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Looking at Breakout: Urgency and predictability direct eye events

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ABSTRACT

We investigated the organization of eye-movement classes in a natural and dynamical setup. To mimic the goals and objectives of the natural world in a controlled environment, we studied eye-movements while participants played Breakout, an old Atari game which remains surprisingly entertaining, often addictive, in spite of its graphic and structural simplicity. Our results show that eye-movement dynamics can be explained in terms of simple principles of moments of prediction and urgency of action. We observed a consistent anticipatory behavior (gaze was directed ahead of ball trajectory) except during the moment in which the ball bounced either in the walls, or in the paddle. At these moments, we observed a refractory period during which there are no blinks and saccades. Saccade delay caused the gaze to fall behind the ball. This pattern is consistent with a model by which participants postpone saccades at the bounces while predicting the ball trajectory and subsequently make a catch-up saccade directed to a position which anticipates ball trajectory. During bounces, trajectories were smooth and curved interpolating the V-shape function of the ball with minimal acceleration. These results pave the path to understand the taxonomy of eye-movements on natural configurations in which stimuli and goals switch dynamically in time.

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1. Introduction

While reading this text, we execute a highly structured and ordered succession of eye-movements (Rayner, 1983). The precise position of each gaze location optimizes the sensitivity of the reading system (Dehaene, Cohen, Sigman, & Vinckier, 2005) and the time spent in each word reflects online syntactic and semantic processing of the read sentence (Kliegl, Nuthmann, & Engbert, 2006). Structuring of eye-movements happens completely unnoticed, resulting in a unified and continuous perception of reading a still page. Reading has been a goldmine for the studies of eye-movements and, more generally of the architecture of mental processes, since it satisfies two conditions of great experimental convenience: (1) eye-movements form a discrete sequence of brief (~30 ms) and rapid (up to 900°/s) saccades between fixations (~300 ms) where the eye remains relatively stationary and (2) fixations are targeted to a region in space easily tagged and mapped to quantitative values of the sentence, word or letter (precise letter of word, number of letters of the word, frequency or expectancy of the word).

Beyond reading, there is also ample evidence for an optimal unconscious structuring of eye-sequences (Eckstein, Drescher, & Shimozaki, 2006; Harris & Wolpert, 2006). The first pioneering

studies of Yarbus (1967) demonstrated that fixations in natural images were targeted to points in the scene which were evidently informative, such as faces, hands or salient objects in the room. Importantly, the sequence of eye-movements varied with the task (for instance, participants looked more to the faces when asked about the ages of the people in the scene) indicating that the measure of information gain to predict eye-movement sequences had to take goals and task objectives into account. In a low-level controlled visual search setup, Geisler and collaborators could determine the precise sequence of eye-movements during visual search based on a model which takes into account known inhomogeneities in receptive field properties of early visual neurons, assuming that each fixation is directed to a point which maximizes the information gain (Geisler, Perry, & Najemnik, 2006; Najemnik & Geisler, 2005, 2008).

A few studies have investigated the dynamics of eye-movements in tasks involving sensorimotor action coordination, as for instance while playing cricket, in which an entangled and nested series of operations are required to achieve a goal (Kato & Fukuda, 2002; Land & Hayhoe, 2001; Land & McLeod, 2000; Pelz & Canosa, 2001; Ranganathan & Carlton, 2007; Regan, 1997; Takeuchi & Inomata, 2009). The main result of these studies is that the visual system constantly anticipates the actions to acquire the necessary information (Hayhoe & Ballard, 2005; Land, 2006; Land & McLeod, 2000).

In short, over the last years we have gained increased understanding of the mechanisms producing fixation sequences in

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natural setups where here by “natural” it is understood not only that the contents of the visual scene inherit statistics of natural scenes but also that the dynamics of goals, objectives, information flow and statistics inherent to the natural world.

In setups in which objects move in an unpredictable way, the smooth pursuit system collaborates with the saccadic system in order to improve tracking (Orban de Xivry & Lefevre, 2007). The appearance of a moving stimulus in the environment elicits smooth pursuit eye-movements with a latency of around 100 ms. Because of this inherent delay, large position errors arise during the visual tracking of a stimulus that changes its trajectory abruptly. Tracking errors also result from the limited velocity and acceleration of the smooth pursuit system. Due to these limitations, the oculomotor system needs to develop strategies to avoid the build up of position error during tracking of a moving target. One strategy is to combine the smooth pursuit movements with catch-up saccades to avoid large position error and eye lagging behind the target (Robinson, 1965).

De Brouwer and colleagues established a general principle of this organization, investigating one-dimensional trajectories with a step in velocity and position after pursuit has been stabilized, using the Rashbass paradigm (de Brouwer, Yuksel, Blohm, Missal, & Lefevre, 2002; Rashbass, 1961) to initiate pursuit without saccades. They found that the pursuit system is flexible and can react to simultaneous changes in position and velocity. The decision to make a saccade is triggered when the prediction of “eye crossing time”, which depends on both position error and velocity error, exceeds a threshold of about 200 ms. The catch-up saccade is triggered at around 125 ms.

Erkelens conceived a complementary paradigm to investigate the dynamics of saccade and smooth pursuit interplay, exploring latencies of saccades and smooth pursuit in response to a moving target that overlaps in time with a pursued target moving in two-dimensional space. He found that when the appearance of the second object coincides with the disappearance of the first, the change in pursuit precedes the saccade, coherent with previous studies which found that pursuit is very fast, faster than saccade initiation (Erkelens, 2006). When the second object overlapped partially in time with the first, directional changes in pursuit occur almost entirely within the accompanying saccade.

The previous studies investigated the coordination of saccade and pursuit in response to unexpected events (Orban de Xivry and Lefevre cite the example of mosquito tracking as an indicator of the intrinsic difficulty of pursuing unpredictable objects even at low speed). If target trajectory is predictable, tracking becomes considerably easier since the oculomotor system can make use of prediction to try and anticipate the future target trajectory during smooth pursuit eye-movements (Bahill & McDonald, 1983; Barnes & Asselman, 1991).

In the most general case, movement combines predictable and unpredictable components. When these signals are applied in orthogonal directions, the predictable component of motion is pursued with almost perfect prediction (Goodwin & Fender, 1973) and is delayed by about 20 ms when the components are non-orthogonal. The pursuit latency to the unpredictable component is of about 110 ms and independent of the orientation similarity of the noise and predictable components (Mulligan, Stevenson, & Cormack, 2005).

Our goal here was to understand in a quantitative manner the organization of the saccadic and smooth pursuit systems in a relatively simple dynamical setup. Our work was inspired by prior experiments analyzing fixations in dynamical sensorimotor setups (Hayhoe & Ballard, 2005; Land, 2006). However, an intrinsic difficulty of this type of experiments is to map eye-movement coordinates to relevant tags of the experiment. In the example of tennis, widely used as a metaphor for complex sensorimotor action

(Wolpert & Flanagan, 2010) the ball moving at very high speeds, the opponent, the net, the lines, all these objects are difficult to identify through a recognition program, are often ambiguous, are not repetitive and hence difficult to group into trials and depend on the history of the game. This limitation makes those works often descriptive, and hardly quantified.

Our solution to this conundrum has been to use old Atari video-games. These games are even today surprisingly entertaining, often addictive and can be arbitrarily hard to play, despite of their graphic and structural simplicity. Also they are presented in a two-dimensional screen, reducing significantly the intrinsic complexity of a natural three-dimensional task.

With this in mind we studied dynamics of eye-movements while participants played *Breakout*, a cult, classic video game. This game has an extremely simple structure. In its original form it consists of a rectangular playing area, a ball bounces off the sides and top of that area. Bricks at the top of the playing area that are touched by the ball disappear, and a paddle in the bottom horizontal position which is controlled by the player trying to keep the ball in the playing area. If the player manages to break all the bricks he wins the game, whereas if the ball falls through the bottom he loses.

2. Methods

2.1. Experimental design: from games to trials

Participants played a modified version of the classic game *Breakout* (Fig. 1a). Their task was to control the paddle to avoid missing the ball off the bottom of the playfield. Raw data consists of a continuous stream of two-dimensional eye positions. Our objective is to explain this data in terms of experimental regressors: the position of the ball, brick and paddle in time.

The game was simplified for experimental purposes: instead of placing several bricks, only one is presented. When the ball hits the brick, it disappears and only reappears after 9 s in a new random position, within a certain height range. We also changed the game to keep the vertical speed of the ball constant (as opposed to the modulus of the velocity, as in the original game). This assured that the time it takes for the ball to go from the paddle, all the way up and down again to the paddle is constant (unless the brick is hit). As a consequence the time-series (of eye-movement data and regressors) could be parsed in a sequence of events and then perform time-locking and event related analysis. We used this particular feature to define a *trial* as the period between two consecutive hits of the ball on the paddle (as long as the brick is not hit). All trials have the same duration (2800 ms), independently of the angle, wall bounces or horizontal movement of the ball or paddle. Fig. 1b shows the vertical position of the eye and the ball in three consecutive trials. So defined, a trial begins with the ball moving up away from the paddle, and finishes at the following bounce on the paddle. Trials are naturally separated in two parts: the first half when the ball moves up, and the second when the ball moves down. Urgency of action increases with trial-time – as the ball approaches the paddle – and hence trial-time will be an important experimental regressor.

2.2. Game

The game was run using a screen resolution of 480×360 px, on a square playfield of 320 px in size (27.9° of visual field). Ball size was 10 px (0.9°), paddle size was 15×8 px ($1.3 \times 0.7^\circ$), and brick size was 32×8 px ($2.8 \times 0.7^\circ$). Depending on the position in which the ball impacts the paddle, the angle of the ball for the subsequent trial is set. For this purpose, the paddle is divided in six equal parts, which define the horizontal velocity to be ± 6.1 , ± 12.2 or $\pm 18.3^\circ/s$. The vertical velocity of the ball is kept constant at $18.3^\circ/s$, and thus

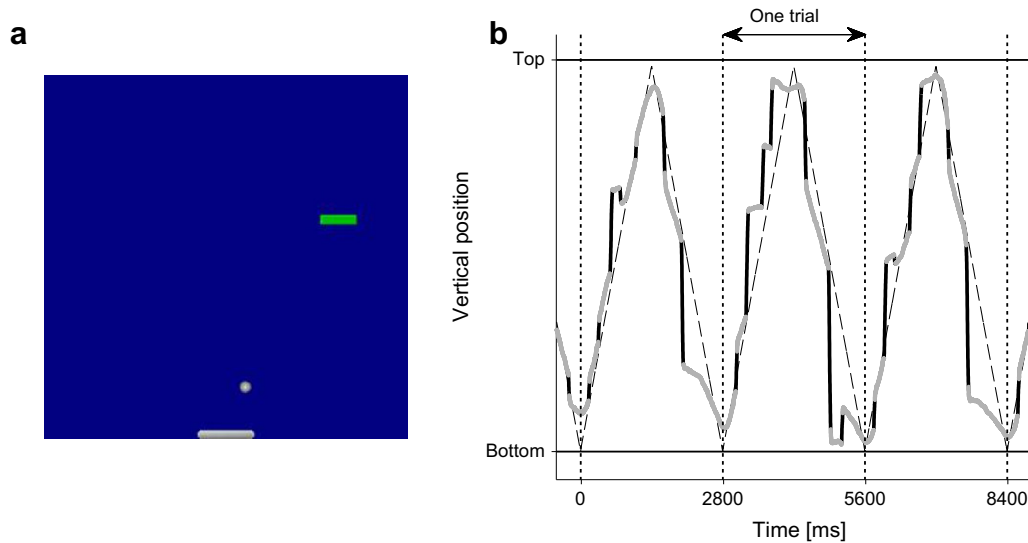


Fig. 1. Experimental design. (a) Image extracted from the implemented version of the *Breakout* game. (b) Vertical position of the ball (dashed line) and eye (continuous line). A trial is defined as the period between two consecutive paddle hits, which is constant (2800 ms) since the y-velocity of the ball is fixed. Eye events (gray line) are defined as the eye-trajectories between two consecutive saccades (black line).

the ball moves along three different diagonal trajectories of angles of 18.4° , 33.7° and 45° with respect to vertical orientation. Absolute ball velocity was then $19.3^\circ/\text{s}$, $22.0^\circ/\text{s}$ and $25.8^\circ/\text{s}$, well below the maximum smooth pursuit velocity (Meyer, Lasker, & Robinson, 1985). Players control the game choosing to impact at different positions of the paddle and hence the deviation from the center cannot be called an error. The ball follows a symmetric, predictable trajectory when it bounces on top and lateral walls.

Paddle is controlled using keyboard that imposes acceleration, with maximum velocity. Eye is tracked at 1000 Hz, but game objects (brick, ball and paddle) were sampled at 70 Hz (screen refresh rate). A linear interpolation was used to resample game objects to 1000 Hz for analysis.

A total of 15 participants played the game for 10 or 15 min. Trial detection was done offline, defined as the period between two consecutive paddle bounces, excluding periods in which the ball hit the brick. Mean trial count per subject was 228 (minimum 94, maximum 326). Mean eye event count per subject was 1661 (minimum 806, maximum 2360).

2.3. Control tasks

A total of 23 subjects completed the fixational control task. It consisted in the visual presentation of a single-line sentence in the center of the screen (font: regular New Courier, 12 point, 0.5° in height, screen resolution 1024×768 px). Once the subjects completed reading the sentence, they directed their gaze to a red dot located in the bottom-left corner of the screen. This triggered the end of the trial. Fixations directed to the first and last word of each sentence were excluded from the analysis.

The pursuit control task was visually identical to the game, with the exception that the paddle and the brick were absent, and the ball performed a predefined sequence of movements with mirror-like bounces on the borders. The ball bounced around the screen for 10 s, and then stopped for 1 s to allow subjects to rest. These blocks were repeated 80 times, with longer pauses every eight blocks. A total of four subjects completed this task.

2.4. Eye tracking

We utilized a desktop-mounted, video-based eye tracker (Eye-Link II; SR Research Ltd., Kanata, Ontario, Canada), at a sampling

frequency of 1000 Hz, in monocular mode. Nominal average accuracy is 0.5° , and space resolution is 0.01° RMS. The tasks were presented on a 19 in. monitor model Samsung SyncMaster 997 MB, at an eye-monitor distance of 50 cm. Eye position was recorded at a resolution of 1024×768 px in all tasks, and offline downsampled to 480×360 px to match screen geometry for the game and pursuit control task. The head was stabilized with a chin rest.

2.5. Saccade, blink and co-occurrence detection

Saccades were automatically detected by a heuristic algorithm implemented within the EyeLink II eyetracker system. Thresholds for automatic saccade detection were: $30^\circ/\text{s}$ for velocity threshold, and $8000^\circ/\text{s}^2$ for acceleration threshold. Saccade detection is robust to large changes of these parameters (changing these parameters to $22^\circ/\text{s}$ and $3800^\circ/\text{s}^2$ respectively resulted in less than 0.1% change in the number of saccades detected).

Blinks are identified when the tracker loses the eye. In the few ms before and after losing the eye the tracker detects the eye in erroneous positions (out of the screen), due to partial occlusion of the pupil. Blinks are defined comprising the interval from the moment in which eye position is lost to the moment in which it is recovered.

For blink-saccade co-occurrence we analyzed each blink, and calculated the mean eye velocity as the last position before and the first position after the blink, divided by blink duration. Finally we defined a blink-saccade co-occurrence if this velocity was larger than the threshold of saccade detection ($30^\circ/\text{s}$).

2.6. Event definition and event velocity

We define an *eye event* as the two-dimensional eye trajectory between two consecutive saccades. For each individual event we calculated a representative eye velocity (horizontal and vertical separately) as the slope obtained from linear regressions performed on the raw, unfiltered eye positions $x(t)$ and $y(t)$ as functions of time (i.e. slope of the single events as seen in Figs. 1b and 2a). The velocity calculated this way results similar but more stable than the actual mean velocity, calculated from initial and final position of the event. It is also comparable to an estimation of the velocity after filtering out the higher frequencies.

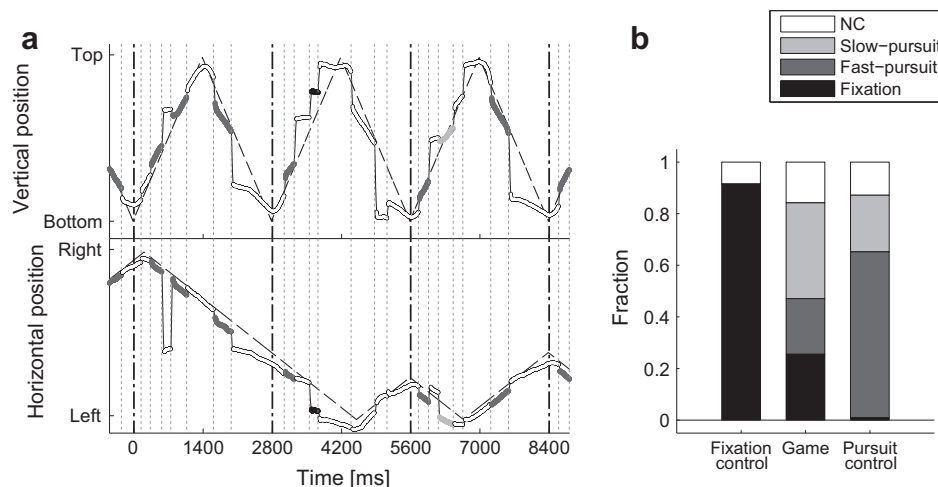


Fig. 2. Categorization of eye-movement types. (a) Horizontal and vertical position of the ball (dashed line) and eye (continuous line and symbols) on three consecutive trials. Grayscale in the eye trajectory indicate the classification of eye events: fixations (black), smooth pursuits (both levels of gray), and unclassified (outlined white). Bounce events are marked in outlined white. Vertical dashed lines indicate saccades separating events. (b) Fraction of event types in the three tasks. As expected, the fixation control task (left) contains mainly fixations and the pursuit control task (right) mostly pursuits. The game (center) contains an intermediate proportion of smooth pursuits and fixations.

2.7. Details of event classification

Once we determined event velocity, this information was used to classify each event as fixation or smooth pursuit. To be classified as *fixation*, absolute velocity must be lower than velocity threshold determined as the 90th percentile of the absolute value distribution during the fixation control task ($\sqrt{V_x^2 + V_y^2} < V_{th}^{fix} = 2.4^\circ/s$), and that mean square error of the linear regression must be lower than 0.1° . The latter ensures that $x(t)$ and $y(t)$ are mainly linear.

To be classified as *smooth pursuit* eye velocity must fall inside the corresponding ellipse. Geometric parameters of the ellipses were chosen to enclose the main cluster of events in the control task, for each angle separately. Results are robust to small changes of all the thresholds.

2.8. Proximity factor

We calculated the distance from the gaze position to the different objects, for each sample and trial. Proximity factors are defined as the percentage of trials in which each distance is shorter than the threshold, in each time step. Proximity factor results are robust, and they are qualitatively preserved if thresholds are changed. We used the value of 30 px (2.6° of visual field) as threshold for gaze–ball distance, gaze–brick and gaze–paddle distance. Note that the gaze can be near to more than one object at once, hence proximity factors do not add up to 100%. Since the block and the paddle are elongated objects, the distance to them is calculated as the minimum of the three distances to one of the ends or the center.

2.9. Advancement and prediction error

To calculate advancement and prediction error we analyzed each sample of each trial separately. For each sample we calculated the geometric distance between the gaze location and every point of the ball trajectory in a period 500 ms before and 500 ms after current ball location (see Fig. 7a). The minimum value of those distances is called *prediction error*. And the distance (measured in ms) between this closest point in the trajectory and the current ball position along ball trajectory is defined as the *advancement*. The advancement measures how far ahead (if positive) or behind (if negative) of the ball the gaze is located, along ball trajectory.

3. Results

3.1. Classification of ocular events during linear ball trajectories

We identified saccades using a standard algorithm which uses velocity and acceleration thresholds (see Section 2). We define an *eye event* as the two-dimensional eye trajectory between two consecutive saccades (Fig. 2a). Our first aim was to classify *eye events* as *fixations* (events in which gaze remains in a fixed position), and *smooth pursuits* (events in which the eye moves at velocity similar to the ball²).

To calibrate the classification algorithm we ran two control experiments. In the *fixation control* task, participants had to read a static line of text that appeared on the center of the screen. A scatter plot of the two-dimensional velocity of each event indicated that all events were clustered close to the origin (Fig. 3a). Since we also included for this classification a condition of minimal square deviation (see Section 2) this assures that gaze during these events is mainly static, appropriately corresponding to fixations. For classification purposes, we considered an event as a fixation when its absolute velocity was lower than the 90th percentile of this distribution (black in Figs. 2 and 3). The same threshold was used to identify fixations in all the experiments.

In the *pursuit control* task participants were instructed to follow a ball moving by the playfield at the same speeds and angles as in the game. We used this task to calibrate smooth pursuit detection, considering the simplest case of eye events during which the ball did not bounce. In this case, the velocity distributions of the ocular events are spread in a wide region, and not just characterized by a single threshold value. One consistent feature was that the absolute value of eye velocities was systematically lower than the absolute value of the ball velocity, the gain was lower than one (Buizza & Schmid, 1986; Meyer et al., 1985). Hence the distributions are not centered in the ball velocity; rather they seem to be bounded by ball velocity. We found that for each given ball movement, the eye velocity is clustered in an ellipsoidal region, roughly located between the fixation threshold and the actual ball velocity

² For simplicity here we did not consider pursuits to the paddle since the paddle did not move during most of the trial and when it moved the velocity was not constant. When considering only events in which the paddle did not move, none of the results presented here changed significantly.

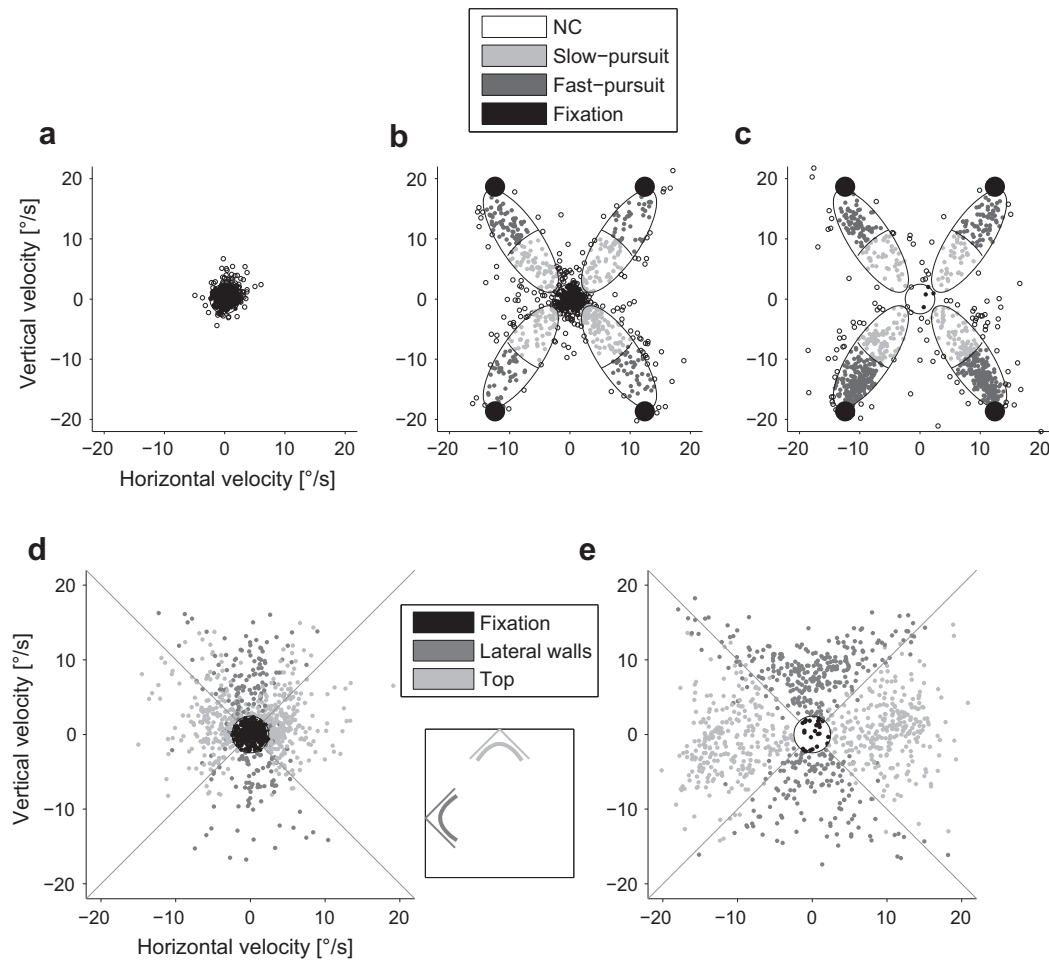


Fig. 3. Distribution of eye event velocities. (a–c) Distribution of eye velocities of the fixation control task (a), the game (b) and pursuit control task (c) for non-bouncing events. Velocity thresholds used to determine fixation (circle) and smooth pursuit (ellipses) are drawn. Large black dots indicate the values of ball velocity. All three panels contain a representative sample of 1000 events. (d and e) Distribution of eye velocities of the game (d) and pursuit control task (e) for bouncing events. Events slower than fixation threshold were categorized as fixations (black). Non-fixational events were categorized as bounces on lateral walls (dark gray), and bounces on top (light gray). Both panels contain a representative sample of 1000 events. Inset: Schematic of bounces on lateral walls or top.

(Fig. 3c). The ellipses are inclined slightly toward the horizontal with respect to the stimulus velocity. This suggests that the gain is higher for the horizontal pursuit than for vertical (Soechting, Rao, & Juveli, 2010). We used these features to classify each event as a smooth pursuit if their velocity falls into the corresponding ellipse (both dark and light gray in Figs. 2 and 3a–c). The parameters of the ellipses were chosen to enclose the main cluster of events in this control task, and subsequently used for the game. With this classification, $80 \pm 11\%$ (SE) of the non-bouncing events fell inside the corresponding ellipses, and was classified as pursuits. Only $1.3 \pm 0.3\%$ of the events was classified as fixations. $18 \pm 4\%$ of the events remained unclassified (outlined white in Figs. 2 and 3). While these classification criteria are certainly arbitrary, it serves for comparisons of event distributions across different tasks.

During each eye event of the game the trajectory of the ball may be a straight line or a bounce (Fig. 2a). We first analyzed eye velocities during linear trajectories of the ball. Eye-movements during bounces on the borders of the screen are analyzed in the next section. Eye velocities were continuously distributed between fixation-like and pursuit-like values (Fig. 3b). Using the classification criteria from the control experiments, $25 \pm 3\%$ (SE) were classified as fixations and $56 \pm 4\%$ as smooth pursuits (Fig. 2b).

Smooth pursuit distributions were different in the game and in the pursuit control task. In both cases velocities extend along the

direction of movement (in fact slightly inclined toward horizontal). However, during the pursuit task, the events are clustered closer to the ball velocity, while in the game the pursuit events have lower velocities, and locate closer to the origin. To quantify this observation, we simply separated smooth pursuit distributions in two categories: *fast pursuits* (or high-gain pursuits), in which the eye follows the ball at a speed close to that of the ball (dark gray in Figs. 2 and 3a–c); and *slow pursuits* (or low-gain pursuits), in which the eye velocity is lower, farther from ball velocity (light gray in Figs. 2 and 3a–c). We measured the mean percentage of slow pursuits (of all smooth pursuit events) which was significantly greater for the game than for the pursuit control task (game: $68 \pm 4\%$, pursuit task: $30 \pm 10\%$; unpaired two-tailed *t*-test: $t(17) = 4.13$, $p = 0.0007$).

3.2. Classification of ocular events during ball bounces

Ocular pursuit has been studied in periodic, non-linear and non-predictable trajectories (Barnes, 2008; Tavassoli & Ringach, 2009). Bouncing events are non-linear but predictable class of movements, which are frequently found in nature. Our game was tailored to investigate eye-movement trajectories during these singularities.

Eye events can be easily identified when projected to the $v_x - v_y$ plane. During linear trajectories of the ball these distributions formed a cluster close to the origin corresponding to fixations,

and clusters elongating in the direction of the ball corresponding to smooth pursuits (Fig. 3a–c). When we projected bouncing events to the $v_x - v_y$ plane we observed a qualitatively different distribution, with points clustering in the meridian axes (Fig. 3d and e). On the non-fixational events, velocity was mainly vertical when the ball hit the lateral walls (dark gray) and mainly horizontal when it hit the top and bottom (light gray). In the game, $82 \pm 6\%$ (SE) of fast events bouncing on the lateral walls fell into the vertical quadrants delimited by the principal diagonals, and $71 \pm 4\%$ of the fast events bouncing on the top fell into the horizontal quadrants (bottom hits on the game were not included because the output angle depends on the position of the paddle, and rebounds are not easily predictable and not necessarily symmetric). Both fractions are significantly larger than 50% (which would have been expected by random distribution), as confirmed by statistical tests (two-tailed t -test lateral walls: $t(14) = 5.12$, $p = 0.0002$; top: $t(14) = 5.54$, $p < 0.0001$). Similarly, in the pursuit control task, $90 \pm 2\%$ (SE) of the fast events bouncing on the lateral walls fell into the vertical quadrants, and $97 \pm 1\%$ of the fast events bouncing on the top fell into the horizontal quadrants. Both fractions are significantly larger than 50%, as confirmed by statistical tests (two-tailed t -test lateral walls: $t(3) = 21.76$, $p = 0.0002$; top: $t(3) = 38.64$, $p < 0.0001$).

The previous analysis revealed that during bounces, the eyes follow the moving object in the non-bouncing direction and stay fixed on average in the bouncing direction. We next investigated the specific pattern of eye-trajectories during bounces. At the bounce, the ball follows a V-shaped trajectory where the component of the velocity longitudinal to the border is preserved, while the perpendicular component is reversed. We found that eye-movements do not follow strictly the V-shape trajectory of the ball. Rather, they follow a curved trajectory, which seemed to smoothly interpolate the ball trajectory avoiding sharp accelerations and minimizing movement in the direction of the reversal (see Fig. 4a).

To quantify this observation we fitted the horizontal–vertical position of each eye event during bounces using a constant-plus-quadratic function as $y(x) = c(x - x_0)^2 + y_0$, where c and y_0 are the curvature and the intercept respectively (which were fitted), and x_0 corresponds to the x -position of the ball at the bounce. The sign of the curvature reflects whether the trajectory is concave or convex which can be compared with the ball trajectory. $88 \pm 2\%$ (SE) of the eye events in the game were curved like the trajectory of the ball (Fig. 3c), and $97 \pm 1\%$ in the pursuit control task (not shown). These values are significantly larger than 50%, as confirmed by statistical tests (two-tailed t -test game: $t(14) = 18.25$, $p < 0.0001$; pursuit control: $t(3) = 40.14$, $p < 0.0001$). We estimated for each bouncing angle, the average the values of c and y_0 . The resulting trajectories $y_{\text{angle}}(x) = \langle c \rangle_{\text{angle}}(x - x_0)^2 + \langle y_0 \rangle_{\text{angle}}$ smoothly interpolated the ball trajectory (Fig. 4b, inset).

In distinct forms of motor movements, smooth interpolations have been suggested to be the result of optimal solutions to cost functions which minimize simultaneously the acceleration (or its derivative), and proximity to the target (Flash & Hogan, 1985; Hogan, 1984; Uno, Kawato, & Suzuki, 1989). Avoiding abrupt velocity changes serves to maximize precision in reaching (Harris & Wolpert, 1998). More importantly, since visibility is known to diminish during saccades (Bridgeman, Hendry, & Stark, 1975) and perception is distorted during accelerated eye-movements, avoiding abrupt movements may serve to improve visibility for better prediction of the ball-trajectories resulting from sudden and intrinsically uncertain change of speed that occurs at the bounce.

While our purpose here is not to provide a full model with cost functions relating velocity to visibility to fit minimal models (see for instance Harris & Wolpert, 2006 for efforts in this direction) a series of observations are globally in accordance with the hypothesis that visibility is maximized during bounces to predict subsequent uncertain trajectories: (1) Blinks are minimal during the

bounces (Fig. 5a). Blink probability during bounces on the paddle differs significantly from the $[-100 \text{ ms}, 100 \text{ ms}]$ period to the $[200 \text{ ms}, 400 \text{ ms}]$ period (paired one-tailed t -test: $t(14) = 4.11$, $p = 0.0005$). Blink probability during bounces on the top (inset of Fig. 4a) also increases from the $[1300 \text{ ms}, 1500 \text{ ms}]$ period to the $[1600 \text{ ms}, 1800 \text{ ms}]$ period, although not reaching significance (paired one-tailed t -test: $t(14) = 1.16$, $p = 0.13$). (2) Eye velocity has a minimum during the bounce time (Fig. 4c and d). A t -test comparing the $[-100 \text{ ms}, 100 \text{ ms}]$ period to the $[200 \text{ ms}, 400 \text{ ms}]$ period confirmed this for both game and control pursuit (paired one-tailed t -test. Game: $t(14) = 8.54$, $p < 0.0001$; control pursuit: $t(3) = 7.83$, $p = 0.004$). (3) Indeed, in accordance with this finding, the most dramatic change during bounces is a drastic inhibition of saccades (Fig. 5b). Saccade probability increases from about 4% during the bounce to a peak of about 25%, more than twice the global mean value, about 230 ms after the bounce. To quantify this observation we performed one-tailed t -tests comparing saccade probability for each time sample to the global mean (gray dashed line). Bars at the top and bottom corresponds to values significantly higher or lower ($p < 0.0005$) than global mean value.

In summary, eye-movements during bounces follow a smooth trajectory which on average interpolates the V-trajectory of the rebound. Just after the bounce, eye velocity is minimal and blinks and saccades are significantly suppressed, suggesting that participants allocate unconsciously attention in a rational manner. Based on these observations we examined whether the dynamics of eye-movements during the course of the game indicates an implicit rational strategy.

3.3. Dynamics of eye-movements reflect a spontaneous organization of attention during the game

While our experimental design had the appearance of a game, it was conceived to be parsed as a sequence of trials (Fig. 2a). This allowed us to investigate the average dynamics of different observables of eye-movements. The trial is naturally parsed in relevant moments; when the ball hits the paddle, the top and the paddle again. Hits on lateral walls are averaged out, since they occur at different phases in different trials.

We first analyzed the distribution of blinks throughout the trial. To maintain normal moisture, eyes must blink, on average, every around 5 s (Carney & Hill, 1982). However, during blinks, visibility is temporary lost. Similarly, fast saccadic movements are necessary to shift the foveal region of the retina to salient parts of the visual scene (Najemnik & Geisler, 2005), but during saccades visibility is severely reduced, a phenomenon referred as saccadic suppression (Bridgeman et al., 1975; Burr, Morrone, & Ross, 1994). Hence a rational strategy would be to avoid blinks and saccades in the more demanding moments of the trial. In the previous section we already showed that eye velocity, blinks and saccades were minimal during bounces, a moment at which the ball direction is likely to be estimated. Here we further investigated such spontaneous and efficient distribution of eye events throughout the course of the trial.

We averaged, for each participant, the blink probability along the time of the trial. We then averaged this event-related blink probability across all participants (Fig. 5a). Most of the blinks occur on the first quarter of the trial once the ball commences its way up, away from the paddle. This corresponds to the less demanding moment of the task as the ball is at maximal time to hit the paddle again and far from all bounces. Few blinks occur on the rest of the trial, apart of a smaller peak after the bounce on the top (see inset of Fig. 5a). Both peaks are found about 300 ms after the bounces. To quantify these observations we divided the trial in four stages and submitted the data to an ANOVA analysis with ball direction (up and down) and trajectory segment (first and second half) as independent factors. We observed a significant effect of

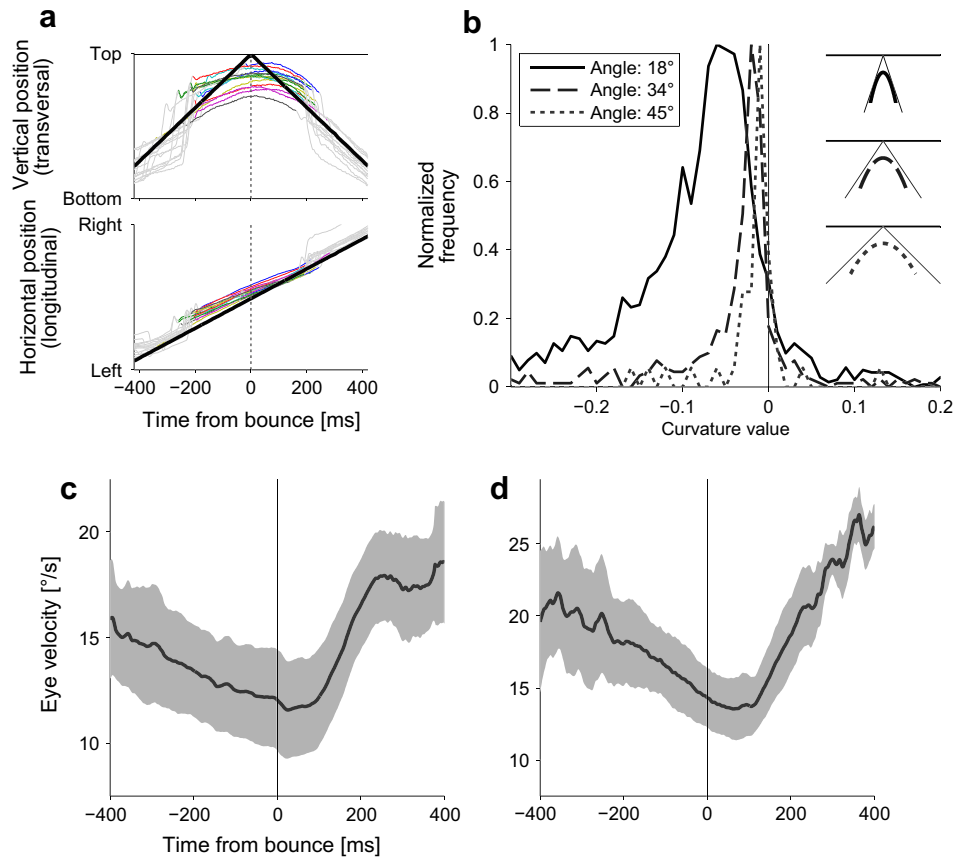


Fig. 4. Following a bouncing object. (a) Longitudinal and transversal position of the eye during a bounce. Different lines indicate the trajectory of representative eye events during bounces. The rest of the trajectory (of the antecedent and subsequent event of each trial) is coded in light gray. The black line indicates the trajectory of the ball. (b) Normalized histogram of curvature of eye-trajectories for each angle. Insets: The eye movement with curvature and intercept averaged from all bouncing events, for each ball angle. (c and d) Mean eye velocity calculated during bounce events is minimum at the top bounces for both game (c) and pursuit control (d). Shades are standard deviations of subjects' means.

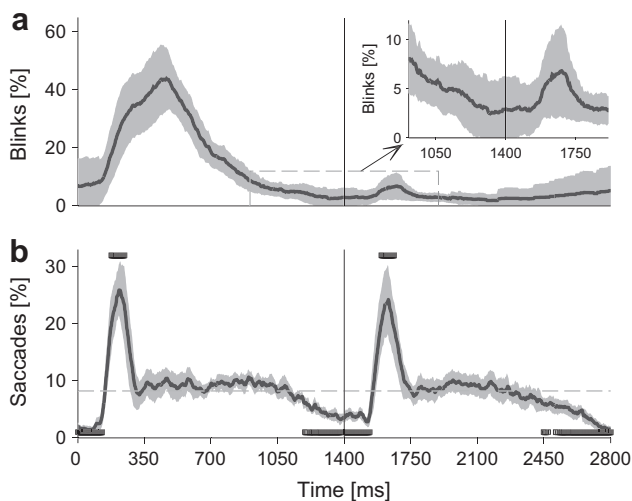


Fig. 5. Dynamics of blinks and saccades throughout the course of the trial. (a) Mean percentage of blinks found throughout the course of the trial. Inset: Detail of the bounce on the top. (b) Percentage of saccades throughout the trial. Gray dashed line corresponds to global mean value. Bars at the top and bottom corresponds to values significantly higher or lower ($p < 0.0005$) than global mean value. Shades are standard deviations of subjects' means.

both factors as well as an interaction (direction: $f_{1,56} = 39.68$, $p < 0.0001$; segment: $f_{1,56} = 20.92$, $p < 0.0001$; interaction:

$f_{1,56} = 19.40$, $p < 0.0001$). This asymmetry indicates that most of the blinks are concentrated in the first quarter of the trial.

We performed the same analysis for saccade probability. Away from bounces, saccades occur at a constant rate. Saccade probability is significantly reduced in the 400 ms period around the bounces, and it peaks around 230 ms after each bounce (Fig. 5b). To quantify this observation we performed t -tests comparing saccade probability for each time sample to the global mean (gray dashed line). Bars at the top and bottom correspond to samples significantly higher or lower than global mean (one-tailed t -test, $p < 0.0005$).

Our previous results showed that blinks are made in the less demanding moments of the trials and that saccades are suppressed during the most relevant moments (bounces and paddle impact). Yet another strategy to economize saccades and blinks would be to produce them simultaneously, as if the system knows that it would not be getting any useful vision during the saccade, so it would be a good time to blink.

To measure blink and saccade co-occurrence we first estimated, for each blink, the position just before the blink (in the last sample before the blink) and just after the blink. We obtained a mean velocity dividing by blink duration and we counted a saccade if this velocity exceeded the saccade threshold, $30^\circ/\text{s}$. Note that this is a lower-bound for saccade occurrence. If mean velocity is greater than $30^\circ/\text{s}$ a saccade has to have occurred, but it is possible that there was a saccade (only during a fragment of the blink) and mean velocity would be less than the saccade threshold. Despite this underestimation of the number of saccades by this method we

found that $75 \pm 5\%$ contained a saccade. We then compared this density of occurrence pairing each blink to an identical time interval in a trial in which there was no blinks. In this no-blink control we found a significantly lower density of saccades $30 \pm 2\%$. The difference in occurrence was highly significant as indicated by a paired two-tailed t -test: after averaging the saccade densities for each subject and blink or no-blink condition $t(14) = 10.96$, $p < 0.0001$.

In the previous analysis we measured the relative dynamics of eye events and blinks during the trial. Another ocular trace of underlying mental algorithms during the game comes from the direction of gaze (Itti & Koch, 2000, 2001; Yarbus, 1967). We calculated, for each participant and each time sample during the trial, the fraction of trials for which the distance between the gaze location and the objects (ball, paddle and brick) was smaller than a fixed threshold (see Section 2 for details).

Overall the time course of object proximity followed an expected trend, although from explicit reports this remained completely unaware to all subjects. Gaze is systematically closer to the ball during the second half of the trial, when the ball is moving down (Fig. 6a). To quantify this observation we submitted the proximity factor to the ball to an ANOVA analysis with ball direction (up and down) and trajectory segment (first and second half) as independent factors. We only observed a significant effect of the direction, and no effect for segment or interaction (direction: $f_{1,56} = 4.34$, $p = 0.04$; segment: $f_{1,56} = 0.71$, $p = 0.40$; interaction: $f_{1,56} = 0.2$, $p = 0.65$). This was confirmed by a post hoc t -test comparing the first and second half of the trial (paired one-tailed t -test; $t(14) = 2.33$, $p = 0.014$). Salient features of the proximity factor of the ball are the bumps at the beginning and end of each half trial. These bumps reflect the particular type of movement in which the eye follows the ball on the bounces, performing the smooth curved trajectory described in the previous section (Fig. 4).

When the ball hits the paddle the gaze is in close proximity to the paddle in a large fraction of the trials (Fig. 6b). Proximity to the paddle drops rapidly to almost zero after the initial movement

of the ball, and ramps up slowly during the second half of the trial, when the ball is moving down. This function is asymmetric; participants are closer to the paddle when the ball is about to impact it than when it has already done it. To quantify these observations we submitted the data to an ANOVA analysis with ball direction (up and down) and trajectory segment (first and second half) as independent factors. We observed a significant effect of both factors as well as an interaction (direction: $f_{1,56} = 9.28$, $p = 0.004$; segment: $f_{1,56} = 5.48$, $p = 0.02$; interaction: $f_{1,56} = 68.61$, $p < 0.0001$). This asymmetry indicates an anticipatory pattern which will become evident in subsequent analysis: participants direct their gaze to the paddle when the ball is about to make contact, but not when it has just made contact and is moving up.

The eye–paddle proximity factor could be trivially explained by the ball trajectory: if participants simply look at the ball, at the moments in which the ball is close to the paddle gaze will also be directed to the paddle. To examine whether this accounts for our observations we superposed the ball–paddle proximity factor to the gaze–paddle proximity factor (dashed line in Fig. 6b). This comparison indicated that while these curves covaried they had qualitatively different patterns. Eye is directed to the paddle more than 300 ms earlier than the ball. In contrast the gaze leaves the paddle quickly (~ 100 ms) after the ball.

The same anticipatory pattern was observed when analyzing proximity to the brick (Fig. 6c). All trials contained at most one brick and the objective of the game was to hit the brick with the ball. Participants' gaze was directed in proximity to the brick in anticipation to the movement of contact. Interestingly proximity to the brick also reflects a marked asymmetry during the trial: the major proportion of gaze directed to the brick occurs during the first half of the trial. As observed with the blink distributions, saccades to the brick are maximal in the less demanding moment of the task as the ball is at maximal time to hit the paddle again. To quantify this observation, we submitted the data to an ANOVA analysis with ball direction (up and down) and trajectory segment (first and second half) as independent factors. We observed a significant effect of both factors as well as an interaction (direction: $f_{1,56} = 69.35$, $p < 0.0001$; segment: $f_{1,56} = 34.17$, $p < 0.0001$; interaction: $f_{1,56} = 12.74$, $p = 0.0007$).

A comparison to ball–brick proximity factor (dashed line in Fig. 6c) indicates that the gaze is directed to the brick earlier than the ball. Mean trial-time of eye–brick proximity occurrence was 1004 ± 21 ms (SE), while mean ball–brick time was 1362 ± 21 ms (paired two-tailed t -test: $t(14) = 10.22$, $p < 0.0001$). Moreover, gaze is located in close proximity to the brick almost five times more frequently than the ball (mean eye–brick proximity factor: $7.00 \pm 0.48\%$, mean ball–brick proximity factor: $1.44 \pm 0.10\%$). Paired two-tailed t -test: $t(14) = 13.02$, $p < 0.0001$).

Another advantage of our experimental design is that we could quantify the degree and the precision of anticipation, measuring in each instant the minimum distance between the gaze and the ball trajectory, restricted to a period of 1000 ms centered at the current ball location to avoid wrapping artifacts.

We define, for each time t (within the 2800 ms of the trial) and time difference t_d within a range $[-500$ ms; 500 ms] the geometric distance between the gaze location at time t , $\vec{G}(t)$ and the position where the ball was t_d ms before (if t_d is negative) or will be after (if t_d is positive) $\vec{B}(t + t_d)$:

$$D(t, t_d) = |\vec{G}(t) - \vec{B}(t + t_d)|.$$

We then define for each t , the advancement t_{adv}

$$t_{adv} = \arg \min_{t_d} D(t, t_d)$$

and the prediction error P_{err} as

$$P_{err} = D(t, t_{adv}).$$

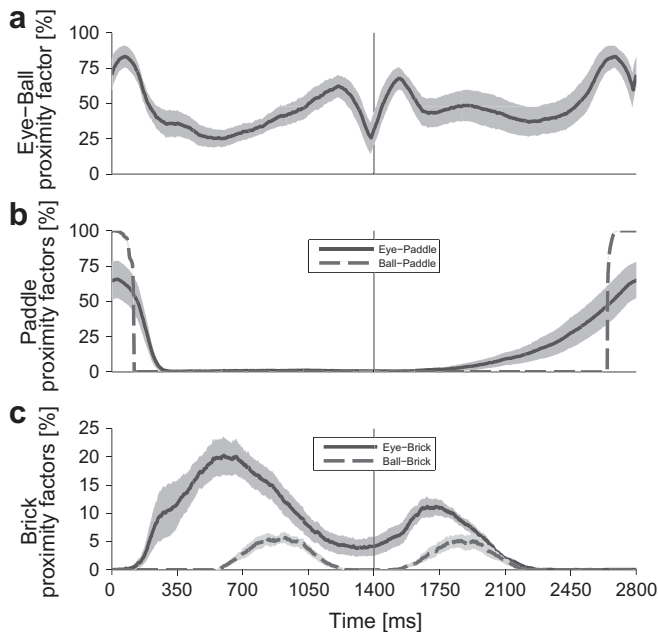


Fig. 6. Proximity factors. (a) Time course throughout the trial of eye-ball proximity factor. (b) Time course of eye-paddle (continuous line) and ball-paddle (dashed line) proximity factors. (c) Time course of eye-brick (continuous line) and ball-brick (dashed line) proximity factors. Shaded areas are standard deviations of subjects' means.

The advancement t_{adv} measures how far ahead (or behind) of the ball the gaze is located, along ball trajectory (see Fig. 7a). As expected by our previous findings, during most of the trial (except during the bounces) the time of advancement was positive (Fig. 7b). We found that the advancement was consistently positive, with a value close to 150 ms, indicating that the gaze is systematically ahead of the trajectory of the ball. We submitted the advancement to an ANOVA analysis with ball direction (up and down) and trajectory segment (first and second half) as independent factors. Neither factors nor the interaction were significant (direction: $f_{1,56} = 3.34$, $p = 0.07$; segment: $f_{1,56} = 1.01$, $p = 0.31$; interaction: $f_{1,56} = 0.02$, $p = 0.89$).

A qualitatively distinct pattern is observed during bounces. About 200 ms before each bounce, the advancement begins a nearly linear decrease which reaches a minimum 200 ms after the bounce, after which advancement increases abruptly. To quantify this observation we performed t -tests comparing advancement values for each time sample to the global mean (gray dashed line). Bars at the bottom correspond to samples significantly lower than global mean (one-tailed t -test, $p < 0.0005$). This dynamics coincides with the inhibition and sudden burst in saccade distributions (Fig. 5b) suggesting a coherent relation between these two observables: when the ball is about to bounce, saccades are postponed to increase ball visibility, and gaze progressively loses anticipation with respect to the ball trajectory. About 200 ms after the bounce, saccades are made with very high probability which sets gaze again in anticipation of the ball trajectory.

Prediction error P_{err} measures the proximity of gaze to the ball trajectory (see Fig. 7c). We found that prediction error is minimal during crucial moments of the bounces as manifested by two effects. First, prediction error was lower while the ball was moving down and approaching the paddle. Second, within each half of

the trial, prediction error reached a minimum during the bounces and peaked during the first half of each segment when the ball was at maximal distance from bounces. These observations were confirmed by an ANOVA analysis of prediction error with ball direction (up and down) and trajectory segment (first and second half) as independent factors. We observed a significant effect of both factors but no interaction between them (direction: $f_{1,56} = 14.28$, $p = 0.0004$; segment: $f_{1,56} = 8.02$, $p = 0.006$; interaction: $f_{1,56} = 0$, $p = 0.99$).

4. Discussion

We investigated the dynamics of eye events in a simple video game, as a model of an ecologic sensory-motor task in which all variables are under experimental control. We found that the distribution of pursuit velocity during events in which the ball moves linearly are very broad and upper bounded by the velocity of the moving object (Buizza & Schmid, 1986; Meyer et al., 1985). In events in which the ball bounces, eye-movements follow a smooth trajectory which on average interpolates the V-trajectory of the rebound.

Harris and Wolpert (2006) have argued that the main sequence of saccades (the consistent relationship between duration, peak velocity and amplitude of saccadic movements) evolved to optimize the trade-off between the duration and the accuracy of the movement (Harris & Wolpert, 2006). In line with this idea, several authors have suggested that the interplay between saccadic and pursuit system optimizes tracking error under unpredictability eliciting catch-up saccades when the error estimated at the moment in which the eye will cross a target exceeds a certain threshold (de Brouwer et al., 2002). Our results are inline with this view, suggesting that smooth interpolation of abrupt changes of velocity (bounces) may result from optimizing a cost function which maximizes tracking accuracy and penalizes abrupt movements. While requiring further investigation, we suggest that penalization of abrupt movements does not merely reflect a “lazy system”; rather, it may serve to improve visibility during relevant moments in which uncertain trajectories ought to be estimated. A series of observations are in good agreement with this simple principle of predictability and urgency of action guiding the organization of eye events.

First, blinks and saccades – which serve different purposes but both inflict a moment of loss of sight – were absent during bounces and virtually all blinks were produced while the ball was moving upwards. After a refractory period of a few hundred milliseconds following the bounce (typical decision times in simple tasks) saccades were maximal.

Second, analysis of the object to which gaze was directed appeared to be guided by urgency and prediction. Fixations to the brick – which are not necessary to maintain the ball in the game – were maximal when the ball is at maximal time to hit the paddle. On the contrary, gaze towards the ball and paddle was maximal when the ball approaches the paddle.

The pattern of anticipation also reflected a consistent organization. Throughout most of the trial, gaze was directed to a point which anticipated the ball by about 150 ms. This is consistent with results obtained in various ball sports, where eyes anticipate the ball trajectory by 100–200 ms (Hayhoe & Ballard, 2005; Land, 2006; Land & Furneaux, 1997; Land & McLeod, 2000). The sole moment of the trial during which gaze was equally advanced (or even behind) of the ball was observed during the refractory period of saccades observed during bounces. This pattern is consistent with a model by which participants postpone saccades at the bounces while predicting the ball trajectory and subsequently make a catch-up saccade. This saccade is targeted to the expected position

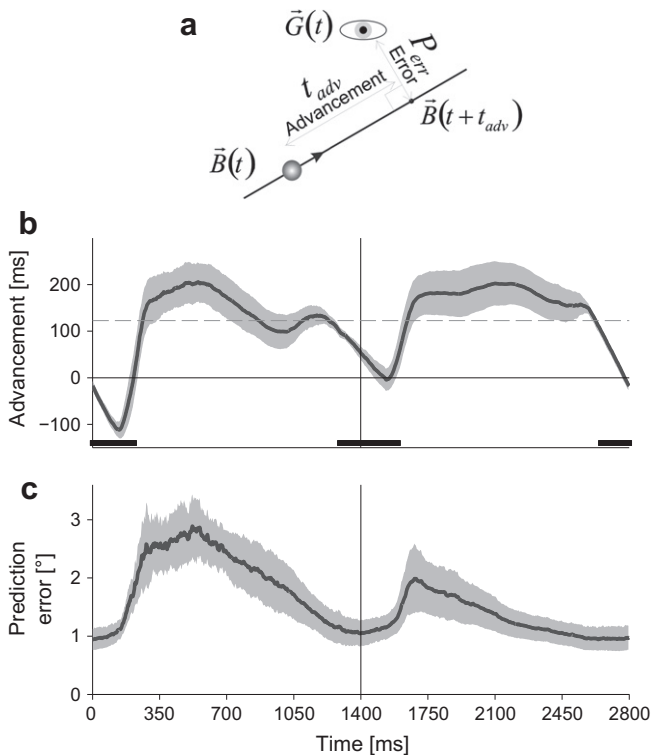


Fig. 7. Prediction and precision of ball tracking. (a) Schematic of the calculation of the advancement t_{adv} and prediction error P_{err} . (b) Advancement of the eye with respect to the current location of the ball. Gray dashed line corresponds to global mean value. Bars at the bottom corresponds to values significantly lower than global mean value. (c) Prediction error of the eye with respect to the trajectory of the ball. Shades are standard deviations of subjects' means.

of the ball ahead of the trajectory after which gaze remains ahead of the ball until the next bounce. Finally, the precision of the anticipated trajectory also varied with urgency, being maximal close to the critical moments of bounces.

Hence, while gaze during the course of the game may be uncoupled from ball position, they are tightly correlated about 300 ms before the moment of paddle bounce. Since eye and paddle trajectories converge at the time of impact, simply driving the paddle from the x -position of the ball leads to perfect play. Since the eye can be moved so much faster than the hand, and is more directly coupled to the ball, using the x -position of the eye to control the paddle, could be a very efficient strategy. This was demonstrated by Michael Dorr, who implemented a version of Breakout controlled by gaze, showing that the game can be played more efficiently when the paddle is controlled by the horizontal component of gaze than when it is controlled by hand (Dorr, Pomarjanschi, & Barth, 2009).

Early studies of ocular movements convincingly showed that a main factor determining gaze location is determined by saliency (Yarbus, 1967). Saliency combines bottom-up (contrast, color, curvature) and top-down elements which relate, at different moments, to task necessity (Navalpakkam & Itti, 2006). The systematic anticipation here observed indicates that, in dynamic setups, salient or relevant points which attract gaze may not be the center of action, but rather the points where action will happen in the immediate future. This is reminiscent of the findings of Geisler and colleagues. They found that, in a visual search task, saccades are not directed to the point where the target is most likely to be, but rather to the point which maximizes the information gain given the spatial inhomogeneities in resolution of the retina (Geisler et al., 2006; Najemnik and Geisler, 2005, 2008).

Summarizing, we investigated the organization of eye-movement classes while participants played Breakout. We observed that eye-movement dynamics can be explained in terms of simple principles of moments of prediction and urgency of action. We observed a consistent anticipatory behavior (gaze was directed ahead of ball trajectory) except during the moment in which the ball bounced either in the walls, or in the paddle. During bounces, trajectories were smooth and curved interpolating the V-shape function of the ball with minimal acceleration, while saccades and blinks were suppressed. About 200 ms after bounces we observed a sharp peak in the density of saccades suggesting that participants postpone saccades at the bounces while predicting the ball trajectory. They subsequently make a catch-up saccade directed to a position which anticipates ball trajectory. This work constitutes a first step aimed to understand eye-movements on natural configurations in which stimuli and goals switch dynamically in time.

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References

- Bahill, A. T., & McDonald, J. D. (1983). Smooth pursuit eye movements in response to predictable target motions. *Vision Research*, 23(12), 1573–1583.
- Barnes, G. R. (2008). Cognitive processes involved in smooth pursuit eye movements. *Brain and Cognition*, 68(3), 309–326.
- Barnes, G. R., & Asselman, P. T. (1991). The mechanism of prediction in human smooth pursuit eye movements. *Journal of Physiology*, 439, 439–461.

- Bridgeman, B., Hendry, D., & Stark, L. (1975). Failure to detect displacement of the visual world during saccadic eye movements. *Vision Research*, 15(6), 719–722.
- Buizza, A., & Schmid, R. (1986). Velocity characteristics of smooth pursuit eye movements to different patterns of target motion. *Experimental Brain Research*, 63(2), 395–401.
- Burr, D. C., Morrone, M. C., & Ross, J. (1994). Selective suppression of the magnocellular visual pathway during saccadic eye movements. *Nature*, 371(6497), 511–513.
- Carney, L. G., & Hill, R. M. (1982). The nature of normal blinking patterns. *Acta Ophthalmologica (Copenhagen)*, 60(3), 427–433.
- de Brouwer, S., Yuksel, D., Blohm, G., Missal, M., & Lefevre, P. (2002). What triggers catch-up saccades during visual tracking? *Journal of Neurophysiology*, 87(3), 1646–1650.
- Dehaene, S., Cohen, L., Sigman, M., & Vinckier, F. (2005). The neural code for written words: A proposal. *Trends in Cognitive Sciences*, 9(7), 335–341.
- Dorr, M., Pomarjanschi, L., & Barth, E. (2009). Gaze beats mouse: A case study on a gaze-controlled breakout. *Psychology Journal*, 7(2), 197–211.
- Eckstein, M. P., Drescher, B. A., & Shimozaaki, S. S. (2006). Attentional cues in real scenes, saccadic targeting, and Bayesian priors. *Psychological Science*, 17(11), 973–980.
- Erkelens, C. J. (2006). Coordination of smooth pursuit and saccades. *Vision Research*, 46(1–2), 163–170.
- Flash, T., & Hogan, N. (1985). The coordination of arm movements: An experimentally confirmed mathematical model. *Journal of Neuroscience*, 5(7), 1688–1703.
- Geisler, W. S., Perry, J. S., & Najemnik, J. (2006). Visual search: The role of peripheral information measured using gaze-contingent displays. *Journal of Vision*, 6(9), 858–873.
- Goodwin, A. W., & Fender, D. H. (1973). Recognition of component differences in two-dimensional oculomotor tracking tasks. *Vision Research*, 13(10), 1905–1913.
- Harris, C. M., & Wolpert, D. M. (1998). Signal-dependent noise determines motor planning. *Nature*, 394(6695), 780–784.
- Harris, C. M., & Wolpert, D. M. (2006). The main sequence of saccades optimizes speed-accuracy trade-off. *Biological Cybernetics*, 95(1), 21–29.
- Hayhoe, M., & Ballard, D. (2005). Eye movements in natural behavior. *Trends in Cognitive Sciences*, 9(4), 188–194.
- Hogan, N. (1984). An organizing principle for a class of voluntary movements. *Journal of Neuroscience*, 4(11), 2745–2754.
- Itti, L., & Koch, C. (2000). A saliency-based search mechanism for overt and covert shifts of visual attention. *Vision Research*, 40(10–12), 1489–1506.
- Itti, L., & Koch, C. (2001). Computational modelling of visual attention. *Nature Reviews Neuroscience*, 2(3), 194–203.
- Kato, T., & Fukuda, T. (2002). Visual search strategies of baseball batters: Eye movements during the preparatory phase of batting. *Perceptual and Motor Skills*, 94(2), 380–386.
- Kliegl, R., Nuthmann, A., & Engbert, R. (2006). Tracking the mind during reading: the influence of past, present, and future words on fixation durations. *Journal of Experimental Psychology: General*, 135(1), 12–35.
- Land, M. F. (2006). Eye movements and the control of actions in everyday life. *Progress in Retinal and Eye Research*, 25(3), 296–324.
- Land, M. F., & Furneaux, S. (1997). The knowledge base of the oculomotor system. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, 352(1358), 1231–1239.
- Land, M. F., & Hayhoe, M. (2001). In what ways do eye movements contribute to everyday activities? *Vision Research*, 41(25–26), 3559–3565.
- Land, M. F., & McLeod, P. (2000). From eye movements to actions: How batsmen hit the ball. *Nature Neuroscience*, 3(12), 1340–1345.
- Meyer, C. H., Lasker, A. G., & Robinson, D. A. (1985). The upper limit of human smooth pursuit velocity. *Vision Research*, 25(4), 561–563.
- Mulligan, J. B., Stevenson, S. B., & Cormack, L. K. (2005). The effect of plaid orientation on pursuit of partially-predictable motion. *Journal of Vision*, 5(8), 440.
- Najemnik, J., & Geisler, W. S. (2005). Optimal eye movement strategies in visual search. *Nature*, 434(7031), 387–391.
- Najemnik, J., & Geisler, W. S. (2008). Eye movement statistics in humans are consistent with an optimal search strategy. *Journal of Vision*, 8(3), 4–14.
- Navalpakkam, V., & Itti, L. (2006). An integrated model of top-down and bottom-up attention for optimizing detection speed. In *Proceedings of the 2006 IEEE computer society conference on computer vision and pattern recognition* (Vol. 2). IEEE Computer Society.
- Orban de Xivry, J. J., & Lefevre, P. (2007). Saccades and pursuit: two outcomes of a single sensorimotor process. *Journal of Physiology*, 584(Pt 1), 11–23.
- Pelz, J. B., & Canosa, R. (2001). Oculomotor behavior and perceptual strategies in complex tasks. *Vision Research*, 41(25–26), 3587–3596.
- Ranganathan, R., & Carlton, L. G. (2007). Perception-action coupling and anticipatory performance in baseball batting. *Journal of Motor Behavior*, 39(5), 369–380.
- Rashbass, C. (1961). The relationship between saccadic and smooth tracking eye movements. *Journal of Physiology*, 159, 326–338.
- Rayner, K. (1983). *Eye movements in reading: Perceptual and language processes*. New York: Academic Press.
- Regan, D. (1997). Visual factors in hitting and catching. *Journal of Sports Sciences*, 15(6), 533–558.
- Robinson, D. A. (1965). The mechanics of human smooth pursuit eye movement. *Journal of Physiology*, 180(3), 569–591.

- Soechting, J. F., Rao, H. M., & Juvela, J. Z. (2010). Incorporating prediction in models for two-dimensional smooth pursuit. *PLoS One*, 5(9), e12574.
- Takeuchi, T., & Inomata, K. (2009). Visual search strategies and decision making in baseball batting. *Perceptual and Motor Skills*, 108(3), 971–980.
- Tavassoli, A., & Ringach, D. L. (2009). Dynamics of smooth pursuit maintenance. *Journal of Neurophysiology*, 102(1), 110–118.
- Uno, Y., Kawato, M., & Suzuki, R. (1989). Formation and control of optimal trajectory in human multijoint arm movement. Minimum torque-change model. *Biological Cybernetics*, 61(2), 89–101.
- Wolpert, D. M., & Flanagan, J. R. (2010). Motor learning. *Current Biology*, 20(11), R467–R472.
- Yarbus, A. L. (1967). *Eye movements and vision*. New York: Plenum Press.