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Predictive eye movements when hitting a bouncing ball

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Predictive eye movements targeted toward the direction of ball bounce are a feature of gaze behavior when intercepting a target soon after it has bounced. However, there is conjecture over the exact location toward which these predictive eye movements are directed, and whether gaze during this period is moving or instead "lies in wait" for the ball to arrive. Therefore, the aim of this study was to further examine the location toward which predictive eye movements are made when hitting a bouncing ball. We tracked the eye and head movements of 23 novice participants who attempted to hit approaching tennis balls in a virtual environment. The balls differed in time from bounce to contact (300, 550, and 800 ms). Results revealed that participants made predictive saccades shortly before the ball bounced in two-thirds of all trials. These saccades were directed several degrees above the position at which the ball bounced, rather than toward the position at which it bounced or toward a position the ball would occupy shortly after the bounce. After the saccade, a separation of roles for the eyes and head ensured that gaze continued to change so that it was as close as possible to the ball soon after bounce. Smooth head movements were responsible for the immediate and ongoing changes in gaze to align it with the ball in the lateral direction, while eye movements realigned gaze with the ball in the vertical direction from approximately 100 ms after the ball changed its direction of motion after bounce. We conclude that predictive saccades direct gaze above the location at which the ball will bounce, presumably in order to facilitate ball tracking after the bounce.

Introduction

People move their eyes to where important information is to be found. When people are asked to look at a scene in the absence of a particular task, the eyes are usually attracted by high contrasts (Parkhurst, Law, & Niebur, 2002; Tatler, Hayhoe, Land, & Ballard, 2011; Treue, 2003) and by sudden changes in the scene (Orquin & Loose, 2013). However, people do not typically just look at scenes for no apparent reason.

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In performing a task, the eyes are usually directed toward task-relevant objects and regions, presumably in order to acquire information that will help guide task execution (e.g., Land, Mennie, & Rusted, 1999). Moreover, since guiding an action takes time, information must sometimes be acquired somewhat in advance of when it is critical for the ongoing action. In that case, gaze shifts must sometimes rely on judgments about where useful information will be found in the near future, rather than always relying on the action itself to guide gaze. Examples of such gaze shifts are that the eyes are regularly directed ahead of the hand and teapot when making tea (Land et al., 1999) and ahead of the foot during walking (Matthis & Fajen, 2014; Matthis, Yates, & Hayhoe, 2018). People have been shown to fixate locations exactly at the moments at which they need information from those locations (Triesch, Ballard, Hayhoe, & Sullivan, 2003). The extent to which gaze should precede the hand or leg depends on the relevant sensorimotor delays and whether there are mechanical issues to consider (Matthis et al., 2018).

One situation that has been used to study predictive eye movements is when attempting to intercept a moving target shortly after it bounces, as for instance occurs in tennis or cricket, where the approaching ball is hit after it has bounced off the ground surface. In these situations, *predictive saccades* move gaze ahead of the ball toward the direction of the ball's anticipated location of bounce (Land & McLeod, 2000; Ripoll, Fleurance, & Caseneuve, 1987). This is an interesting situation, because the eyes move to a position at which useful information is expected to appear sometime in the future, rather than useful information necessarily being present when the eyes arrive there. Predictive saccades occur immediately prior to bounce irrespective of the ball speed (Croft, Button, & Dicks, 2010), suggesting that they have a functional purpose rather than being a simple compensation for a ball that is traveling too fast to be tracked by the eyes. Moreover, recent evidence suggests that predictive saccades may be guided by an internal model of ball motion (Diaz, Cooper, Rothkopf, & Hayhoe, 2013; Hayhoe, Mennie, Sullivan, & Gorgos, 2005), with complex predictions made by integrating the observer's experience from prior trajectories with real-time information about the ball's trajectory (Diaz et al., 2013). Accordingly, predictive saccades offer promise as a model for understanding the basis of sensorimotor predictions.

In the 1980s, Ripoll and colleagues revealed that skilled table-tennis players use predictive saccades to move their eyes ahead of an approaching ball's trajectory when attempting to hit it (Ripoll & Fleurance, 1988; Ripoll et al., 1987). They tested five of the best table-tennis players in France and showed that rather than pursuing the ball with their gaze until the bounce and then adjusting gaze to the ball's motion after the bounce, the players (after an initial period of tracking) produced a saccade that moved gaze ahead of the ball's trajectory toward the anticipated position at which the ball would bounce. After the bounce, the players attempted to pursue the ball again, but often fell behind. The results provided one of the first indications that skilled interception involves the use of motion-trajectory information to generate predictions about the future position of the ball, and that there may be some advantage in generating predictions rather than trying to smoothly track the ball with the eyes throughout the entirety of its flight.

Almost 15 years later, Land and McLeod (2000) published their seminal work claiming that the ability to generate early predictive saccades constitutes an important element of skill during interception. In that study, the eye movements of three cricket batsmen of different skill levels were tracked while the batsmen attempted to hit balls projected toward them. All three batsmen made predictive saccades that redirected gaze toward the location of bounce, after which gaze was said to "lie in wait" for the ball's arrival. Critically, Land and McLeod reported a systematic relationship between the skill of their three participants and the timing of saccades, with the more skilled batsmen found to produce earlier predictive saccades. This finding was interpreted as evidence to suggest that skilled athletes may have developed a better propensity for prediction, and that the ability to generate earlier predictions may help explain a skilled batsman's advantage in the game. Moreover, Land and McLeod's model of ball-flight prediction suggested that information at ball bounce was crucial for anticipating the position at which the ball would ultimately arrive.

There remains controversy about whether skilled athletes do actually generate earlier predictive saccades during interception. In a recent study of 23 elite and 20 club-level cricket batsmen, Sarpeshkar, Abernethy, and Mann (2017) were unable to find evidence to support the claim that better batsmen generate earlier predictive saccades. In fact, there was evidence to suggest that the elite batsmen in some cases made *later* predictive saccades, delaying their eye movements when attempting to intercept the most challenging ball trajectories. Similarly, Mann, Spratford, and Abernethy (2013) compared the eye and head movements of two of Australia's best-ever cricket batsmen to those of two competent but less-skilled club batters and found no difference in the timing of the predictive saccades. They did, however, find evidence that the elite batsmen were *more consistent* in the timing of their saccades. Moreover, the elite batsmen were better characterized by the movement of their *heads*. Specifically, the elite batsmen were more likely to match the downward rotation of their head to that of the ball, meaning that the ball was maintained in a consistent egocentric direction in a head-centered frame of reference. In sum, the ball was being pursued by the *head* while predictive saccades were moving the eyes in advance to future locations along the ball's trajectory, including the anticipated location of ball bounce.

The idea that predictive saccades redirect gaze toward the exact location of bounce has been questioned by other studies that show that prebounce saccades may actually target gaze toward a location *beyond* the bounce (Diaz et al., 2013; Hayhoe et al., 2005; Land & Furneaux, 1997). As a case in point, Diaz et al. (2013) have shown that novice racquetball players produce predictive saccades that target where the ball will be at a very specific moment in time *following* bounce. In that study, participants were required to hit balls, in a virtual environment, that followed one of three trajectories differing according to the prebounce (and therefore postbounce) velocity of the ball. Diaz et al. found that irrespective of the ball trajectory, participants directed their saccades in such a way that gaze landed where the ball would be approximately 170 ms after the bounce. What was most remarkable was that after the elasticity of the ball was experimentally manipulated to alter the postbounce ball velocity, the novice participants almost immediately adapted their saccades so that gaze would continue to be relocated to where the ball would be 170 ms after bounce. The fact that these saccades were generated before the bounce provides evidence to suggest that they were produced using a combination of both real-time information about prebounce ball trajectory and prior information about the elasticity of the ball. Moreover, the findings imply that there might be something particularly meaningful or performance facilitating about a time delay of 170 ms between bounce and realignment of ball and gaze.

At this point it is unclear why some studies would report that predictive saccades redirect gaze toward the bounce while others suggest that gaze redirects beyond bounce. Different situations may require different predictive strategies. For instance, in some situations it may be advantageous to move gaze beyond bounce, whereas in others it might not. A real cricket ball's path after the bounce may be much less predictable than that of a virtual racquetball, making it less advantageous to anticipate how the ball will proceed after it bounces. Another possible difference is related to the time constraints inherent in different hitting tasks. In the study by Diaz et al. (2013), participants had about 800 ms available between the moment of bounce and the time that they could hit the ball. In that situation there is sufficient time to reestablish pursuit after the bounce and make alterations to the action on the basis of real-time information that becomes available after ball tracking recommences. In contrast, less than 300 ms was available after bounce in the cricket and some table-tennis studies, where saccades were reported to move to the bounce location itself. In those situations, there may be little point in moving gaze beyond bounce because sensorimotor delays mean that it may become too late to adjust movements after ball tracking has been reestablished (Brenner & Smeets, 1997; McLeod, 1987; Sarpeshkar & Mann, 2011), if indeed gaze tracking could be reestablished at all. In this sense, the temporal constraints of the task might influence the nature of the predictions made.

An alternative explanation for the conjecture over the landing point of the saccades could be that one consistent predictive strategy might exist during interception (i.e., either toward or beyond bounce) but that methodological limitations in some studies could have led to a misinterpretation of the direction toward which prebounce saccades were directed. Because results in studies of natural interceptive actions are often interpreted on the basis of footage from mobile (head-mounted) eye trackers, Diaz et al. (2013) have conjectured that in tasks where it is difficult to distinguish between the ball trajectory at and beyond bounce (such as cricket batting), gaze may have been misinterpreted as being directed toward rather than beyond the bounce. Specifically, if the ball were to be looming toward the participant's head following bounce, then it would be difficult to disentangle whether gaze were directed toward bounce or some location beyond it. Further, there have historically been limitations in the temporal (and spatial) accuracy of mobile eye-tracking systems used in studies of natural interceptive actions (e.g., a frame rate of 30–40 Hz), and this could have also led to misinterpretations of the actual location of gaze in high-speed tasks such as cricket batting and table tennis (Kredel, Vater, Klostermann, & Hossner, 2017; Mann, Causer, Nakamoto, & Runswick, 2019).

The aim of this study was to determine the location toward which predictive eye movements are made when hitting a bouncing ball. We tracked the eye movements of novice participants who attempted to hit approaching balls in a virtual tennis environment. By manipulating the time from bounce to contact (300, 550, or 800 ms), we sought to determine whether the direction toward which predictive saccades were directed was influenced by the temporal constraints of the task. In addition, given the influence of prior information in generating predictive saccades, we expected that ball trajectories presented in a blocked fashion (where the predictability of a ball's trajectory is high) would result in earlier saccades that relocated gaze farther along the future trajectory than trials presented in a random fashion. We therefore presented balls both as blocks of trials with the same time from bounce to contact and in blocks in which all three times were randomly interleaved.

Method

Participants

Twenty-three right-handed participants (*M* ± *SD* age = 21.3 ± 1.1 years) with minimal experience playing tennis (0.8 ± 1.9 years) volunteered to take part in the study. Participants provided written informed consent to take part in a procedure approved by the Scientific and Ethical Review Committee of the Faculty of Behavioural and Movement Sciences at Vrije Universiteit Amsterdam according to the tenants of the Declaration of Helsinki.

Apparatus and stimuli

A custom-made virtual-reality tennis environment was created using the Unity game engine (Unity Technologies, San Francisco, CA). The virtual environment consisted of a room in which there was a tennis court whose dimensions matched those of a regular court (23.77 × 10.97 m). Tennis balls could be launched from and toward any location on the court, with the ball trajectories following standard Newtonian laws.

An HTC Vive head-mounted display VR system (HTC Corporation, New Taipei City, Taiwan) was used for the experiment. The HTC Vive consists of a headset, two controllers, and two lighthouses which emit infrared laser sweeps to localize the headset and controllers. The HTC Vive has been reported to have excellent spatial and temporal precision (accuracy up to 1.5 cm and jitter < 0.5 mm; Borrego, Latorre, Alcañiz, & Llorens, 2018; latency up to 22 ms; Niehorster, Li, & Lappe, 2017) and to be particularly suitable for the examination of tasks where the movement of participants through virtual space is limited (Niehorster, Li, & Lappe, 2017).

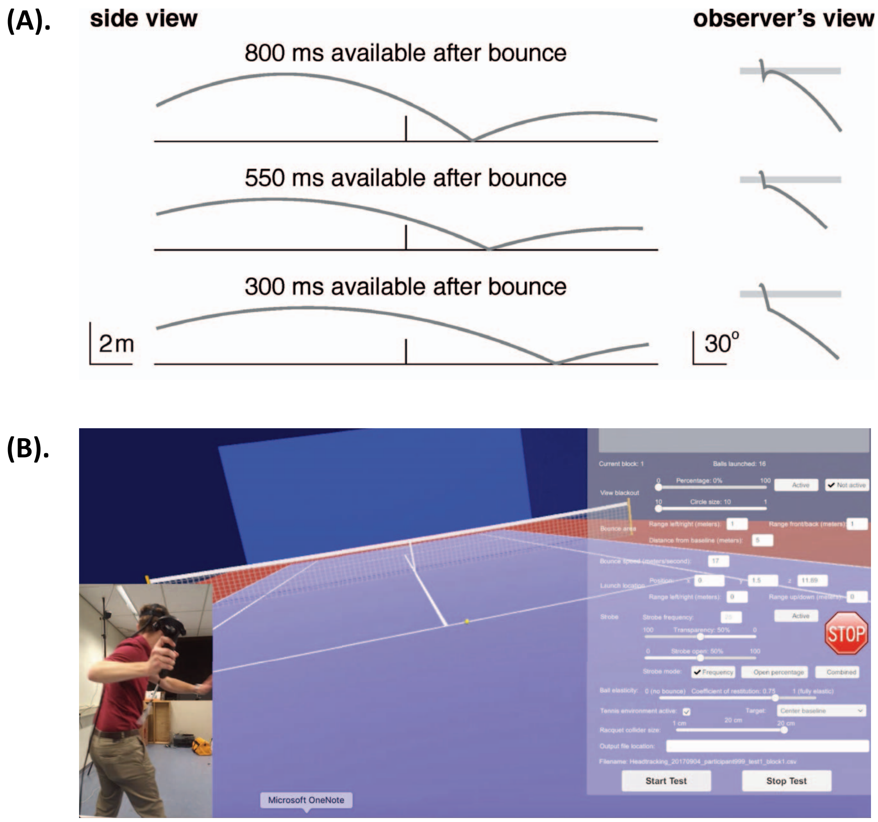
Participants wore the Vive headset to view the virtual environment and attempted to hit the ball using a virtual tennis racquet that was controlled by one of the Vive controllers sampling at 90 Hz. The postcontact direction of the ball was calculated by considering the approach velocity of the ball and the angle, velocity, and angular velocity of the racquet. Although the racquet appeared to be of regulation size, its thickness for the purposes of calculating collisions between racquet and ball was exaggerated to 20 cm to account for tunneling issues resulting from the limited sampling rate of the HTC Vive system, whereby the racquet is represented as a succession of discrete locations in space rather than a continuous trajectory.

An SMI eye tracker (Sensorimotor Instruments GmbH, Teltow, Germany) fitted into the VR headset was used to measure eye movements during the task (sampled at 90 Hz). The SMI eye tracker is a binocular system that was used to determine a single (cyclopean) direction of gaze. Head direction was recorded by measuring the position and orientation of the headset. Calibration was performed using SMI's built-in 5-point on-screen calibration that spanned 26° of visual angle horizontally and 23° vertically. The calibration measured the mean error between each of the measured locations of gaze and their respective on-screen calibration targets. Only calibrations where the mean error was less than 1° were accepted; calibrations were repeated in any cases where the error exceeded 1°. We used autocorrelation of the eye and head traces recorded when rotating the head during fixation (VOR task; see Matthis et al., 2018) to determine that there was a five-frame ($\approx$55 ms) delay in recording eye direction relative to the head and accounted for this delay in our calculations of eye direction relative to the head.

Procedure

Participants stood at the center of the baseline (11.89 m from the net) on their side of the simulated tennis court and were instructed to hit approaching balls over the net so that the ball landed within the opposite side of the court. They controlled the launch of the ball by pressing a trigger on the back of the Vive controller. Balls were launched from the opposite baseline (23.78 m away) from a height of 1.7 m above the ground and 2 m to the left of the center of court (from the viewpoint of the receiver). Balls always passed through a position 1 m above the ground and 1 m to the right of the center of the baseline, though participants were free to hit the ball before (or after) it reached this point. The movement of the balls from the left to the right of the right-handed participants ensured that we could observe changes in gaze in both the horizontal and vertical directions. The ball elasticity, which specified the ratio of post- to prebounce vertical velocity, was set at 0.65 for all trials.

We presented three different *time-after-bounce* ball trajectories that differed in the time available from bounce to contact (300, 550, 800 ms from bounce to arrival at the baseline; Figure 1). Accordingly, the ball trajectories were constrained by the location of launch, arrival, and time from bounce to arrival. Note in the observer's view in Figure 1 how the ball clearly moved upward after the bounce when the time after bounce was 800 ms (top panel), tended to initially loom toward



Current block: 1 Balls launched: 16

View blackout: Percentage: 0% (0–100); Active; ✓ Not active; Circle size: 10 (10–1)

Bounce area: Range left/right (meters): 1; Range front/back (meters): 1; Distance from baseline (meters): 5

Bounce speed (meters/second): 17

Launch location: Position: x 0, y 1.5, z 11.89; Range left/right (meters): 0; Range up/down (meters): 0

Strobe: Strobe frequency: [illegible]; Active; Transparency: 50% (100–0); Strobe open: 50% (0–100); Strobe mode: ✓ Frequency; Open percentage; Combined

Ball elasticity: 0 (no bounce) Coefficient of restitution: 0.75 1 (fully elastic)

Tennis environment active: ☑ Target: Center baseline

Racquet collider size: 1 cm 20 cm 20 cm

Output file location:

Filename: Headtracking_20170904_participant999_test1_block1.csv

Figure 1. Experimental setup. (A) The three ball trajectories as seen from the side (left; orthographic projection) and from the observer's vantage point (right; perspective projection). The vertical line in the side view and gray horizontal bar in the observer's view represent the net. (B) A screenshot of the tennis court as seen by the participant, with the control panel on the right used to program ball-flight characteristics (not seen by participants) and the inset showing a participant performing the task.

the participant following bounce in the 550-ms condition (middle panel), and moved down in the participant's field of view when there was only 300 ms available after the bounce (bottom panel). Participants attempted to hit 75 practice balls to become accustomed to hitting balls in the virtual environment (25 trials for each of the three ball trajectories, in random order) and then performed five sets of 30 trials in which eye movements were measured. The first and last of these sets contained 10 trials of each ball trajectory that were presented in a random order. The remaining three sets each contained 30 blocked trials of a single trajectory. The order in which the three sets of blocked trials were presented was counterbalanced across participants.

Data analysis

To identify saccades, we determined the velocity of the eyes at each moment by dividing the distance between the eye direction on the next and previous samples by the time between those samples, and then determined the acceleration of the eye at each moment by dividing the difference between the velocities on the next and previous samples by the time between those samples. We determined the median absolute acceleration during the trial, and defined saccades as portions of the eye traces between which the acceleration was more than five times this median absolute acceleration or less than negative five times this median absolute acceleration. In addition, the amplitude of the overall change in eye orientation during a saccade had to be at least 1° and gaze had to be moving at least 20% faster than the ball (to avoid the detection of pursuit rather than saccades). Occasional eye movements that fulfilled these criteria but were immediately preceded or followed by missing data were not considered, because they were likely to be blinks. We categorized the saccades as *corrective saccades* if gaze was closer to the ball at the end of the saccade than it was at the beginning, and as *predictive saccades* if gaze was closer to the ball at the beginning than at the end. We were primarily interested in predictive saccades that took place during the final 400 ms prior to bounce.

When evaluating the contributions of the eyes and head to changes in gaze (as in the examples in Figure 2), we show head rotation and ball position in a coordinate system that is fixed in space with an origin at the head, with the exception that eye orientation is shown in a

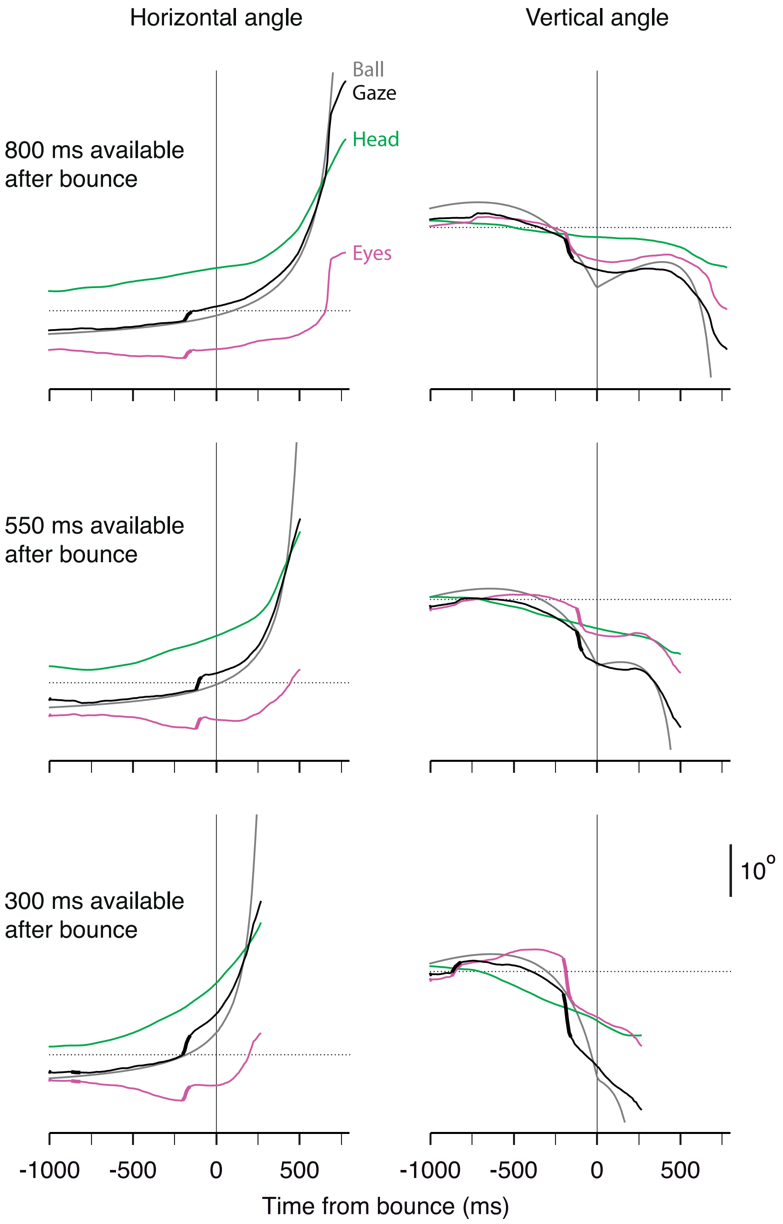


Figure 2. Angular eye and head movements of one participant during one trial for each of the three time-after-bounce ball trajectories. The plots show the first trial with a predictive saccade within the 400 ms prior to bounce in a session in which all three ball trajectories were randomly interleaved. Purple traces: eye-in-head rotation. Green traces: head rotation in space. Black traces: eye in head and head in space combined to give approximate gaze trajectories. Gray traces: ball-in-space trajectories. Thick parts of the eye and gaze trajectories indicate saccades. The left and right panels show the horizontal and vertical components of the same trial. The dotted horizontal lines represent orientations straight ahead with respect to the head for the eyes, and straight down the court at eye height for the head, ball, and gaze.

coordinate system that is fixed to the head with its origin in the orbit. In these cases, we combine the eye movements relative to the head with the head's orientation in space to determine the two-dimensional gaze direction in space, and therefore we are considering the head's pitch and yaw but ignoring its roll. Much of our remaining analysis is based on plotting the position of the ball within the field of view. For our analysis of the position of the ball with respect to gaze, we do consider head roll. We combine the direction of gaze with respect to the head with the three-dimensional position and orientation of the head in space and the three-dimensional position of the ball in space to determine where gaze was oriented relative to the ball in head-centered coordinates. To determine whether participants looked ahead of the ball's trajectory, we plotted the ball's head-centric position with respect to gaze at two particular moments of interest: the moment

	Blocked			Random			
	800 ms	550 ms	300 ms	800 ms	550 ms	300 ms	Total
Percentage of trials with contact between racquet and ball	78	61	58	66	56	60	65
Percentage of trials with ball hit over the net	16	9	7	10	9	6	10

Table 1. Participants' success rates for hitting the virtual ball in each of the experimental conditions.

the predictive saccade ended and the moment of the bounce. We did not exclude any of the trials in which participants made predictive saccades, but in some figures we have weighted the data by our confidence in the eye-movement recordings to some extent by making the size of the plotted dots inversely proportional to the median angular distance between gaze and ball during the time period in which we expected good pursuit (between 1,000 and 200 ms before the bounce). We also calculated the horizontal and vertical velocity of the eyes relative to the head, and of the head and ball in space across the time course of each trial. Since it became evident that the eyes and head were not always static near the moment of the bounce, we determined how the head, eyes, and ball moved for the time periods from −100 to 0 ms, 1 to 100 ms, and 101 to 200 ms relative to the moment of bounce.

We established the percentage of trials with predictive saccades and the median times at which predictive saccades occurred relative to bounce, and used 3 (time after bounce: 300, 550, 800 ms) × 2 (presentation order: random, blocked) repeated-measures analyses of variance to test for differences between conditions ($\alpha = 0.05$). For comparing the horizontal and vertical orientations of gaze relative to the ball across various pairs of groups of trials, we used Wilcoxon signed-rank tests on the aggregate data ($\alpha = 0.001$).

Results

Participants managed to make contact with 65% of the virtual balls projected toward them, but only succeeded in hitting 10% of them over the net (see Table 1). It was more difficult to hit the ball when there was less time between bounce and contact.

Most saccades that were classified as predictive occurred during the final 400 ms before the bounce, irrespective of the differences between the prebounce trajectories that were needed to realize the different time-after-bounce conditions (aqua-colored curves in Figure 3). Of the 3,480 trials, 80% (2,779) had a saccade that started during the final 400 ms before the bounce, with two-thirds of all trials (67%; 2,325 trials) containing a predictive saccade that moved gaze farther ahead of the ball during the last 400 ms before the bounce. Predictive saccades occurred more frequently when the time after bounce was only 300 ms (Table 2)—main effect of time-after-bounce, $F(2, 44) = 9.074$, $p < 0.001$—with the difference in the frequency of saccades across time-after-bounce conditions being more pronounced in the blocked trials than in the random trials—significant time-after-bounce × Presentation order interaction, $F(2, 44) = 3.401$, $p = 0.042$. The predictive saccades did not occur earlier in trials in which the ball trajectories were blocked (Table 2, Figure 3; no significant effects of presentation order, time-after-bounce, or their interaction).

We now turn to a consideration of the direction toward which gaze was located at the completion of the predictive saccades. Unless mentioned otherwise, for the following analyses we consider only trials in which a predictive saccade was initiated between 400 ms before the bounce and the moment of the bounce. Figure 4 shows that if gaze were held still at the end of the saccade, then the vertical elevation of gaze in the 800-ms condition would have coincided with the vertical elevation of the ball about 150–200 ms after bounce (similar to the 170 ms described by Diaz et al., 2013). However, in the horizontal direction, gaze at the end of the predictive saccades was slightly behind where the ball would later bounce (red and blue vertical lines are to the right of gaze in the top panel at $t = 0$ ms). This provides the first indication that predictive saccades do not simply bring gaze to a future position on the ball's trajectory. Considering the absolute distance of the ball from where gaze landed at the end of the predictive saccades, the ball passed closest to gaze at 83 ± 19 ms after bounce for the randomly presented trajectories ($M \pm SD$ across participants) and 121 ± 18 ms after the bounce for the blocked trajectories (see also the first minima following bounce in the curves shown in Figure 5).

The predictive saccades also landed above and to the left of the bounce point when there was less time to pursue the ball after the bounce (time after bounce of 550 or 300 ms; central and lower rows in Figure 4). Since the ball bounced lower in those conditions, it rarely realigned vertically with where gaze was directed at the end of the saccades. When there was 550 ms after the bounce, the ball passed closest to the saccade endpoints at 82 ± 11 and 86 ± 15 ms after the bounce for the random and blocked trajectories, respectively. When the time after bounce was 300 ms, the ball moved away from the saccade endpoints immediately after the bounce

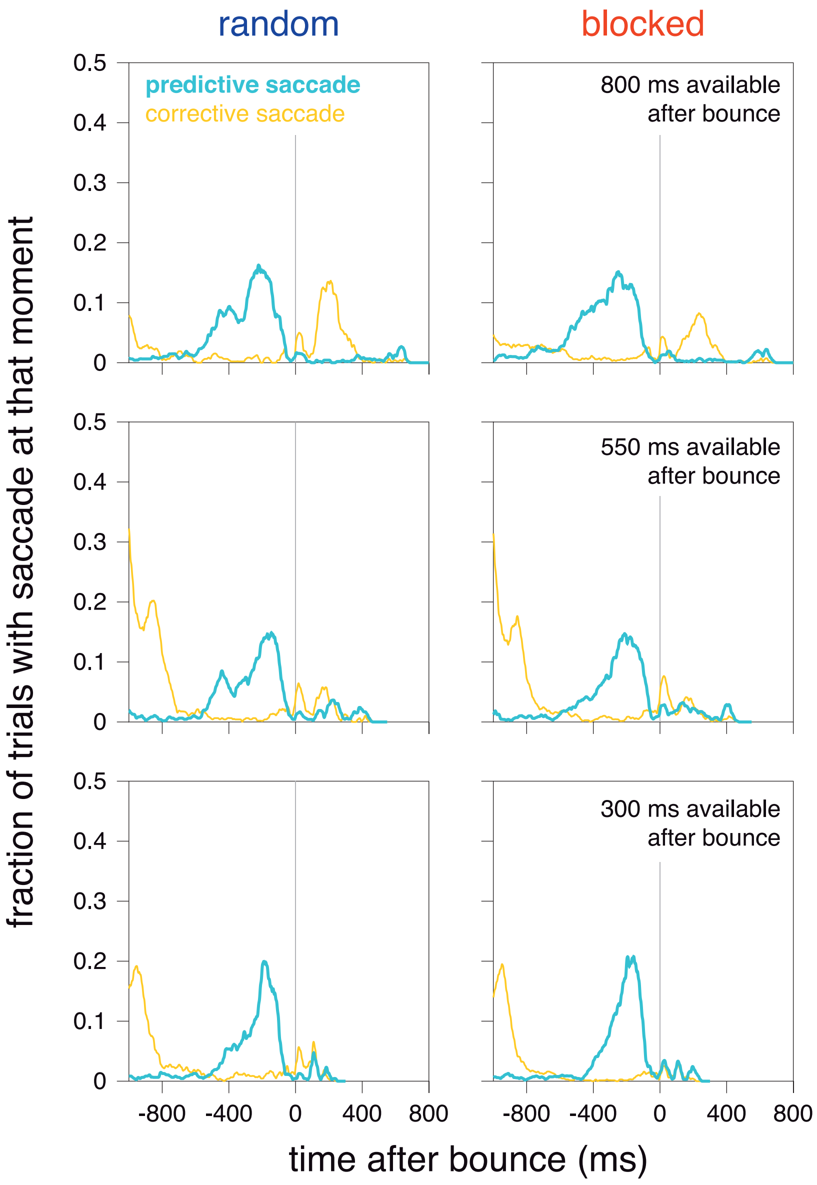


Figure 3. Occurrence of saccades as a function of time for each ball trajectory. Rows compare the time-after-bounce conditions and columns compare the random (left) versus blocked (right) trials. Predictive saccades (aqua) are saccades that end with gaze farther from the ball than it started. Corrective saccades (yellow) are saccades that end with gaze closer to the ball. It may appear as though more saccades were found soon after release in the trials where there was 550 ms available from bounce to contact, but this is largely an artifact, because we show only the final 1,000 ms before bounce, and those trials had the shortest time from release to ball bounce.

Time after bounce (ms)	% of trials with a predictive saccade		Timing of predictive saccade (ms relative to bounce)	
	Random	Blocked	Random	Blocked
800	67.5	62.0	−164	−140
550	65.1	64.1	−102	−110
300	74.6	79.0	−139	−152

Table 2. Predictive saccades across each of the three time-after-bounce conditions. All values are averages across the 23 participants.

(Figure 5). These findings suggest that the 170-ms delay found by Diaz et al. (2013) when the time after bounce was 800 ms does not generalize to different ball trajectories. Prior knowledge of the ball trajectory had little influence on the landing position of the saccades, although the saccades did appear to land slightly higher when the trajectories were blocked than when they were randomly interleaved if there was 800 ms after the bounce.

If the goal were to be looking at a certain point when the ball bounced, then we might expect gaze to be

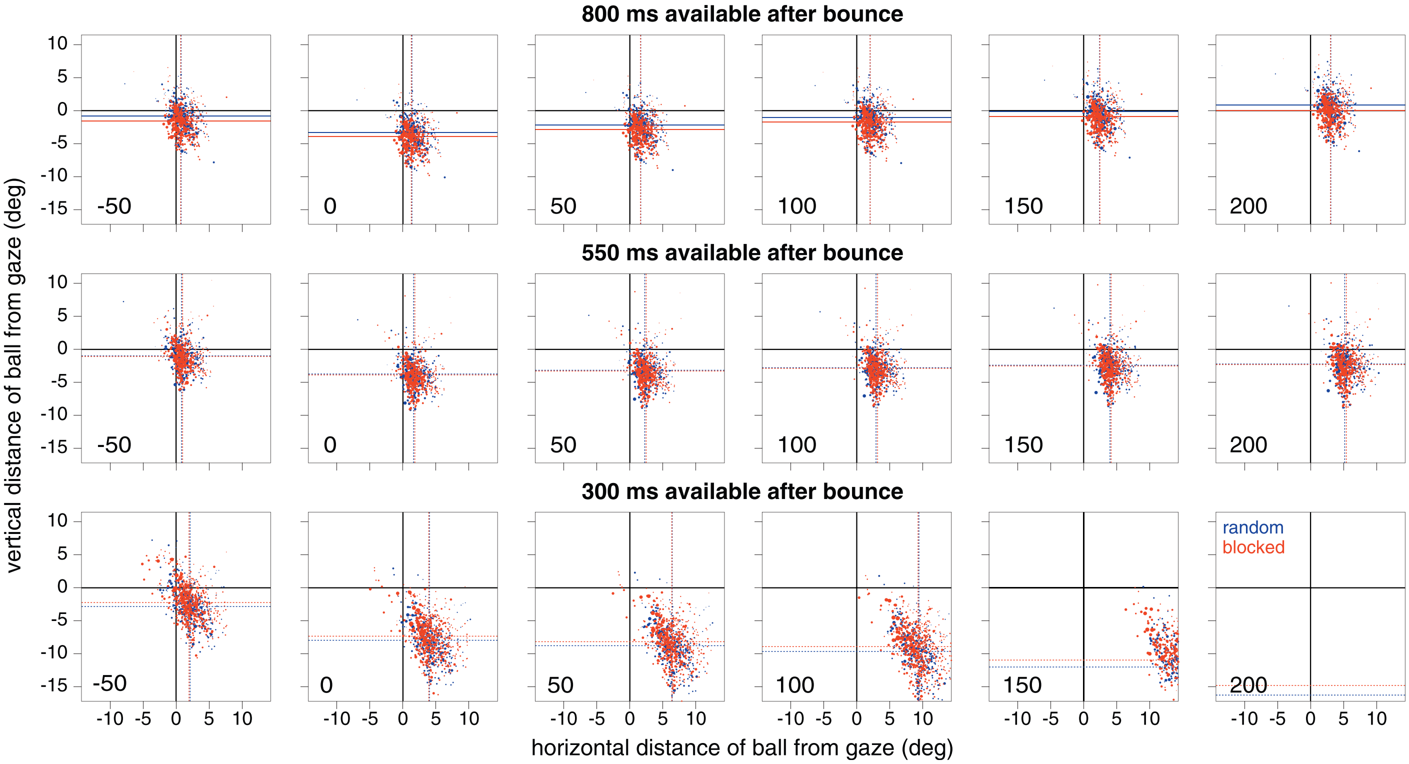


Figure 4. Position of the ball relative to the location in space toward which gaze was directed at the end of each prebounce predictive saccade. Angles between ball and gaze are presented in head-centered coordinates (horizontal is along the interocular axis, using the head orientation at the end of the saccade). The different panels within each row show the position of the ball at various times relative to the moment of the bounce (times in milliseconds indicated by the numbers in the lower left corners). Each dot is one trial. Dot sizes are inversely proportional to the median distance between gaze and ball between 1,000 and 200 ms before the bounce. When trajectories were randomly interleaved the dots are blue, and when presented in separate blocks the dots are red. The red and blue horizontal and vertical lines indicate the corresponding median values (solid lines indicate a significant difference between the random and blocked conditions). Some trials fall outside the panels, particularly for time points well after bounce in the 300-ms time-after-bounce condition.

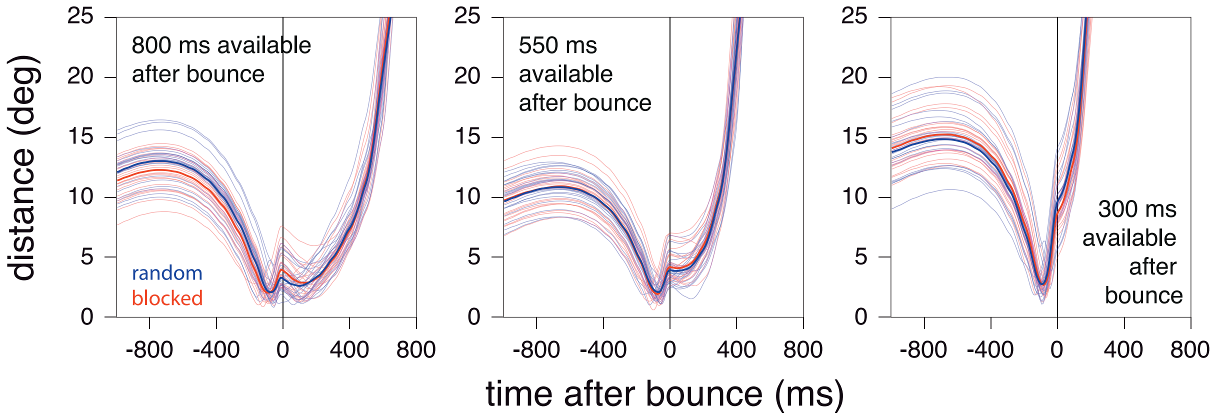


Figure 5. Median angular distance between the position of the ball throughout its trajectory and the location toward which gaze was directed at the end of the prebounce predictive saccade. The position of the ball is expressed as the time at which the ball reaches each part of the trajectory. The horizontal and vertical components of the position of the ball with respect to gaze are shown in Figure 4 for several moments near the time of the bounce. Each thin curve represents one participant. The thick curves show the overall median distances. Color coding as in Figure 4.

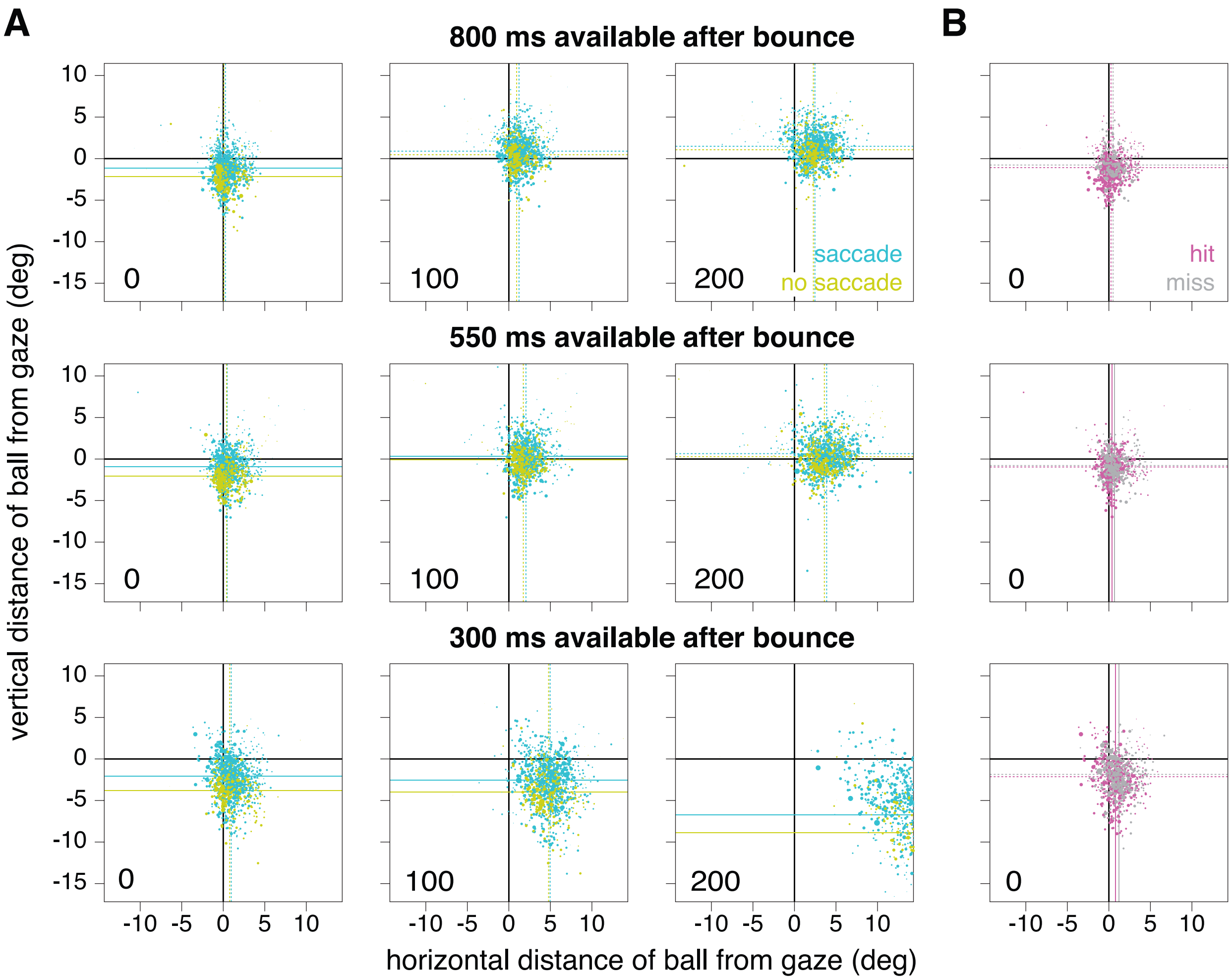


Figure 6. Position of the ball relative to the direction toward which gaze was directed at the moment of the bounce when comparing (A) trials with and without a predictive saccade (blue and yellow, respectively) and (B) when the participant did and did not make contact with the ball (purple and gray, respectively). Plots are shown in head-centered coordinates using the head orientation at the time of the bounce (because we show the ball relative to gaze—i.e., the eye + head direction—at bounce). Colored lines indicate median values as in Figure 4 (solid lines reflect that the two medians differ significantly). Figures combine the data from both the blocked and randomly interleaved trajectories.

directed toward that position irrespective of whether or not gaze was brought there by a predictive saccade. Figure 6A compares the position of the ball relative to gaze at the moment of the bounce (and at two later times) when there was a predictive saccade and when there was none. The results show that saccades relocate gaze to a position that is systematically closer to the ball at the moment of bounce irrespective of the time after bounce. In other words, the absence of a predictive saccade resulted in gaze remaining farther above the ball at bounce than when a saccade was performed. The presence or absence of a saccade appeared to have little consequence on participants' ability to realign their gaze with the ball following bounce in the 800- and 550-ms time-after-bounce conditions, but a saccade did assist in postbounce tracking when the temporal constraints were tighter in the 300-ms condition. However, the location of gaze at bounce appeared to be of little consequence in determining whether a person would hit the ball or not. Figure 6B shows that there was no difference in the vertical location of gaze at bounce when participants did or did not hit the ball. There was some suggestion that players were more likely to hit the ball when gaze was more *horizontally* aligned with the ball at bounce in the 300- and 550-ms conditions (but not the 800-ms condition), though the differences are marginal.

Figure 6A (left column) shows that gaze was directed just above the ball at the moment of the bounce for all time-after-bounce trajectories. Figure 7 shows this in more detail, in the same format as Figure 4, and only when a predictive saccade was performed prior to bounce. The only difference between Figures 7 and 4 is that in Figure 7 the position of the ball was determined relative to where gaze was directed *at the moment of the bounce* rather than at the end of the saccade. The fact

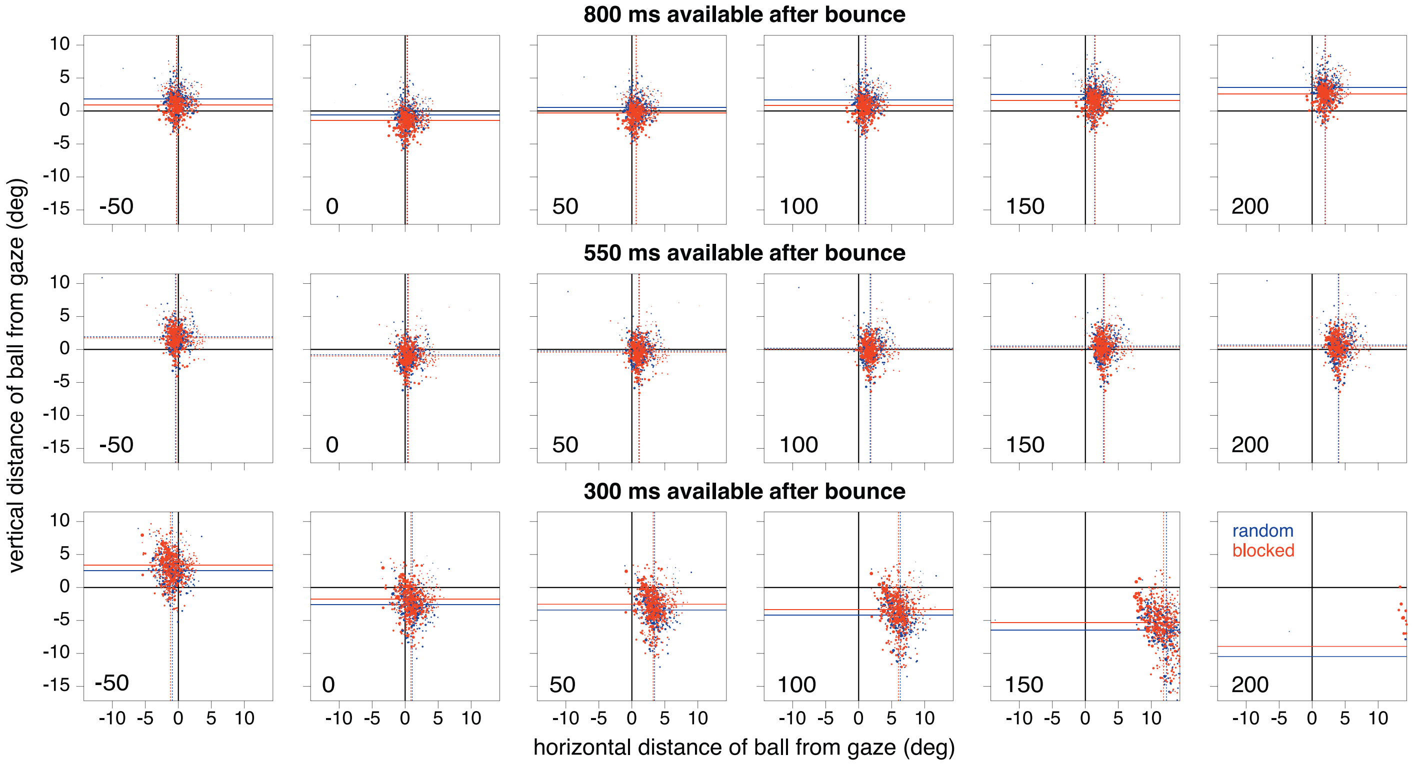


Figure 7. Position of the ball relative to the direction in space toward which gaze was oriented at the moment of the bounce. Plots are shown in head-centered coordinates using the head orientation at the time of the bounce. Further details as in Figure 4.

that the two figures are different shows that gaze did not lie in wait at the end of the saccade but continued to move, possibly in anticipation of the ball's trajectory, between the end of the saccade and when the bounce took place. Intriguingly, gaze at the moment of bounce was directed immediately above the ball irrespective of whether the ball would subsequently move upward in the visual field (800-ms condition), loom toward the participant (550 ms) or move downward following bounce (300 ms).

Figures 4 and 7 show ball positions at various times relative to where gaze was directed at a *single* moment: at the end of the predictive saccade (Figure 4) or at the moment of the bounce (Figure 7). The differences between the figures suggest that gaze does not remain stationary after the saccade to wait for the bounce to occur but instead keeps moving in anticipation of the ball's motion. To examine the degree to which the eye and head movements anticipated and adjusted to the target motion *after* the bounce, we determined the actual position of gaze relative to the ball leading up to and following bounce (Figure 8). If gaze changed in anticipation of how the ball would proceed after bounce, we expected to see changes in gaze within the first 100 ms after the bounce that would approximately match those of the ball's motion. If gaze was *not* anticipatory and only reacted to real-time information about ball trajectory after bounce, then we expected gaze to start matching the ball's motion only about 100 ms after the bounce (because of the sensorimotor delay). A comparison of Figures 7 and 8 reveals that gaze does follow the ball reasonably well in the horizontal direction, and also aids in vertical tracking to some extent. However, it is less clear whether gaze was already tuned to the ball's motion during the first 100 ms after the bounce. We therefore examined in more detail how the eyes and head were moving near the time of the bounce (Figure 9).

Figure 9 shows the mean angular velocities of the eyes and head during the periods leading up to and following the bounce. Before the bounce (Figure 9A), the ball's motion (shown in gray) was downward and slightly to the right, irrespective of the trajectory. What is most remarkable is a relative separation of roles for the eyes and head: Head rotation shifted gaze to the right and slightly downward (shown in green), whereas the eyes shifted gaze almost exclusively downward (shown in pink). While the head movements compensated more or less entirely for the ball's rightward motion, just before the bounce the downward movements of the eyes and head were much less than the ball's, reflecting both that predictive saccades often occurred more than 100 ms prior to bounce, and the ultimate position of gaze above the ball at the moment of bounce.

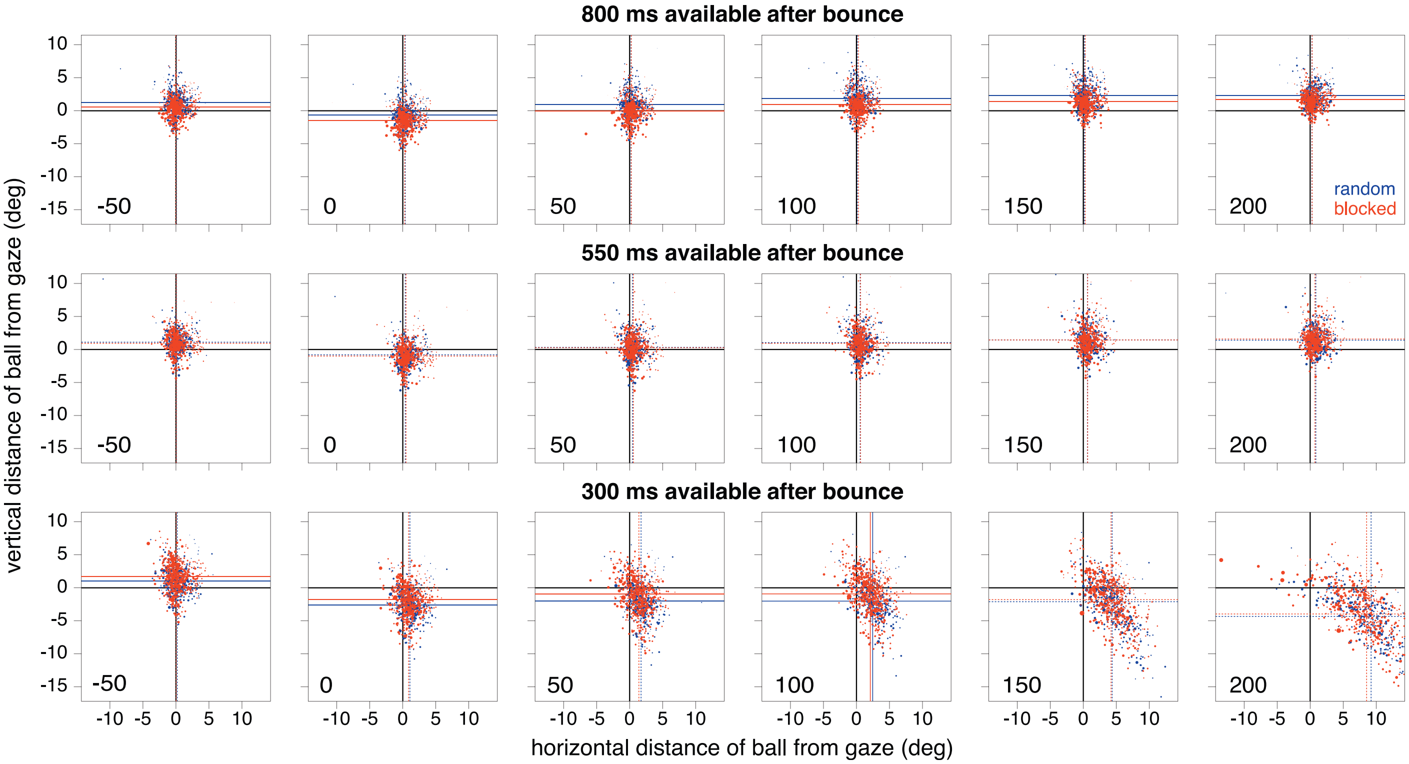


Figure 8. Position of the ball relative to gaze at moments relative to ball bounce. Plots are shown in head-centered coordinates using the head orientation at each moment. Further details as in Figure 4.

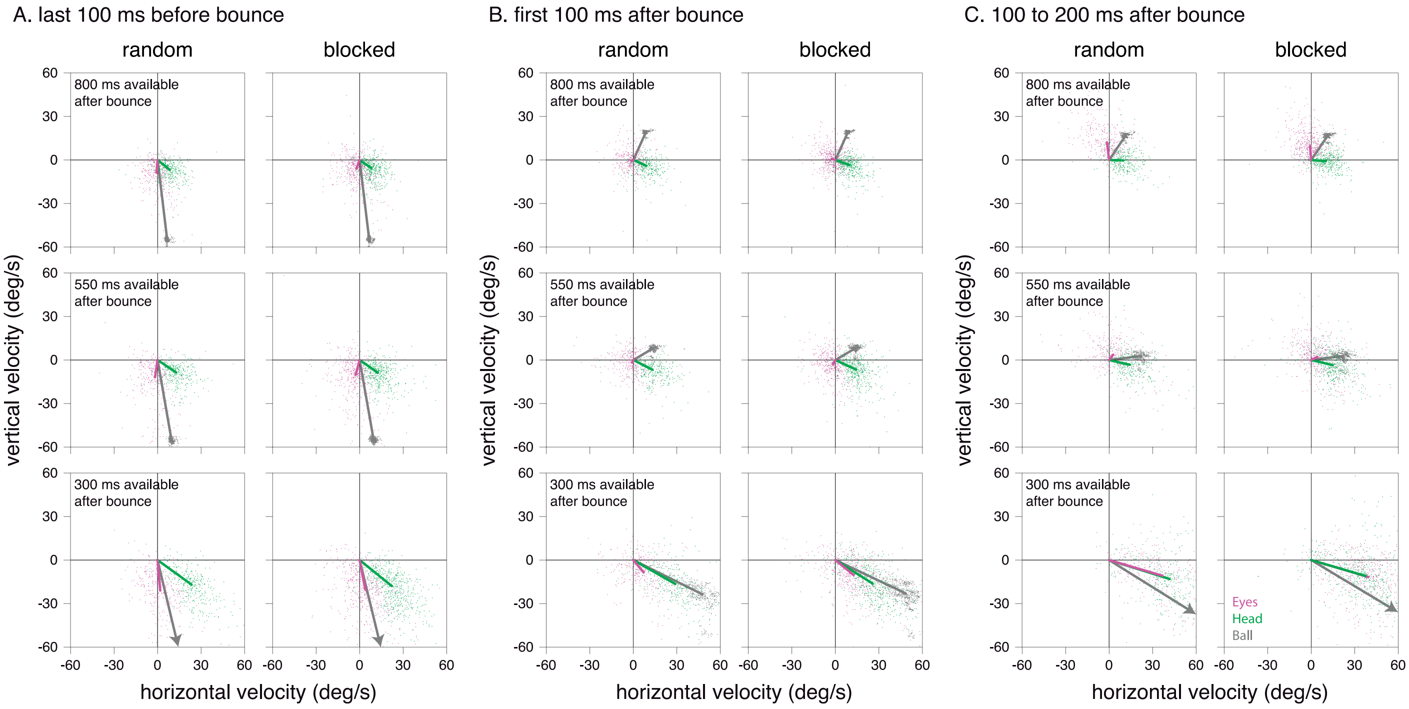


Figure 9. Mean angular velocities with respect to the position of the head of the ball (horizontal defined in space; gray), of rotations of the head (horizontal defined in space; green), and of the eyes in the head (horizontal defined with respect to the head; pink) during (A) the final 100 ms before the bounce, (B) the first 100 ms after the bounce, and (C) 100–200 ms after the bounce. Each dot represents a single trial. The thick lines indicate the overall median values, including values that fell outside the visible range. Arrows at the ends of some gray lines indicate that the median values fell outside the image in that direction.

After the bounce, the ball moved quite differently for the three trajectories (shown in gray in Figure 9B and 9C). We were particularly interested in whether the eyes moved in accordance with the ball's motion during the first 100 ms after the bounce, because the eyes would only be able to do so if the participant anticipated how the ball would move after it bounced. During the first 100 ms after the bounce, the head continued to move as it had been moving before the bounce (shown in green in Figure 9B), with these movements helping to track the sideways trajectory of the ball. The eyes barely moved at all during the first 100 ms after bounce, suggesting that eye movements to pursue the target may not be planned before the bounce. During the second 100 ms after the bounce (Figure 9C), the head continued to track the ball laterally (reflecting the low horizontal misalignments between gaze and ball in Figure 8) and the eyes tended to adjust gaze to match the vertical ball position. The exception was the fast 300-ms condition, where the eyes also moved laterally to contribute to the unsuccessful attempt to keep gaze on the ball (see lower right panels of Figure 9)—a point we return to shortly. Collectively, these results confirm that gaze itself was far from stationary near the time of the bounce. The head followed the general motion of the ball. The eyes moved downward toward the ball but kept gaze above the ball in anticipation of its vertical deflection at the time of the bounce. It appears that motion after the bounce (and therefore 100 ms of postbounce ball motion) must be observed before the eyes really adjust adequately to the change in direction.

To further investigate the relative contributions of the eyes and head to changes in gaze during ball flight, we examined the horizontal and vertical angular velocities of the ball, head, and eyes as a function of time throughout the trial (Figure 10). As we already suspected, the vast majority of horizontal gaze tracking (left column) was achieved by rotating the head. The eyes contributed only when the ball's angular velocity exceeded about 20°/s. The eyes played a more prominent role in *vertical* gaze tracking (right column), with both the eyes and head contributing throughout the trial, though the head tended to contribute in a somewhat damped manner compared to the eyes. The vertical velocity of the eyes increased rapidly before bounce, presumably partly because of predictive saccades. Nevertheless, gaze velocity was delayed with respect to the ball whenever there was a fast change in ball velocity (the black lines lie to the right of the gray curves), suggesting that the ability to predict precisely how the ball would move was limited.

Given that the ball always passed through a selected location on the court when approaching the participant (1 m above the ground and 1 m to the right of the center of the baseline), a possible limitation of our study would be that participants could have tried to hit the ball at that position with a single stereotyped movement of the virtual racquet irrespective of the ball trajectory. To check whether they did so, we examined the variability in racket position relative to the position of contact between racquet and ball (Figure 11). The results were clearly inconsistent with what would be expected if participants produced stereotyped movements toward a single location in space. First, if participants were to adopt a stereotyped movement, there should be no change in the variability in position leading up to the moment of contact between racquet and ball. However, the variability in the position of the racquet in depth decreases up to the location of contact (Bootsma & van Wieringen, 1990). This pattern is easy to understand if participants vary the velocity of the racquet across trials. Second, the lateral variability in the position of the racquet *increased* in the lead-up to contact, rather than staying constant or decreasing. This would not be expected if participants were aiming for the same location on each trial. Finally, lateral and vertical standard deviations of 20 cm or more for the position of the racquet are not consistent with attempts to precisely reproduce the same movement at the same place. Moreover, if participants sought to perform a single stereotyped movement across all trajectories, then the ball would need to be hit precisely at the baseline. However, participants on average were clearly not doing so. The gray curve in Figure 11 shows that the ball was hit, on average, almost 50 cm in front of the position at which all three trajectories converged. Clearly, hitting movements were tailored to the ball trajectories when the three trials were randomly interleaved, because the ball would effectively arrive at different locations in each of the three conditions when hit 50 cm in front of the baseline. A similar pattern of variability was found in the blocked condition, where the standard deviation was determined separately for each of the three blocks (which each contained only identical trajectories) and was then averaged across the three blocks. It seems that stereotyped actions were not performed even when the ball trajectories were blocked and therefore known in advance.

Control experiment

So far we have been attributing all differences that we see between the three time-after-bounce conditions to the difference in time available after the bounce. A possible limitation of the present study is that the three conditions also differed in where the ball bounced relative to the observer and slightly in the vertical velocity at bounce (7.22, 6.85, and 7.89 m/s, respectively, in the 300-, 550-, and 800-ms conditions). To make sure that it was really the timing that mattered,

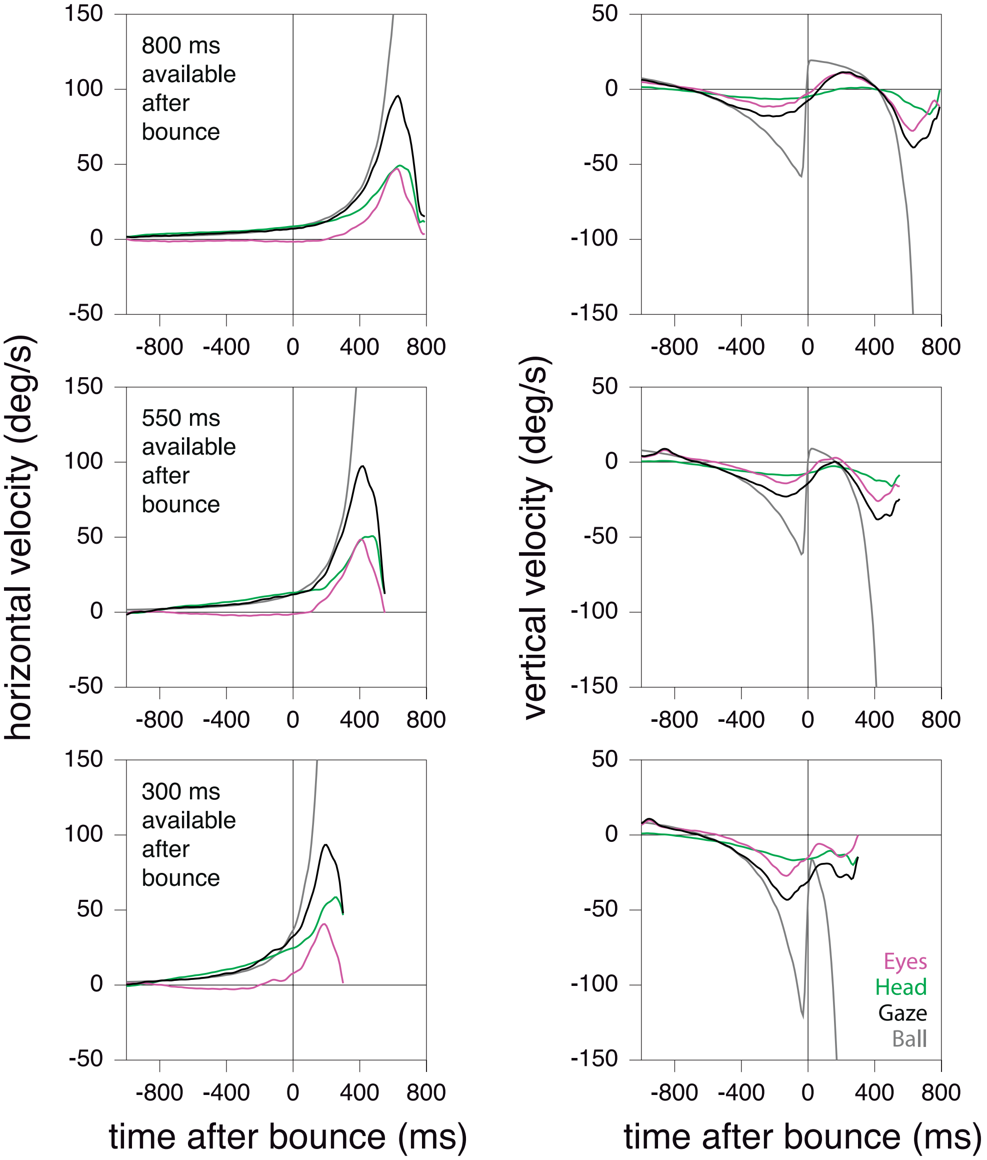


Figure 10. Horizontal and vertical angular velocities of the ball (gray), gaze (black), head (green), and eyes (pink) as a function of time relative to the moment of bounce. Lines show the means of the median values for individual participants, irrespective of whether the different trajectories were randomly interleaved or blocked. Note that by taking the median velocity we emphasize the smooth component of pursuit, because saccades will only contribute to the pink curves if they are timed consistently across trials. Such precise timing might occur near the time of the bounce for some participants. Note that gaze often lags behind the ball when the ball accelerates. In these plots the separation into horizontal and vertical is not perfect because the directions are defined in space coordinates for the ball and head, but in head coordinates for the eyes (as in Figure 2).

we conducted a control experiment that replicated the three time-to-bounce times (300, 550, and 800 ms) but with all balls bouncing at the same location on the court and traveling at the same vertical speed immediately prior to bounce. Moreover, given our finding that saccades were placing gaze above the ball at the time of the bounce, we took the opportunity to manipulate the elasticity of the ball between conditions to determine the degree to which the postbounce trajectory of the ball influenced where gaze was directed by the time of the bounce. To do so, we had 13 new novice participants complete the same VR tennis task, this time attempting to hit 30 trials in each of six blocked conditions presented in a randomized order—3 time-after-bounce conditions (300, 550, 800 ms) × 2 ball-elasticity conditions (lower elasticity, higher elasticity)—in which the ball always bounced at the same location (5 m from the baseline and 0.37 m to the right of the court midline). Changes in the time after bounce were achieved by varying the motion of the ball, the location of launch, the ball elasticity, and the location

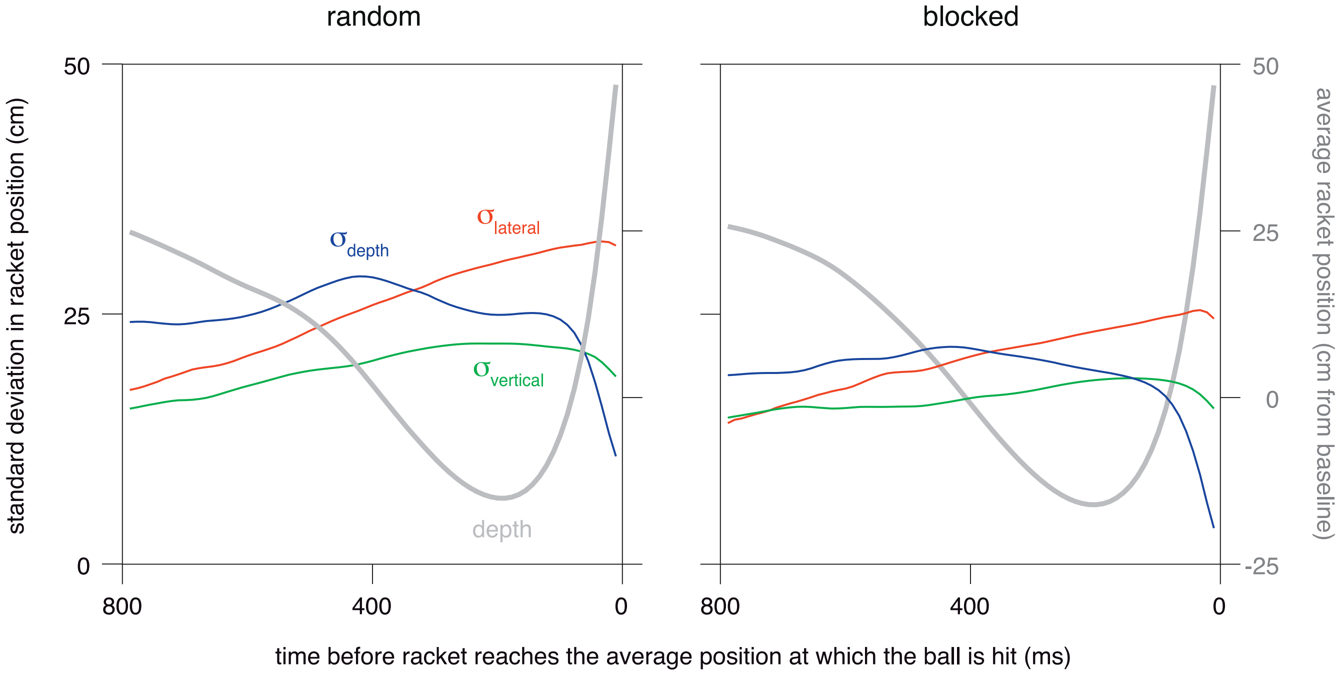


Figure 11. Variability of the virtual racquet position relative to each participant's average position of contact between racquet and ball in the random and blocked conditions. The standard deviation of the racquet position was averaged across participants for the depth (blue), lateral (red), and vertical (green) directions. The standard deviation was determined separately for each trajectory when the trajectories were blocked (after which the values were averaged), but it was determined across all trajectories when they were randomly interleaved. The average racquet position in depth relative to the baseline is shown in gray (see right axis), with positive values indicating that the racket was in front of the baseline.

of arrival (Table 3). All other procedures were identical to those in the original experiment.

The direction of gaze with respect to the ball for the three times-after-bounce was very similar to that of the original experiment, suggesting that it is the time-after-bounce that is the critical difference between the conditions. Importantly, at the time of the bounce, gaze was directed lower—that is, closer to the bounce position—when the elasticity was lower. This was the case for all three times-after-bounce, despite the fact that the prebounce trajectories were always identical for the two ball-elasticity conditions (Figure 12). This provides support for the claim by Diaz et al. (2013) that prior knowledge of ball elasticity is taken into account when guiding gaze in anticipation of a bounce. The head tracked the horizontal movement of the ball, as it did in the main experiment, but from this experiment it is evident that the head moves in anticipation of the ball's trajectory, because the head movements already differ in accordance with the elasticity during the first 100 ms after the bounce (Figure 13).

Remarkably, even after the eyes had time to respond to the perceived motion after bounce (i.e., >100 ms after bounce), it was the head rather than the eye movements that continued to differ in line with the ball elasticity. It seems that the head is performing the real-time tracking of the ball to adapt to the different elasticities, while the eyes move in the same direction, for at least the first 200 ms after bounce, irrespective of the postbounce trajectory (see in particular the 300-ms condition in Figure 13C, where the green lines differ between ball-elasticity conditions but the pink lines do not). Accordingly, these predictive head movements ensure that that there is no difference in the vertical position of the ball relative to gaze for the balls with different elasticity about 100 ms after the bounce (red and green horizontal lines overlap 100 ms after the bounce in Figure 12).

Discussion

The aim of this study was to determine the location toward which predictive eye movements were directed when hitting a bouncing ball. We examined the gaze of 23 novice tennis players who attempted to hit balls that varied in the time from bounce to contact in a virtual environment. Participants made predictive saccadic eye movements shortly before the bounce in two-thirds of the trials. These saccades took gaze toward the vicinity of the bounce point, but contrary to previous suggestions, gaze didn't lie in wait for the ball to arrive following the saccade. Instead, there was a distinct

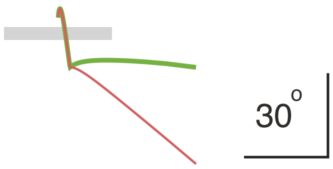
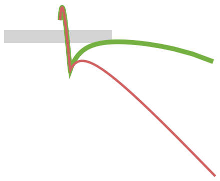
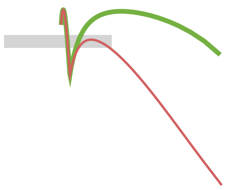
Time-after-bounce condition	Launch location (x,y,z) (m)	Elasticity condition	Ball elasticity	Arrival location (x,y,z) (m)	Observer's view (red = lower elasticity, green = higher elasticity)
300ms	0.00, 1.70, 23.78	Lower	0.733	0.47, 1.10, 0.00	
		Higher	0.924	0.47, 1.50, 0.00	
550ms	0.16, 1.70, 15.13	Lower	0.670	0.47, 1.10, 0.00	
		Higher	0.770	0.47, 1.50, 0.00	
800ms	0.23, 1.70, 12.04	Lower	0.750	0.47, 1.10, 0.00	
		Higher	0.820	0.47, 1.50, 0.00	

Table 3. Ball trajectories in the control experiment. *Notes*: Spatial coordinates are reported in meters relative to an origin at the center of the baseline where participants stood (positive values are, respectively to the right, upward, and straight ahead along the midline of the court from the participant's viewpoint). The location of bounce—$(x, y, z) = (0.37, 0.00, 5.00)$ m—and the vertical velocity immediately prior to bounce (7.03 m/s) were identical in all six conditions.

separation of roles for the head and eyes, with the eyes remaining stationary until they could react to post-bounce visual information—so until about 100 ms after the bounce—and the head continuing to follow the motion of the ball between the moment of the saccade and beyond, when the eyes started following the ball. Accordingly, a strategy emerged whereby the saccade and head movements combined to ensure that gaze was systematically directed several degrees above the point at which the ball would bounce, irrespective of whether the ball moved upward or downward in the participant's visual field after the bounce (Figure 4). This direction of gaze did not coincide with a future point on the ball's trajectory, with the reactive eye movements and predictive head and eye movements altering the direction of gaze so that it realigned with the ball soon after bounce (Figure 8). Gaze relied on prior information in addition to real-time information, but there is still much to be examined with regard to the extent to which it did so. The eye and head movements did not differ between trials in which ball trajectories were predictable and ones in which they were not (i.e., presented in an interleaved or blocked fashion), suggesting that participants relied heavily on real-time information about ball flight. However, our novice participants did take into account prior knowledge of the elasticity of the ball to tailor their eye movements to the postbounce ball trajectory even before the ball bounced.

There has been conjecture over the location toward which saccades redirect gaze: Several studies have found gaze to be directed above or beyond the bounce point (Diaz et al., 2013; Hayhoe, McKinney, Chajka, & Pelz, 2012; Hayhoe et al., 2005), while others have reported that gaze is directed toward the location of the bounce itself (e.g., Land & McLeod, 2000; Mann et al., 2013; Ripoll, Bard, & Paillard, 1986; Ripoll et al., 1987; Sarpeshkar et al., 2017). We expected that a possible reason for this discrepancy might be that the time constraints after the bounce differed between the

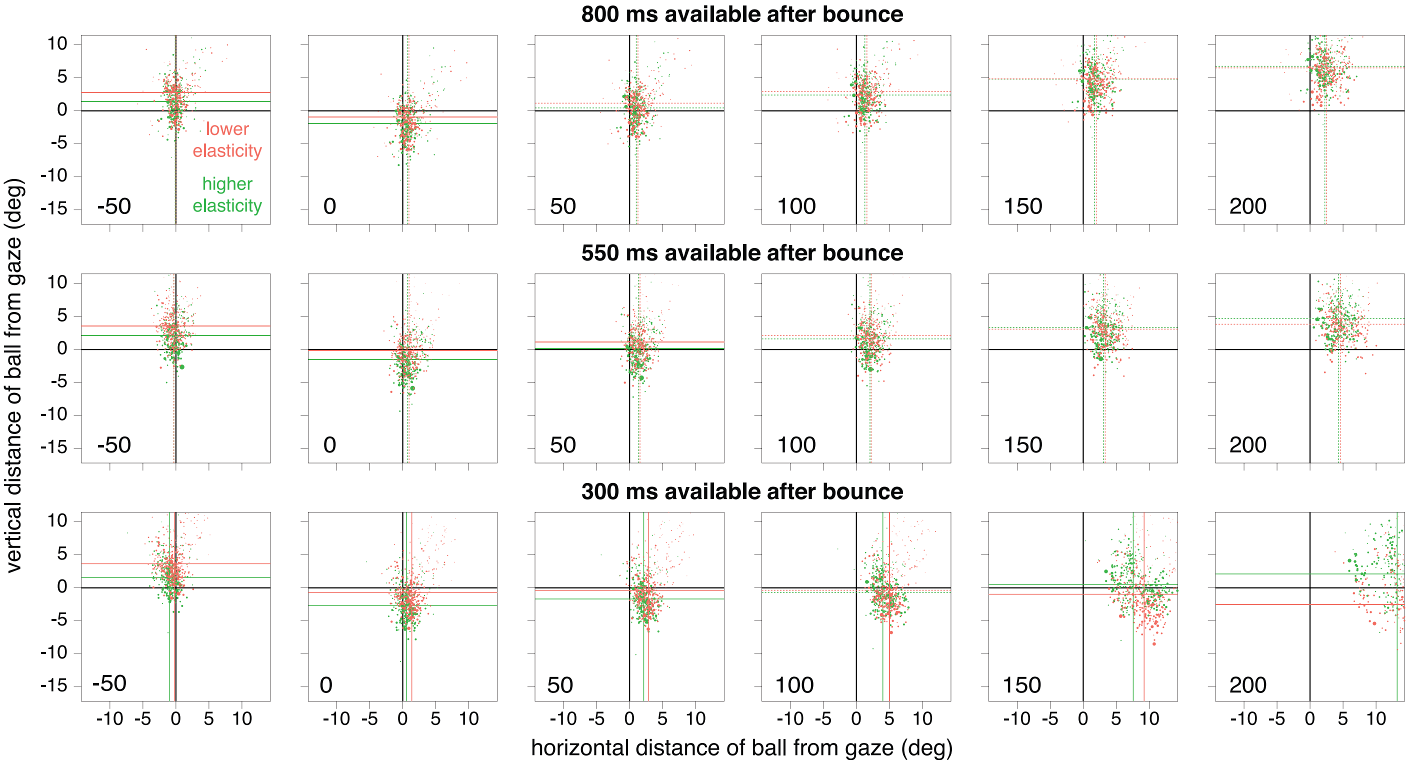


Figure 12. Position of the ball (dots) relative to the location in space toward which gaze was directed at the moment of bounce (black crosshairs) in the control experiment. Trials with low elasticity are shown in red and trials with high elasticity in green. Other details as in Figure 7.

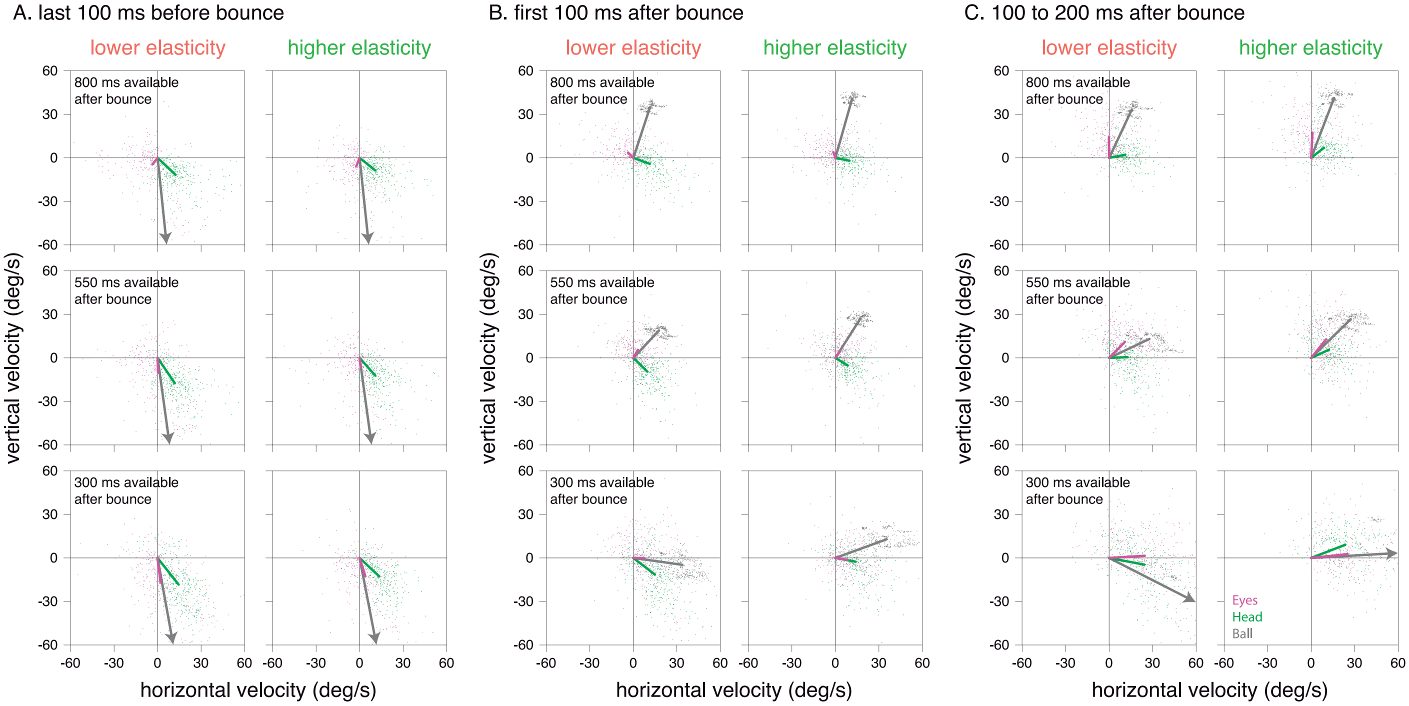


Figure 13. Mean angular velocities with respect to the position of the head for the ball (gray), head (green), and eyes in head (pink) in the control experiment during (A) the final 100 ms before the bounce, (B) the first 100 ms after the bounce, and (C) 100–200ms after the bounce. Each panel shows the six combinations of time after bounce (800, 550, 300 ms) and ball elasticity (lower and higher). Other details as in Figure 9.

studies: Saccades toward the bounce point itself are mainly reported in studies in which there was little time between bounce and contact. We examined whether this was indeed the reason for the discrepancy by manipulating the time between bounce and contact. We found that differences in the time from bounce to contact were unlikely to be the reason for the contrasting findings across studies. In our study, predictive saccades consistently brought gaze to a point above the bounce, irrespective of the time available after the bounce.

Methodological limitations are likely to be the best explanation for why gaze has previously been misinterpreted as being directed toward rather than above the bounce. Studies which report gaze being directed *toward* the bounce (Land & McLeod, 2000; Mann et al., 2013; Sarpeshkar et al., 2017) have typically examined performance in tasks with high temporal constraints (such as cricket batting) while using mobile eye trackers with low temporal (and perhaps spatial) accuracy that may not have been precise enough to detect gaze being directed several degrees above rather than toward the bounce at the very moment that the saccade ended. Eye and head movements immediately following the saccade result in gaze being directed very close to the ball by the time of actual ball bounce (Figure 7). It is possible that some of those studies which interpreted saccades to end *beyond* bounce may have failed to account for those eye and head movements that follow the saccade, which could have led to a misinterpretation of the endpoints of the saccades as being farther along the trajectory than they really were. Finally, the coordinate system that is used to describe the data may influence the description to some extent. Diaz et al. (2013) defined the vertical with respect to gravity. In the present study, “vertical” is defined with respect to the head. Thus, the coordinate systems differ by the head roll. Although this does not change the angular distance between gaze and ball, it can influence the extent to which gaze is considered to be above the ball. Importantly, future positions of the ball are defined in the same coordinates, so the extent to which gaze anticipates the motion of the ball is not affected.

A key challenge to overcome when examining gaze in tasks where an object is approaching in depth is to determine the precise location toward which gaze is directed. Due to geometric limitations in judging distance from the orientations of the two eyes (Brenner & Smeets, 2000), gaze is generally specified by a single vector direction with respect to the head rather than by a Cartesian location in space, as we also do here. This limitation introduces a possible ambiguity near the moment of the bounce when the ball is adopting a head-on trajectory toward the observer, because gaze oriented directly above the ball could alternatively correspond to a strategy to look toward the trajectory of the ball either before or after it bounced. In order to minimize this ambiguity, we launched balls from the left of the court and directed them toward the participant’s right, rather than adopting a head-on trajectory. By doing so, we could observe that the direction of gaze at the end of the predictive saccades was closer to the ball’s position 50 ms before the bounce than it was to its position at any time after the bounce, irrespective of the remaining time after bounce (Figure 4; also see Figure 5). This at first would appear to suggest that saccades may have been targeting the ball position immediately *before* bounce, though we find this unlikely. Rather, we think this is probably an artifact resulting from the constant horizontal head rotation. The saccades moved the eyes downward to place gaze just above the bounce location (vertical component), relying on the ongoing head rotation to align gaze with the ball at the time of the bounce (horizontal component; see Figure 8). Support for the idea that the saccade endpoint is related to the ball’s position after the bounce, rather than its position before the bounce, can be found in our control experiment, where we show that a change in the ball elasticity changes the landing position of the predictive saccade even though this change does not affect the prebounce trajectory (see also Diaz et al., 2013). In addition, it appears unlikely that predictive saccades direct gaze toward a ball position *after* bounce because gaze was directed above the ball’s position at bounce even when the ball loomed toward the participant after bouncing (550-ms condition) or even when it moved *down* in the visual field after bounce (300-ms condition). The saccades appeared to systematically direct gaze immediately above the bounce location.

In our study we presented trials both in a random manner, whereby the three possible ball trajectories were randomly interleaved, and in a blocked manner, whereby each of the three possible trajectories was presented separately. We expected that if predictive saccades provide a reflection of the degree to which the ball trajectory can be predicted (Land & McLeod, 2000), then we would find more predictive behavior in terms of more frequent and/or earlier predictive saccades in the blocked condition when the ball trajectory was known in advance. There were differences in the frequency of saccades between the random and blocked conditions, but not in a consistent manner that would reflect superior prediction in the blocked condition. Although more predictive saccades were found in the blocked condition when the time after bounce was only 300 ms, *fewer* predictive saccades were found when the time-after-bounce was 800 ms. There was no indication that the predictive saccades occurred earlier in the blocked trials (Table 2), suggesting that prior knowledge of the ball flight did not assist in making earlier predictions—a finding that is somewhat in contrast to Land and McLeod's claim that earlier saccades reflect a superior capacity for prediction. In sum, it might have been reasonable to expect to find consistently more predictive behavior in the blocked condition, when the predictability of the ball trajectory was high, but the results show that this was largely not the case.

There has been some suggestion that predictive saccades may prepare the eyes to rapidly adapt to a discontinuity in ball flight following bounce (e.g., Hayhoe et al., 2012; Mann et al., 2013), and the results of our study lend support to this hypothesis. First, we have shown that although the head tends to do much of the ball tracking throughout ball flight, the eyes generally account for more of the change in vertical velocity after bounce than the head does (Figure 10), presumably because it is easier to make rapid adjustments to the movement of the eyes than to the movement of the head. Second, the comparison of trials with and without a predictive saccade shows that gaze was more closely aligned with the ball after bounce in trials where there *was* a predictive saccade than in those without a saccade (Figure 6), particularly when the time constraints were more severe, suggesting that the saccades assist in more quickly adapting to the particularly fast discontinuities in ball flight. Third, saccades were found more frequently when the discontinuity in ball flight following bounce was greatest. If predictive saccades do assist in adapting to abrupt discontinuities in ball flight after bounce, then they should be found more regularly when there is a greater discontinuity in trajectory, and particularly if the trajectory is known in advance. Although the apparent direction of the ball's motion changed from downward to upward following bounce in the 800-ms time-after-bounce condition, the largest angular change in vertical velocity was actually found in the 300-ms condition, where the ball continued to move downward in the participants' visual field following bounce (see right column in Figure 10). And it was in this 300-ms condition that the most saccades were found, with the increase further exaggerated in the blocked condition, when participants knew the trajectories in advance. It is less clear why there would not *always* be a saccade in these conditions, but nonetheless, the findings collectively provide support for the idea that the saccades assist in adapting to rapid discontinuities in ball flight following bounce. Given previous findings that there are specific differences in the way that *skilled* athletes generate saccades (e.g., earlier or more consistent saccades; see respectively Land & McLeod, 2000; Mann et al., 2013), it seems prudent for future studies to examine whether these differences help skilled athletes to better realign gaze with the ball following bounce.

Another point that is clear from the findings of our study is that the 170-ms delay from bounce to re-alignment between ball and gaze found in the study by Diaz et al. (2013) of novice racquetball players is not a guiding control strategy that holds under different time constraints. In that study, participants appeared to use predictive saccades to relocate gaze in such a way that there was a consistent time delay (~170 ms) from the time the ball bounced to the moment the ball caught up with gaze. Participants adapted their predictive saccades (or possibly the changes in gaze immediately after) to maintain this time delay after a change in the elasticity of the ball, suggesting that there could have been a functional reason for maintaining a 170-ms delay. If so, then a 170-ms delay should have been found in other situations and under differing time constraints. In our study we included a condition where the time from bounce to contact matched that in the study by Diaz et al. (800 ms) and incorporated additional conditions with reduced time delays. When we assumed that gaze was held steady following a predictive saccade, our results in the 800-ms condition approached those of Diaz et al., at least in the vertical direction (Figure 4). However, the 170-ms delay was not found when the time constraints changed, showing that it is not a general feature of predictive saccades. Actually, it is clear that the ongoing head movements and corrective eye movements after the bounce help to realign gaze with the ball much earlier than 170 ms after bounce (Figure 8).

A considerable proportion of the changes in gaze found in our task were a result of changes in the direction of the *head* rather than the eyes. Most of the lateral ball tracking was performed by moving the head, while vertical ball tracking relied almost equally on contributions from the head and eyes (see Figure 9). The head was even shown in the control experiment to anticipate the changes in ball trajectory immediately following bounce in accordance with changes in ball elasticity, suggesting that the head plays a vital role in real-time tracking of the target. These findings reflects those of Mann et al. (2013) that ball tracking in cricket batting is achieved largely through head rotation, with world-class cricket batters better able to couple the rotation of their head to that of the ball to maintain the ball in a consistent direction relative to their head. Apparently, less-skilled tennis players also attempt to track the ball with their head until the ball is very nearby. There are several reasons why tracking with the head may be advantageous. First, predictions about where the ball will be in the future may be more accurate when the ball is maintained in a single egocentric direction relative to the head, rather than being calculated by transforming retinotopic coordinates into a head-centered frame of reference. Second, keeping the head oriented toward the target makes it easier to make fast small adjustments to gaze by moving the eyes. This is what we see happening in the vertical direction: The head follows the overall anticipated vertical (and horizontal) motion, whereas the eyes typically respond to abrupt changes, such as the changes that occur due to the ball bouncing off the ground. The results of our study highlight the need for future studies to consider the individual contributions of the eyes *and* head to changes in gaze during interception.

Tracking a moving target with the eyes helps to predict its future location (Brenner & Smeets, 2011; de la Malla, Smeets, & Brenner, 2017; Spering, Schutz, Braun, & Gegenfurtner, 2011), possibly because an efference-copy signal generated from the smooth-pursuit eye movements can be exploited to facilitate prediction (Spering et al., 2011). However, an efference copy resulting from movement of the extraocular muscles would have been of limited use alone in facilitating prediction of ball trajectory in our task, and in other hitting actions, because the eyes contribute only a proportion of the ball tracking. If efference-copy signals were to play a role in prediction, it would need to be on the basis of movement of the extraocular muscles *and* the muscles that rotate the head. The finding that elite batsmen rely on head more than eye movements could even suggest that efference copies related to head movements may be more reliable than those for the eyes.

In general, our study shows that the head and eyes move in a manner that keeps gaze close to the ball. Predictive saccades often help by moving gaze ahead of the ball when it is possible to anticipate where and when the ball's trajectory will change. The head follows the ball's smooth lateral motion, whereas the head and eyes both move vertically to keep gaze on the ball. This makes sense because eye movements can obviously be adjusted much faster than can head movements. Together, the saccades and ongoing smooth eye and head movements ensure that gaze remains close to the ball near the time of the bounce. When there is ample time to adjust arm movements on the basis of information acquired after the bounce, gaze continues to follow the ball quite well after the bounce. When there is little time to adjust to the trajectory after the bounce, gaze is directed such that the ball is near where we look just after the bounce, before it starts moving at such a high angular velocity that gaze might not be able to track it very well anymore.

Keywords: gaze, eye movements, interception, tennis, prediction

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