errors decreased in the eye-movement condition compared with the fixation condition. An ANOVA revealed a significant main effect of eye state ($F(1,16) = 14.074$, $p < 0.005$), and a significant main effect of distance-to-nearest-approach ($F(3,16) = 8.630$, $p < 0.005$). There was no significant interaction between eye state and distance-to-nearest-approach ($F(3,16) = 0.505$, $p = 0.685$ ns). However, the magnitudes of TTC estimation errors were larger than those predicted by the geometric model.

In the second condition, we varied the simulated object velocity over values of 35, 40, 45, and 50 km/h with the simulated distance-to-nearest-approach of 7.5 m. Figure 5(b) shows the mean TTC estimation errors for the three observers as a function of velocity. In the same way as the first condition, TTC estimation errors were reduced when the observers tracked the simulated approaching sphere with pursuit eye movements. An ANOVA revealed a significant main effect of eye state ($F(1,16) = 27.284$, $p < 0.0001$), and a significant main effect of velocity ($F(3,16) = 91.822$, $p < 0.0001$). There was no significant interaction between eye state and velocity ($F(3,16) = 0.168$, $p = 0.916$ ns). However, the magnitudes of TTC estimation errors were larger than those predicted by the geometric model.

These results showed a qualitatively similar pattern to the TTC estimation errors predicted by the geometric model [eqs. (5) and (6)] for the first and second conditions. This is consistent with the results of experiment 1. However, even though the method of Gray and Regan[14,25] was used to remove any effect of motor delay on TTC estimates, these were overestimated more than the theoretical/geometric values from the geometric model as shown in

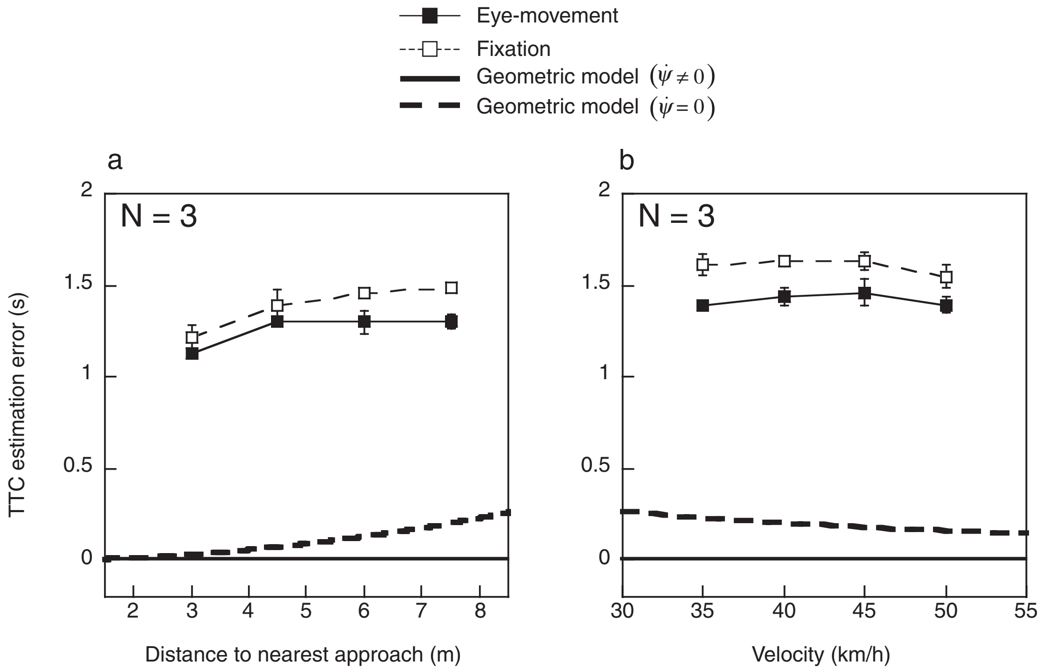

Fig. 5. Results of experiment 2. (a) Mean TTC estimation errors for the three observers as a function of distance-to-nearest-approach (the simulated object velocity = 40 km/h). (b) Mean TTC estimation errors for the three observers as a function of velocity (the simulated distance-to-nearest-approach = 7.5 m). Errors in TTC estimates were calculated by subtracting the actual TTC from the estimated TTC. The open and solid squares represent the fixation and eye-movement conditions, respectively. The thick dashed and thick solid lines represent the geometric predictions for $\dot{\psi} = 0$ and $\dot{\psi} \neq 0$, respectively ($\dot{\psi}$ is the rate of change of visual direction of the approaching object). Error bars are standard errors.

Figs. 5(a) and 5(b). This indicates that the human visual system has a perceptual bias that is not included in the geometric model, suggesting that the human visual system estimates TTC in a different way from the model.

5. General Discussion

The present study indicated that TTC judgments during pursuit eye movements are improved more than those during fixation. This is consistent with the previous finding of Tresilian.[20] We confirmed that the trends of the difference in TTC judgments between the fixation and eye-movement conditions are consistent with the theoretical/geometric consequences pointed out by ref. 5. However, we found that the magnitude of TTC judgments is greater than those predicted by the theoretical consequences.

Why was TTC estimation improved when an approaching object was tracked by pursuit eye movements? One reason is that the extra-retinal signal given by the eye movements provides the rate of change of visual direction of an approaching object in estimating TTC.[20] This is one of the two predictions from the geometric model [see eqs. (5) and (6)]. The present study indicated that the trend of our results is qualitatively consistent with the geometric model prediction represented by eqs. (5) and (6). Also, in our experiment, TTC judgments during pursuit eye movements were conducted under the situation that the target was only visible in the display. It has been shown that, when only an approaching object is visible, the extra-retinal signal given by pursuit eye movements provides the rate of change of visual direction of the object in estimating TTC.[20] Thus, in our experiment, the extra-retinal signal seems to work in this estimation during pursuit eye movements.

Another reason is that keeping the object on the fovea allows the visual system to get a better estimate of any change in size. Regan and Vincent showed that the discrimination threshold for TTC is better when the object is foveated than when it is not.[27] In the present study, when observers judged TTC during fixation, they viewed the target in the peripheral visual field; this would lead to degradation in TTC estimates. However, if this were true, one would expect that the TTC estimation error during fixation would have simply increased with the distance to nearest approach from the eye for all simulated velocities. But when the simulated velocity of the target was 100 km/h, the TTC estimation error during fixation did not increase with the distance to nearest approach (see Fig. 4). Thus, the differences in TTC estimation errors between the fixation and eye-movement conditions cannot be explained only by the reason that keeping the target on the fovea provides a better estimate of TTC.

The present study showed that TTC estimates were overestimated more than the theoretical values predicted by the geometric model. In experiment 2, we presented observers with information that was geometrically sufficient to estimate the TTC of the approaching object. In addition, we used the method of Gray and Regan[14,25] to remove any effect of motor delay on TTC estimates. However, observers overestimated TTC even though they used pursuit eye movements in the estimation, indicating that the human visual system has a perceptual bias that is not included in the geometric model. This suggests that the human visual system estimates TTC in a different way from the geometric model, although the effect of pursuit eye movements on TTC estimates for human observers is qualitatively consistent with the model prediction.

Alternatively, the TTC overestimation may have been caused by the TTC estimation task used in the present study: observers needed to predict the motion trajectory of the target after the target had disappeared from the display. The prediction of the motion trajectory may produce a perceptual bias in estimating TTC. In future investigations, it would be informative to develop a new TTC estimation task that does not include the prediction of the motion trajectory.

Our findings have important implications for physiological work on the processing of TTC judgments in the human brain. Primate cortical area MST (medial superior temporal) receives both the extra-retinal signal of pursuit eye movements[28] and the retinal signal of optic expansion producing a sensation of motion-in-depth.[29] More recently, a human fMRI study has suggested that cortical area MT+ (Middle temporal complex) is activated in estimating TTC.[30] Thus, our findings suggest that cortical area MST may be closely related to TTC estimation in humans.

Many studies of TTC have dealt with the situation that the effect of the extra-retinal signal given by pursuit eye movements on TTC estimation is little shown.[9–12,24] Welchman *et al.* did not find differences in the estimation of the direction of three-dimensional object motion between fixation and pursuit.[24] In their experiment, the distance to the point of nearest approach was very short. As the geometric model describes, there are few differences in TTC estimation between fixation and pursuit in the case of a short distance to the nearest approach [see Figs. 2(a) and 2(e)]. However, the differences in TTC estimation between fixation and pursuit are quite dramatic in a long distance to the nearest approach [see Figs. 2(d) and 2(h)]. The discrepancy between our results and the results of Welchman *et al.*[24] may be explained by considering the difference in the simulated geometric parameters.

In conclusion, we have demonstrated that TTC judgments during pursuit eye movements are improved more than those during fixation, and that the difference in TTC estimates between fixation and pursuit is qualitatively consistent with the geometric model prediction. These findings suggest that the extra-retinal signal given by pursuit eye movements provides the rate of change of visual direction of an approaching object. This is consistent with the previous finding of Tresilian.[20] Furthermore, our findings revealed that human observers overestimate TTC, although the effect of pursuit eye movements on TTC estimates is qualitatively consistent with the geometric model prediction. This suggests that the human visual system calculates TTC during pursuit eye movements in a different way from the geometric model of TTC estimation.

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References

1) D. N. Lee: Perception **5** (1976) 437.
2) R. W. McLeod and H. E. Ross: Perception **12** (1983) 417.
3) V. Cavallo and M. Laurent: Perception **17** (1988) 623.
4) W. Schiff and M. L. Dietwiler: Perception **8** (1979) 647.
5) D. N. Lee and D. S. Young: in *Brain Mechanisms and Spatial Vision*, ed. D. Ingle, M. Jeannerod, and D. N. Lee (Matrinus Nijhoff, Dordrecht, Netherlands, 1985) p. 1.
6) J. R. Tresilian: Perception **19** (1990) 223.
7) J. R. Tresilian: J. Exp. Psychol.: Human Perception Perform. **17** (1991) 865.
8) R. J. Bootsma and R. R. D. Oudejans: J. Exp. Psychol.: Human Perception Perform. **19** (1993) 1041.
9) D. Regan and R. Gray: Vision Res. **41** (2001) 3321.
10) J. R. Tresilian: Trends Cognitive Sci. **3** (1999) 301.
11) D. Regan and R. Gray: Trends Cognitive Sci. **4** (2000) 99.
12) I. P. Howard and B. J. Rogers: *Seeing in Depth* (I Porteous, Toronto, 2002) Vol. 2, p. 519.
13) H. Heuer: Perception **22** (1993) 549.
14) R. Gray and D. Regan: Vision Res. **38** (1998) 499.
15) S. K. Rushton and J. P. Wann: Nat. Neurosci. **2** (1999) 186.
16) M. F. Land and P. McLeod: Nat. Neurosci. **3** (2000) 1340.
17) P. McLeod, N. Reed, and Z. Dienes: Nature **426** (2003) 244.
18) A. T. Bahill and J. D. McDonald: Vision Res. **23** (1983) 1573.
19) D. R. Geruschat, S. E. Hassan, and K. A. Turano: Optometry Vision Sci. **80** (2003) 515.
20) J. R. Tresilian: J. Exp. Psychol.: Human Perception Perform. **20** (1994) 154.
21) C. A. Baker and W. C. Steedman: Human Factors **4** (1962) 343.
22) P. R. DeLucia: J. Exp. Psychol.: Human Perception Perform. **17** (1991) 738.
23) P. R. DeLucia and R. Warren: J. Exp. Psychol.: Human Perception Perform. **20** (1994) 783.
24) A. E. Welchman, V. L. Tuck, and J. M. Harris: Vision Res. **44** (2004) 2027.
25) R. Gray and D. Regan: Curr. Biol. **10** (2000) 587.
26) H. Levitt: J. Acoust. Soc. Am. **49** (1971) 65.
27) D. Regan and A. Vincent: Vision Res. **35** (1995) 1845.
28) W. T. Newsome, R. H. Wurtz, and H. Komatsu: J. Neurophysiol. **60** (1988) 604.
29) H. Sakata, M. Kusunoki, and Y. Tanaka: in *Brain Mechanisms of Perception and Memory*, ed. T. Ono, L. R. Squire, M. E. Raichle, D. I. Perrett, and M. Fukuda (Oxford University Press, Oxford, 1993) p. 166.
30) D. T. Field and J. P. Wann: Curr. Biol. **15** (2005) 453.