Research Article

How Dogs Navigate to Catch Frisbees

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ABSTRACT—*Using micro-video cameras attached to the heads of 2 dogs, we examined their optical behavior while catching Frisbees. Our findings reveal that dogs use the same viewer-based navigational heuristics previously found with baseball players (i.e., maintaining the target along a linear optical trajectory, LOT, with optical speed constancy). On trials in which the Frisbee dramatically changed direction, the dog maintained an LOT with speed constancy until it apparently could no longer do so and then simply established a new LOT and optical speed until interception. This work demonstrates the use of simple control mechanisms that utilize invariant geometric properties to accomplish interceptive tasks. It confirms a common interception strategy that extends both across species and to complex target trajectories.*

With little training, dogs can be remarkably good at chasing and catching airborne objects like Frisbees, even when the objects travel through complex trajectories that may dramatically change directions. In the present study, we tested whether dogs utilize the same simple viewer-based navigational heuristics that have been established for human baseball fielders catching fly balls (McBeath, Shaffer, & Kaiser, 1995a, 1996; McLeod & Dienes, 1993, 1996; McLeod, Reed, & Dienes, 2001; Michaels & Oudejans, 1992; Shaffer & McBeath, 2002). Using these heuristics, a pursuer controls the geometric relationship between him- or herself and the target, maintaining an optical image of the target that travels along a straight-line, constant-speed trajectory. We refer to these geometric relationships as optical linearity and optical speed constancy, respectively. Behavior consistent with the maintenance of optical linearity and speed constancy has been found in a variety of navigation-related domains (Adams, 1961; Bruce, Green, & Georgeson, 1996, pp. 267–285; Roscoe, 1968; Toates, 1975, pp. 151–257; Vishton & Cutting, 1995; Wickens, 1992, pp. 466–481). In the experiment reported here, we investigated whether nonhuman species intercepting targets use the same simple control mechanisms that baseball outfielders use to catch fly balls.

When baseball outfielders run to catch fly balls, they use natural, geometrically invariant properties to optically maintain control over the balls. When balls are headed off to the side, fielders select a running path that maintains a linear optical trajectory (LOT) for the ball relative to home plate and the background scenery. In our previous work, we found evidence indicating that the optical information available to the outfielder can be simply analyzed by examining it as a unified two-dimensional (2D) optical image. The geometry of the unified 2D optical image is shown in the top left panel of Figure 1, where α and β specify the vertical and lateral optical angles, respectively, between the ball and its initial optical location (home plate); ψ specifies the optical trajectory projection angle, or the observed angle of ball movement in the picture plane relative to the background horizon. In short, an LOT results when the fielder's running speed and direction maintain a rate of change in the horizontal optical angle, β, that matches the rate of change in the vertical optical angle, α. This is equivalent to maintaining a constant angle of the ball in the picture plane, ψ, as shown in the top right panel of Figure 1. To maintain a constant rate of lateral change, the outfielder remains fixated on the image of the ball while running along a path so as to actively rotate his or her vantage at a constant rate. This typically results in the fielder running fastest laterally at the start, getting a little ahead of the ball, and then easing up somewhat at the end.

A number of researchers have noted that when fielders run off to the side to catch fly balls, they simultaneously maintain a constant increase in the tangent of the vertical optical angle, tan α, which serves as a complementary cue to optical linearity (McBeath, Shaffer, & Kaiser, 1995b; McLeod et al., 2001). As the ball rises, tan α increases at a rate that is a function of the running path selected by the fielder. The fielder arrives at the correct destination by selecting a running path that keeps optical ball speed constant, achieving optical acceleration cancellation (OAC) in the vertical direction. This is shown in the bottom panel of Figure 1, where the optical ball trajectory is like that of an imaginary elevator rising from home plate at constant velocity.

We have shown previously that for balls headed to the side, the LOT is the dominant strategy, and OAC serves as a complementary cue for movement of the ball in the vertical direction (Shaffer & McBeath, 2002). In that work, we confirmed that for missed balls, both the LOT and the OAC strategies must eventually break down as the image of the ball curves toward the horizon. Yet even in those degenerative cases, fielders select a lateral path that continues to keep the image moving along a linear trajectory well after speed constancy is abandoned.
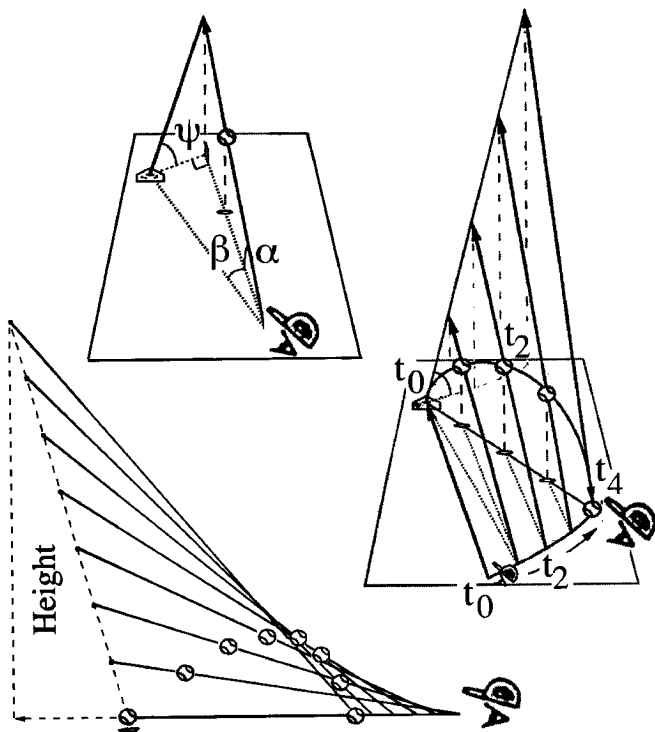
Fig. 1. The linear-optical-trajectory (LOT) model. The top illustrations show the view from a center-field bleacher as a fielder converges on a ball headed to his or her right. The trapezoidal box represents the perspective projection of the ground plane. The optical trajectory is shown with vectors from the fielder's position through the ball. The LOT model specifies that outfielders catch fly balls by running along a path that maintains a monotonically increasing linear optical trajectory of the ball. The illustration at the top left shows how the vertical optical angle (α), lateral optical angle (β), and projection plane optical angle (ψ) are defined. Operationally, α and β, respectively, are defined as the ongoing sums of all instantaneous vertical and lateral angular changes in the position of the target image. The illustration at the top right shows how the LOT heuristic maintains a constant projection angle across time (t_0–t_4). The fielder selects a running path such that the lateral optical ball movement remains proportional to the vertical optical ball movement. Because equal lateral optical angles span smaller distances for nearer than farther objects, the fielder ends up slowing down laterally as the ball approaches. The resultant running path curves slightly and circles under the ball. The bottom illustration is a side view of a fielder intercepting a fly ball in equal temporal intervals. This view shows a ball trajectory (with air resistance) and the fielder approaching from the right while maintaining optical acceleration cancellation. Mathematically, the fielder keeps the tangent of the vertical optical angle increasing at a constant rate.

Recently, McLeod et al. (2001) questioned the LOT strategy, noting that there appears to be systematic optical curvature of the ball image near the end of trajectories, particularly in the extreme case of infield pop-ups. In a reanalysis of their pop-up data, we explained that the LOT model still provides an excellent fit, accounting for a median of more than 97% of the variance (McBeath, Shaffer, & Sugar, 2002; McBeath, Shaffer, Sugar, & Roy, 2002). We also replicated the conditions of McLeod et al. and confirmed that the terminal optical curvature is consistent with threshold-level errors expected for LOT control theory with nonideal, real-world participants. The optical curvature is attributable to the increase in optical ball size near terminus, coupled with a combination of individual differences in

aggressiveness and handedness. Some fielders systematically err in the laggardly direction, whereas others favor running ahead, and balls exhibit more terminal optical curvature as the destination point of the fielder's hand is extended away from his or her eyes.

McLeod et al. (2001) also observed that fielders often initiate lateral movement within the 220 ms before the optical trajectory appears to curve, in seeming contradiction to LOT theory. We noted that this supposition is a misinterpretation of control theory, an interpretation that a control mechanism can respond to errors only reactively (McBeath, Shaffer, Sugar, & Roy, 2002). Using robotic modeling, we confirmed that anticipatory movement to the side is easily accounted for by the parameter-level setting of an active feed-forward mechanism, and that the inclusion of such a mechanism leads to behavior that matches that of humans (Sugar & McBeath, 2001; Suluh, Sugar, & McBeath, 2001). In short, there has been some debate concerning the range of generality of the LOT mechanism for interception, and this has led to insights regarding realistic thresholds, systematic individual differences, and parameter settings of control variables.

Use of the LOT and simultaneous maintenance of OAC in the vertical direction have been proposed as generic strategies that are geometrically constrained to ensure collision between a pursuer and its target. If so, then these strategies may be used to intercept any of a variety of types of moving targets both in domains outside of baseball and by other species. In the present study, we tested whether dogs use similar optical tracking strategies when trying to catch a Frisbee. This task provided a method of testing two different aspects of the generality of the LOT and OAC strategies. First, it allowed us to test whether these two strategies are used across species. Second, it allowed us to test whether these strategies are used irrespective of the flight complexity of the target being pursued. Baseball trajectories are somewhat predictable once initiated, even though aerodynamic drag and ball spin cause them to deviate from perfect parabolic motion (Brancazio, 1985; Watts & Bahill, 1990, pp. 133–149). However, Frisbees can dramatically change direction and speed depending on factors such as how they are thrown, gusts of wind, and the Frisbee angle during flight (Bloomfield, 1999). Thus, it is possible that a strategy like the LOT coupled with OAC may be used only until the occurrence of an unpredictable perturbation in the trajectory of the Frisbee, and then a separate strategy or set of strategies may be initiated.

METHOD

Participants
One springer spaniel, Romeo, and one Border collie, Lilly, participated in the experiment. Both were experienced in catching Frisbees.

Procedure
We mounted a Supercircuits in-line weather-resistant micro-video camera (Model PC75WR) on each dog's head with ace bandages in order to obtain the optical trajectories of Frisbees as the dogs navigated toward them. Each camera was wired to a battery pack and to a transmitter that the dog wore on its back. The equipment setup on Lilly is shown in Figure 2. The signal from the camera was transmitted to a receiver attached to a remote VCR, so that the VCR recorded the image from the micro-video camera.

Frisbees were launched at a variety of angles, all off to the side of the dog's initial position, at varying force from a distance of between 9

Fig. 2. Lilly the dog with the camera attached to her head and battery packs and transmitter located in a "doggie backpack" on her back. This picture was taken during a training trial in which Lilly was getting accustomed to the equipment.

Fig. 3. The optical trajectories of Frisbees on seven representative trials. Frisbee position is plotted as the lateral visual angle, β (in degrees), by the vertical visual angle, α (in degrees), at each 1/30-s video frame. The line over each of the trajectories is the estimate of the best-fit line used to compute the R^2 value. Open symbols are optical trajectories for Lilly, and filled symbols are optical trajectories for Romeo.

and 19 m. The dogs ran between 2 and 14 m to catch the Frisbees. We coded 63 trials in which the dog kept the Frisbee within the field of view of the camera and eventually caught the Frisbee. For these trials, we separately analyzed the Frisbee trajectory for an LOT and vertical OAC.

On five additional trials, we deliberately threw the Frisbee to one side at an angle such that it began moving in the opposite direction at greater speed in midflight. These trials on which the Frisbee changed direction and speed dramatically were analyzed separately to test the fit of a pair of LOTs and pair of OAC rates (i.e., a double LOT and OAC).

For each trial, we measured the trajectory of the Frisbee from the perspective of the moving dog. We recorded the ongoing instantaneous optical position of the center of the Frisbee relative to distant background markers each 1/30 of a second. We defined α and β, respectively, as the ongoing sums of all instantaneous vertical and lateral changes in the position of the Frisbee image. We also recorded the vertical speed pattern of the optical trajectory (plotted as tan α by time).

RESULTS AND DISCUSSION

For each of the first 63 trials, we plotted the ongoing optical position of the Frisbee in terms of α (the vertical visual angle) by β (the lateral visual angle) and determined the best-fit linear function to assess the variance accounted for by a straight-line optical trajectory (i.e., an LOT). A linear function accounted for a median of 93% of the variance in the optical movement of the Frisbee ($Mdn = 89\%$ for Romeo and 97% for Lilly). This provided significant support for the use of the LOT strategy as measured by a sign test, $z = 10.55$, $p < .001$.

Figure 3 shows sample optical trajectories while the dogs chased and caught Frisbees. The lines over the trajectories are estimates of the best-fit lines used to compute the R^2 values and help illustrate that the trajectories remained close to straight lines. Each optical trajectory, or path of the Frisbee from the perspective of the camera positioned on the dog's head, was maintained along a straight line that
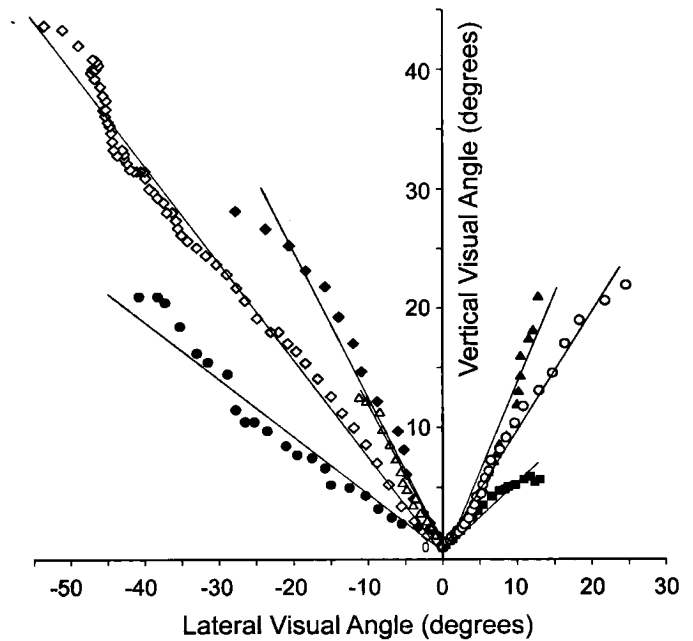
continued to rise throughout the Frisbee trajectory. The sample trajectories in this figure are remarkably similar to ones showing the LOTs maintained by outfielders running to catch fly balls and support the premise that dogs utilize the same strategy to catch Frisbees as baseball outfielders use to catch fly balls (McBeath et al., 1995a). The findings for the optical trajectories support the notion that the LOT is a generic tracking strategy used not only by humans pursuing ballistic objects, such as in baseball, but also by dogs chasing Frisbees.

We also analyzed the same 63 trials to test whether the dog simultaneously kept the Frisbee moving at a constant optical speed in the vertical direction. To test this, we plotted the acceleration of the vertical optical angle (i.e., tan α) by time and found that a linear function accounted for a median of 94.12% of the variance in the vertical tangent, tan α ($Mdn = 94.18\%$ for Romeo and 93.87% for Lilly). This result supports the hypothesis that the dogs were keeping the image of the Frisbee moving at a constant rate in the vertical direction. Thus, dogs catching Frisbees appear to maintain a path that nulls acceleration of the vertical optical angle α (i.e., OAC) and use the OAC as a complement to the LOT. These results replicate our previous findings with outfielders catching fly balls headed off to the side.

We analyzed separately the optical paths from the five trials in which the Frisbee began moving in a new direction and at a new speed during midflight. Figure 4 shows sample optical trajectories from these trials. In these cases, the optical path of the Frisbee was moving in one direction and then suddenly began moving in a dramatically different direction. As Figure 4 shows, the dogs did not appear to abandon the LOT strategy, but simply chose one LOT strategy before the large perturbation and then a new LOT strategy after the perturbation. For
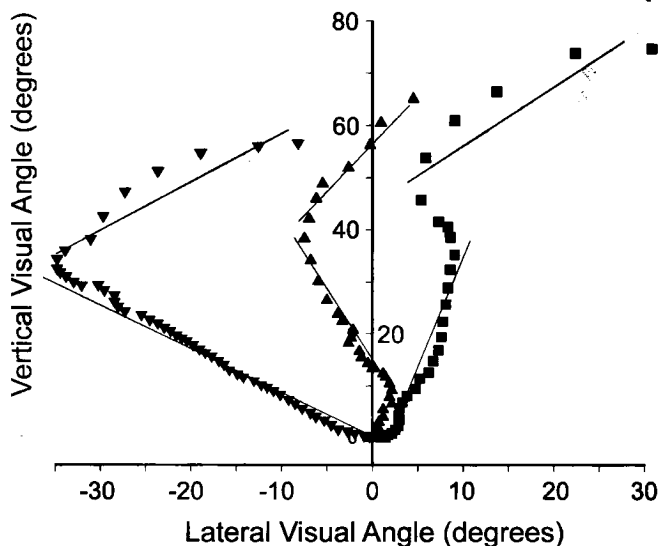
Fig. 4. The optical trajectories of Frisbees on three representative trials in which the Frisbee was deliberately thrown to make a large perturbation in its trajectory. Frisbee position is plotted as the lateral visual angle, β (in degrees), by the vertical visual angle, α (in degrees), at each 1/30-s frame. The line over each of the trajectories is the estimate of the best-fit line used to compute the R^2 value.

these five trials, we found that two lines (i.e., a double LOT) accounted for a median of 91% of the variance in optical movement. The data provided significant support for the use of the LOT strategy, as indicated by a sign test, $z = 4.35$, $p < .001$.

As Figure 4 shows, not only did these optical trajectories appear to fall along two separate straight lines, but they also displayed two characteristic optical speeds along the two lines. We found that two rates of optical speed constancy accounted for a median of 92.36% of the variance in the rate of change of the vertical tangent. Thus, both before and after the Frisbee made its shift, the dogs maintained temporal constancy to a large degree, at the same time that they maintained an LOT. This result supports our previous findings showing that for aerial targets headed off to the sides of pursuers, temporal constancy in the vertical direction is maintained as a secondary cue complementary to spatial linearity.

GENERAL DISCUSSION

Our findings with dogs catching Frisbees further support the generality of viewer-based navigational strategies and control heuristics (Cutting, Springer, Braren, & Johnson, 1992; Cutting & Wang, 2000; Royden & Hildreth, 1996). Behavior consistent with maintaining spatiotemporal constancy between a pursuer and a moving target is found in many domains. For example, airplane pilots are very accurate at spatial tasks of error nulling and pursuit tracking that allows them to maintain constant angle position relative to a target. They also appear to use a strategy of maintaining constant angular changes to guide their turning radius when approaching a runway from an oblique angle (Beall & Loomis, 1997). In general, both aircraft and boat pilots can produce a collision course with another moving craft by maintaining an angle of heading or bearing angle that remains constant relative to the image of the other craft (Pollack, 1995).

Further evidence of the generality of viewer-based interception strategies comes from research with predators tracking prey, and with organisms tracking potential mates, which has shown that adjustments in position are made to maintain control of relative angle of motion between the pair. Tracking research with hoverflies and teleost fish (*Acanthaluteres spilomelanurus*) indicates that they "lock on" to the motion of their target in a manner that maintains optical angle constancy to guide their pursuit (Collett & Land, 1978; Lanchester & Mark, 1975). Maintenance of optical angle constancy to guide pursuit has also been found in tethered flies and free-flying houseflies (Collett & Land, 1975; Reichardt & Poggio, 1976). Research investigating the predator-prey characteristics of bats, birds, and dragonflies has found that they maintain a constant optical angle between themselves and their prey (Jablonski, 1999; Olberg, Worthington, & Venator, 2000; Simmons, Fenton, & O'Farrell, 1979). Finally, our work with automated mobile robots confirms the viability of viewer-based strategies like the LOT and OAC for interception of moving projectiles.

The LOT with concomitant use of OAC appears to be a generic tracking strategy that can be used by a pursuer to navigate toward a moving target in the environment. Additionally, neither the LOT nor the OAC strategy needs to be constrained to the domain of relatively simple, predictable target trajectories, such as in baseball. The current study supports the generality of the use of viewer-based spatiotemporal constancy cues in navigation both across species and across targets varying in flight-path complexity. The present work indicates that when the path of a moving target is sufficiently altered, maintenance of linearity is momentarily disrupted, and then the pursuer adopts a second LOT and OAC that are maintained until interception (i.e., a double LOT). Thus, an LOT-with-OAC strategy can be generalized to situations with complex target movement. In general, pursuers try to maintain a single LOT and OAC, and when the behavior of the target is sufficiently altered, they appear to simply adopt a newer, updated LOT and OAC. In short, the LOT and OAC strategies appear to be widely used viewer-based navigational heuristics for pursuing and intercepting moving targets in three-dimensional space.

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