

Divergence between oculomotor and perceptual causality

Jeremy B. Badler

Laboratory of Neurophysiology (NEFY), Center for Systems Engineering and Applied Mechanics (CESAME) and Institute of Neuroscience (IoNS) Université catholique de Louvain, Brussels, Belgium



Philippe Lefèvre

Center for Systems Engineering and Applied Mechanics (CESAME), Institute of Information and Communication Technologies, Electronics and Applied Mathematics (ICTEAM) and Institute of Neuroscience (IoNS) Université catholique de Louvain, Brussels, Belgium



Marcus Missal

Laboratory of Neurophysiology (NEFY), Center for Systems Engineering and Applied Mechanics (CESAME) and Institute of Neuroscience (IoNS) Université catholique de Louvain, Brussels, Belgium



When two objects such as billiard balls collide, observers perceive that the action of one caused the motion of the other. We have previously shown (Badler, Lefèvre, & Missal, 2010) that this extends to the oculomotor domain: subjects make more predictive movements in the expected direction of causal motion than in a noncausal direction. However, predictive oculomotor and reactive psychophysical responses have never been directly compared. They should be correlated if they tap into the same mental processes. To test this, we recorded oculomotor responses to launching stimuli, then asked subjects to manually classify those stimuli as causal or noncausal. Overall the psychophysical classifications matched the oculomotor biases, although correlations across subjects were mostly absent. In subsequent experiments, 50% of the trials had a 300-millisecond delay after the collision to impede the perception of causality. Subjects maintained their causal oculomotor bias but used different classification strategies, usually grouping the stimuli either by delay or by direction. In addition, there was no evidence that the two response types were correlated on a trial-by-trial basis. The results suggest divergent processes underlying oculomotor responses to and judgments of causal stimuli.

Keywords: launching effect, predictive movement, psychophysics, human

Citation: Badler, J. B., Lefèvre, P., & Missal, M. (2012). Divergence between oculomotor and perceptual causality. *Journal of Vision*, 12(5):3, 1–15, <http://www.journalofvision.org/content/12/5/3>, doi:10.1167/12.5.3.

Introduction

The physical laws that govern the world cause objects to behave in a predictable way. For example, when one mobile object collides with another of approximately equal mass, the second one will move in a predictable way. This reaction is an example of physical causality, where the action of one object causes the reaction of another. Human adults (Michotte, 1946/1963; Scholl & Tremoulet, 2000), as well as young children and babies (Gopnik, Sobel, Schulz, & Glymour, 2001; Leslie & Keeble, 1987; Saxe & Carey, 2006), are able to perceive causality and are highly sensitive to violations of it. For a simple collision event, such violations include temporal or spatial gaps at the

collision, and motion angles or speed ratios that seem to be at odds with the laws of physics (Michotte, 1946/1963; Schlottmann & Anderson, 1993; Schlottmann & Shanks, 1992; Straube & Chatterjee, 2010; Young, Rogers, & Beckmann, 2005). The perception of causality holds across different cultures (Morris & Peng, 1994), though it may be altered or impaired in certain neurological or psychiatric conditions such as autism (Ray & Schlottmann, 2007) and schizophrenia (Tschacher & Kupper, 2006). Evidence suggests that other primate species (Hauser & Spaulding, 2006; O'Connell & Dunbar, 2005), as well as corvids (Chappell, 2006; Seed, Tebbich, Emery, & Clayton, 2006), might be able to perceive and even reason based on causality as well (but see Penn & Povinelli, 2007).

Since seminal work by Albert Michotte (1946/1963), causality has been well-studied in the perceptual domain (Wagemans, van Lier, & Scholl, 2006). However, except for an early exploratory study (Hindmarch, 1973), oculomotor data have only recently been used to quantify the responses to causal stimuli. Badler, Lefèvre, and Missal (2010) were the first investigators to examine the influence of causal stimuli on predictive eye movements. They instructed human observers to track the second moving target following a collision in a simple action–reaction launching display (Michotte, 1946/1963). The reaction target could move either in a logical, causal direction (as would be predicted by transfer of momentum) or in a noncausal direction, orthogonal to the causal motion. Subjects' eye movements tended to be biased towards the causal direction, and movements in that direction tended to have shorter latencies relative to movements in the noncausal direction. These biases disappeared when the causal interaction was eliminated from the display, either by introducing a time delay between the initial collision and reaction target motion, or by the presence of a spatial gap between the launcher and reaction targets.

An obvious question left unanswered by Badler, Lefèvre, and Missal (2010) was the role of perception—that is, did subjects actually perceive the motions in individual trials as causal or noncausal? Typically, causal perception is assessed by having subjects directly judge or classify stimuli (e.g., Falmier & Young, 2008; Schlottmann & Shanks, 1992; Straube & Chatterjee, 2010; Young, Rogers, & Beckmann, 2005), and the original study implicitly assumed that subjects would consider orthogonal motion to be noncausal and vice versa. However, other studies have shown substantial variability in how subjects actually respond, even among Michotte's contemporaries (Beasley, 1968; Gemelli & Cappellini, 1958). Ratings are also sensitive to prior training or instructions (e.g., Falmier & Young, 2008; Young, Rogers, & Beckmann, 2005). To assess the question in the present study, subjects were again tested on the oculomotor causality task and were additionally asked to classify the stimuli as causal or noncausal. The classifications were then used as a measurement of causal perception, to which the oculomotor metrics were compared. If the oculomotor response is linked with perception, predictive eye movements might reflect the initial state of the subject; i.e., an expectation of whether the upcoming motion will be causal or not. Thus the eye movements and classifications should be correlated, especially if they are derived from the same underlying mental process. As with the ratings, one might expect the eye movements to be also influenced by prior experience and individual subject differences. What we found instead was a divergence: although oculomotor re-

sponses and perceptual classifications were congruent for the simplest task, they often differed when stimuli were more complex. Eye movements were consistent across subjects and seemed to be dominated by the context created by multiple stimuli, whereas classifications were more variable and may have been based on a rapid, heuristically based evaluation of each stimulus.

Methods

Experiment 1

Twelve healthy right-handed subjects (eight women; mean age 28.3 years, *SD* 5.0) were used for the experiment. Subjects AF and MH were completely naïve as to the design and purpose of the study. The other subjects were also naïve as to the purpose, but had previously viewed different versions of causally based stimuli. Subjects GT and KT participated in a previous study (Badler, Lefèvre, & Missal, 2010). All subjects were either native speakers of or highly fluent in French or English, and all instructions for the psychophysics task were given in the preferred language of each. All subjects gave their consent to participate, and all procedures were approved by the ethics committee of the Faculty of Medicine at the Université catholique de Louvain and adhered to the Declaration of Helsinki.

The experimental methods were mostly identical to those used previously (Badler, Lefèvre, & Missal, 2010, Experiment 2). Subjects were seated in a darkened room facing a dimly lit CRT monitor (Sony Trinitron, 800 × 600 pixels, 100 hertz). Their chins and foreheads rested on a padded frame 70 centimeters from the screen. Eye movements were recorded at 1,000 hertz using an EyeLink 1000 tower-mounted camera (SR Research Ltd., Mississauga, Ontario, Canada). At the beginning of each session, subjects viewed sequentially presented calibration points of $\pm 5^\circ$ and $\pm 10^\circ$, horizontal and vertical. The calibration trial was used for offline computation of offsets and gains.

The visual stimulus (Figure 1) consisted of a “tool,” a launcher target and a reaction target. All appeared simultaneously at the beginning of the trial. The tool was a static red octagon 1.35° wide, always located in the center of the screen. The launcher target was a green dot 0.5° in diameter that appeared in one corner of the screen at 12° radial eccentricity. After 750 milliseconds it moved towards the central tool with a diagonal trajectory at a velocity of $30^\circ/\text{s}$. The reaction target was a white dot with the same characteristics as the launcher except that it began adjacent to the tool, oriented 135° from the incoming launcher trajectory. At the moment when the launcher target impacted the

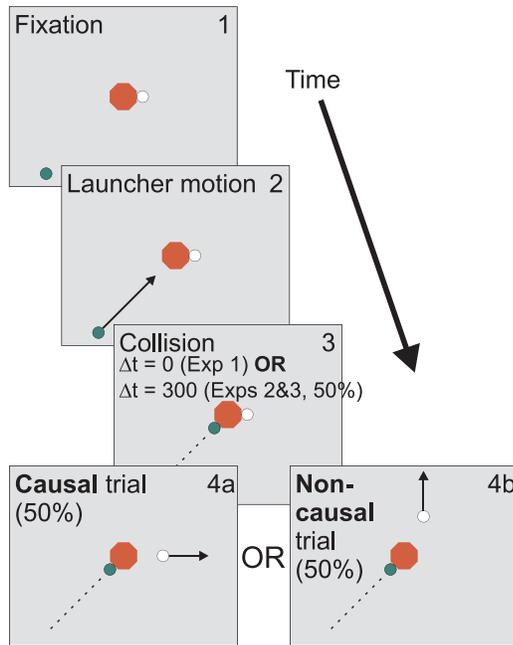


Figure 1. Stimulus sequence. Each trial began with the appearance of the tool octagon, the launcher target, and the reaction target (panel 1). After a fixation interval of 750 milliseconds, the launcher target began to move toward the tool (panel 2). After the collision (panel 3), the reaction target began to move either immediately (**Experiment 1**) or immediately 50% of the time and after a 300-millisecond delay the other 50% of the time (**Experiments 2 and 3**). In causal trials (50%), the reaction target moved in the direction consistent with conservation of momentum (panel 4a). In noncausal trials (50%), the target moved in the orthogonal direction (panel 4b). Note that in the actual stimulus, the background was much darker and the targets were not circumscribed with black lines.

tool, the launcher stopped, and the reaction target began to move. With equal probability, the reaction target moved either directly or orthogonally away from the tool. The former trajectory is defined as the *causal direction*, and the latter the *noncausal direction*. Both reaction trajectory angles were equally distant from the launcher trajectory (135°). The excursion of the reaction target lasted 500 milliseconds, which carried it off of the visible screen. The tool and launcher remained visible for an additional 250 milliseconds. The screen was then blanked for an intertrial interval of 1,000 milliseconds during the oculomotor task and for 2,000 milliseconds during the psychophysics task. The initial position of the launcher target was randomized in a balanced fashion to one of the four corners of the screen. The “handedness” of the reaction target (i.e., whether it lay to the left or right of the launcher path) was also randomized and balanced with the initial launcher position. The motion direction of the reaction target was randomized independently for each trial (0.5 probability to be either causal or noncausal). Motion in

any of the four cardinal directions was possible, depending on the initial geometry of the targets and the causal/noncausal status of the trial.

For the oculomotor task, the subjects were instructed to simply fixate on the white (reaction) target and track it when it began to move. There was no mention of the word “cause” or its relatives, nor was any information given about the movement angle of the reaction target. For the psychophysics task, subjects were instructed to remain fixated on the tool for the entire trial. They were also given a manual response box and a set of printed instructions, consisting of a question and two possible answers corresponding to the two buttons of the response box. The English instructions were as follows: “Which statement most closely describes what you perceive? (Left side:) The green dot caused the white dot to move. (Right side:) The green dot did NOT cause the white dot to move.” The French version was: “Quelle proposition décrit le mieux ce que vous percevez ? (Left side:) Le point vert a causé le déplacement du point blanc. (Right side:) Le point vert n’a PAS causé le déplacement du point blanc.” The box was positioned at a comfortable distance in front of the subjects, and their hands were positioned symmetrically on either side. The “causal” response was always the leftmost button and the “noncausal” response was always the rightmost. The experimenter read the instructions to the subject and also informed them that there was additional time between each trial so response accuracy was more important than quickness. Several subjects were confused by the task, and after the first trial block they were given the additional instruction that they should try to place each trial into one of the two categories indicated by the buttons. Due to the inconsistency of the first block performance, only blocks 2–5 (trials 49–240) were included in the analysis for all subjects. A single block normally consisted of 48 trials (several oculomotor blocks for subject BP were run with 24 trials, due to eye fatigue).

Trial blocks were presented sequentially during the experimental session. Oculomotor blocks were recorded over two separate sessions for subjects AZ, BP, CM, CS, GT, KT, and NS; subjects AF, KY, MH, OK, and OM completed data collection in a single session. The psychophysics blocks always followed the oculomotor blocks. A minimum of five blocks (240 trials) was performed for each task. Subjects were permitted to take short breaks between blocks if needed.

Eye movement recording and elementary analysis procedures (e.g., saccade and smooth pursuit detection) were identical to those previously described (Badler, Lefèvre, & Missal, 2010). Once again, all trials were verified by an operator, and the first trial of every block was automatically rejected to avoid surprise effects. For the oculomotor task, trials in which pursuit onset was

obscured or indeterminate (for example, when it coincided with a blink) were rejected. For the psychophysics task, trials in which the subjects failed to respond within 750 milliseconds of the onset of reaction target motion were rejected. The total rejection rates over all subjects were 9.8% for the oculomotor task and 4.0% for the psychophysics task.

Experiment 2

A total of 18 subjects were used for [Experiment 2](#). Eight of them (six women; mean age 29.8 years, *SD* 5.6) had participated in [Experiment 1](#) and were classified as “experienced.” The remaining 10 (seven women; mean age 29.1 years, *SD* 6.0) were naïve, although subject BD had participated in an earlier pilot experiment using similar stimuli. All subjects in both groups were right-handed, with the exception of SK in the naïve group.

The stimulus conditions were nearly identical to those of [Experiment 1](#), except that 50% of the trials had a 300-millisecond delay imposed between the launcher target collision and the reaction target motion. The delay trials were randomly interleaved in both the oculomotor and psychophysical block types and were balanced with the reaction target direction. Thus, each of the four possible combinations (causal or noncausal \times no-delay or delay) was presented exactly 120 times during the session (60 oculomotor trials + 60 psychophysics trials). The instructions to the subjects remained the same; they were not informed about the presence of the delay. Data were collected during a single session for all subjects. Trial rejection rates were comparable to those of [Experiment 1](#) (6.9% oculomotor task, 3.7% psychophysics task).

Experiment 3

A total of 14 subjects were used for [Experiment 3](#). Eight of them (six women; mean age 30.0 years, *SD* 5.7) had participated in [Experiment 2](#), and were classified as “experienced.” The remaining six (five women; mean age 27.7 years, *SD* 0.8) were naïve. All subjects in both groups were right-handed.

The stimulus conditions were similar to those of [Experiment 2](#). The principal change was the introduction of dual-task blocks, for which subjects were required to track the reaction target as well as classify the trial as causal or noncausal. A standard experimental session had the following structure: two baseline blocks of oculomotor-only trials, 24 practice trials that included the response box, five more blocks with the response box, and two final oculomotor-only blocks. Instructions for the psychophysics task were only given after the initial oculomotor blocks, and practice trials

were not included in the analysis. For subject ES only, the structure was 3-5-1 instead of 2-5-2, and the final oculomotor block of subject NS was lost due to a hardware failure. In addition, subject LF found the response-box trials difficult to the point of frustration and was not required to track the reaction target for the last two blocks. The timing of stimulus events was also changed slightly: the reaction target traveled for 600 milliseconds, the tool and launcher remained visible for an additional 1,500 milliseconds, and the intertrial interval was always 1,000 milliseconds. Note that unlike the previous experiments all trial blocks used the same time structure, and subjects were not told that they had extra time to respond during the dual task.

Rejection criteria were modified slightly as well. Psychophysical responses were permitted for the entire trial duration. Oculomotor responses that were absent or late (>600 milliseconds after reaction motion onset) were classified as Not a Number (NaN) in the subsequent analyses, but were not by themselves a rejection criterion for a trial that otherwise had a valid psychophysical response. Otherwise the criteria were the same as those in [Experiments 1](#) and [2](#). Rejection rates for [Experiment 3](#) were comparable to previous values (4.8% oculomotor task, 6.1% dual task).

Data analysis and statistics

All analyses were performed using MATLAB (The MathWorks Inc., Natick, MA) To facilitate comparison between trials with different geometric configurations, the *x*- and *y*-axes were rotated and/or inverted in order to make the causal direction always rightward (0°) and the noncausal direction always upward (90°). Time zero was defined as either the moment of collision between the launcher target and the tool, or the onset of reaction target motion (see below). Note that the two alignment methods are identical for all trials without a time delay. Most statistics were computed on all subjects individually, using a Bonferroni-corrected alpha of 0.0042 (0.05/12) for [Experiment 1](#), 0.0028 (0.05/18) for [Experiment 2](#), and 0.0036 (0.05/14) for [Experiment 3](#). *P*-values between the corrected alpha and 0.05 were considered marginally significant. Population-based tests were also performed as described below, using an uncorrected alpha (0.05). Since many distributions had obvious deviations from normality, for consistency nonparametric tests were used in all cases. In the text, the abbreviation *df* indicates degrees of freedom.

For the oculomotor task, direction and time were mostly analyzed as described previously (Badler, Lefèvre, & Missal, 2010). Smooth pursuit eye movements and saccades were detected using time-constrained velocity and acceleration thresholds,

respectively. Initial movement direction was calculated by averaging instantaneous direction (the arctangent of the x - and y -velocity components) over the duration of the movement (saccades) or its first 100 milliseconds (pursuit). More details can be found in the cited study. For the direction analysis, the first smooth pursuit movement that occurred in the window of collision time ± 100 milliseconds was selected in each trial. This interval captures the majority of predictive smooth pursuit (Heinen, Badler, & Ting, 2005) while avoiding most visually guided movements (Krauzlis & Miles, 1996). For Experiment 3 only, if pursuit was not initiated within the window but a saccade was, the onset of the saccade was used instead. Movements with directions $< -30^\circ$ or $> +120^\circ$ were excluded ($< 1\%$ for all experiments) because they were not directed toward either potential target trajectory. Trials were aligned with respect to collision onset, and for Experiments 2 and 3 the no-delay and delay trials were grouped together. For each subject, a sign test was used to determine whether the median direction of movements in the predictive interval deviated significantly from 45° , the midpoint between the causal and noncausal reaction directions. A signed-rank test was used to assess the direction deviation over the subject population. In Experiments 2 and 3, the average prediction directions of naïve and experienced subjects were compared using a rank-sum test.

For the time analysis, movements were preclassified as being in the causal direction if they fell within the cone of $0^\circ \pm 30^\circ$, and in the noncausal direction if they were within $90^\circ \pm 30^\circ$. Pursuit movements that occurred at any point after the onset of launcher target motion were examined (saccades were not considered). Trials were aligned on the onset of reaction target motion, and once again no-delay and delay trials were grouped. A Friedman nonparametric two-way ANOVA was used to test whether the median latencies toward the causal and noncausal targets were different over all subjects, and rank-sum tests were done for each subject individually. A rank-sum test was also used to assess whether experienced subjects differed from naïve ones in Experiments 2 and 3.

A trial history analysis was performed using both the direction and the time data. For each subject, trials were divided into two groups based on whether the reaction motion of the preceding trial was in the causal or noncausal direction. Medians of the two groups were then compared using a rank-sum test. For Experiments 2 and 3, the presence or absence of a time delay in the preceding trial was also used as a criterion.

In Experiment 3, the oculomotor data were examined over the three phases of the session: the pre-instruction single-task blocks in the beginning, the dual-task blocks in the middle, and the post-instruction

single-task blocks at the end. For each subject, the direction bias values in the three groups were compared using a Kruskal-Wallis nonparametric one-way ANOVA. For the timing data, directly computing the causal/noncausal latency difference for each group was not possible, since the movements were not paired. Instead, latencies were divided into causal-directed and noncausal-directed movements as usual, then the asymmetry A of each distribution \mathbf{x} was calculated using the formula:

$$A(\mathbf{x}) = \text{Abs}(\text{Median}(\mathbf{x}) - \text{Mean}(\mathbf{x})) \quad (1)$$

Next, the causal/noncausal difference was computed using the median of the less asymmetric distribution:

$$\Delta = \mathbf{x}_C - \text{Median}(\mathbf{x}_N) \text{ if } A(\mathbf{x}_C) > A(\mathbf{x}_N) \quad (2)$$

$$\Delta = \text{Median}(\mathbf{x}_C) - \mathbf{x}_N \text{ otherwise} \quad (3)$$

where \mathbf{x}_C and \mathbf{x}_N are the vectors of causal and noncausal latencies, respectively, and Δ is the difference distribution. The difference distribution was calculated separately for each group, and the three groups were compared with the Kruskal-Wallis ANOVA as before. As for all of the individual subject tests, a Bonferroni-corrected alpha (0.0036) was used.

For all experiments, the psychophysical task trials were organized based on the subject's response (causal = \mathbf{C} , noncausal = \mathbf{N}), the direction of the reaction target motion (causal or $0^\circ = \mathbf{dC}$, noncausal or $90^\circ = \mathbf{dN}$), and where applicable, the postcollision time delay (causal or 0 milliseconds = \mathbf{tC} , noncausal or 300 milliseconds = \mathbf{tN}). Thus for example, a response of "noncausal" to a reaction target that moved at 0° after a time delay is denoted $\mathbf{N dC tN}$. For Experiment 1, error trials were considered to be those where the response did not match the stimulus: a causal response to a target moving in the noncausal direction, and vice-versa (i.e., $\mathbf{C dN}$ and $\mathbf{N dC}$). Thus for each subject, an error rate was calculated by dividing the number of error trials by the total number of trials. A latency analysis was also performed by comparing causal response, causal stimulus ($\mathbf{C dC}$) trials with noncausal response, noncausal stimulus ($\mathbf{N dN}$) trials, using the same statistical tests as the oculomotor time data (rank-sum for individual subjects and Friedman ANOVA for the subject population). As with the oculomotor time data, latency values were aligned on reaction target motion.

For Experiments 2 and 3, an error analysis was no longer applicable. Instead, subjects were grouped according to whether they classified stimuli based on the reaction target direction or on the postcollision time delay (see Results). Naïve and experienced subjects were then compared using a MATLAB implementation of Fisher's exact test (Trujillo-Ortiz, Hernandez-Walls,

Castro-Perez, Rodriguez-Cardozo, Ramos-Delgado, & Garcia-Sanchez, 2004) to determine whether they tended to belong to different groups. Each subject's group also determined how their response latency data were aligned (on the collision or on reaction motion onset), and which subset of data were used for the causal versus noncausal latency comparison. Specific details are given in the Results section. As usual, significance was assessed by rank-sum (individuals) and Friedman tests (population).

Correlations between oculomotor and psychophysical data were computed for all experiments. Two simple linear regressions were performed on the subject population, using median responses: oculomotor direction bias versus psychophysical causal/noncausal response latency difference, and pursuit causal/noncausal response latency difference versus the same psychophysical latency difference. For Experiment 3, two within-subject tests were also performed. First, initial movement direction values were grouped according to whether the psychophysical response on the same trial was causal or noncausal, and the two groups were then compared using a rank-sum test. Second, movement latency was compared to psychophysical response latency using an iteratively reweighted robust regression function (MATLAB's `robustfit`). Causal-only, noncausal-only, and pooled data were tested. For this analysis only, the psychophysical latencies were aligned on reaction target motion (the same as the oculomotor latencies) regardless of the subject.

Results

Experiment 1

The oculomotor results of the first experiment confirmed the findings of Badler, Lefèvre, & Missal (2010). For smooth pursuit movements in the predictive zone, subjects showed a marked bias towards the causal direction (signed rank sum = 0, $df = 11$, $p < 0.001$; Figure 2A). Predictive saccades occasionally occurred during the interval as well, and though not frequent enough for statistical analysis, they had the same causal bias as the pursuit movements (not shown). Pursuit movements throughout the trial oriented in the causal direction also had shorter latencies than movements oriented in the noncausal direction (median difference 39 milliseconds; Friedman $\chi^2 = 8.3$, $df = 23$, $p < 0.005$; Figure 2B). A history analysis (see Methods) revealed that neither movement direction nor latency were significantly influenced by the causal versus noncausal direction status of the immediately preceding trial, for any subject.

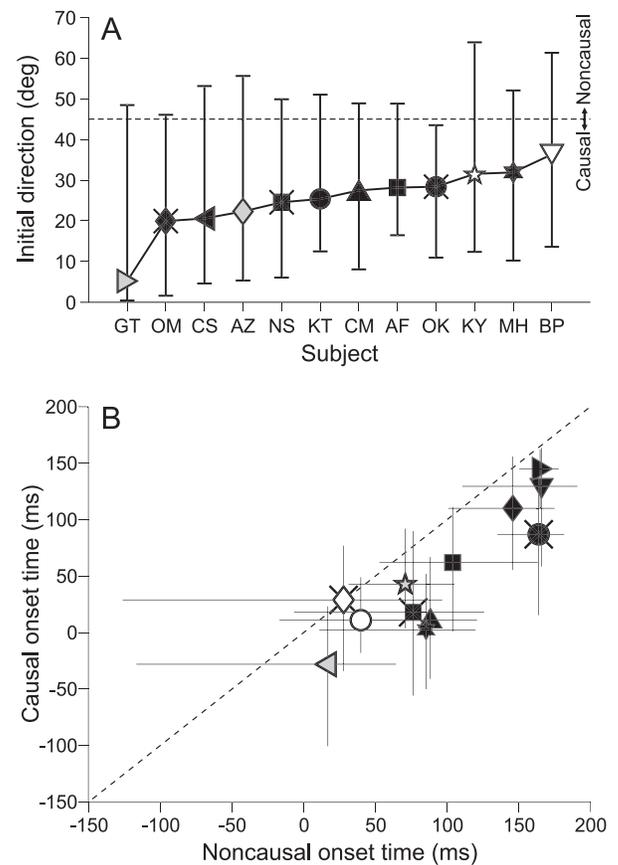


Figure 2. Oculomotor results, Experiment 1. (A) Median predictive pursuit direction for all subjects. The dashed line indicates the midpoint between the causal and noncausal directions (45°). Filled symbols indicate points significantly below 45° ($p \leq 0.0042$); shaded symbols indicate marginal significance ($p \leq 0.05$). Note the consistent preference to move in the causal direction. (B) Median onset time for pursuit movements in the causal direction versus movements in the noncausal direction, for all subjects. Filled and shaded symbols indicate significant or marginally significant latency differences, analogous to panel A. Note that most subjects lie below the diagonal; i.e., their movements in the causal direction tend to occur with shorter latency than movements in the noncausal direction. For both panels, error bars indicate interquartile range.

After the oculomotor trial blocks, subjects began the psychophysical trial blocks where they needed to evaluate the same stimuli they had just tracked. All subjects were able to categorize the majority of stimuli correctly (Figure 3A); that is, they responded “causal” when the reaction target moved in the causal direction and “noncausal” in the opposite case. Incorrect classification rates ranged from 32% (subject KY) to 0% (subject OM), though the majority of subjects made few mistakes ($<10\%$, 9/12 subjects). Subjects also showed a consistent pattern of response latencies—in general, causal responses occurred more quickly than noncausal responses (median difference 107 millisecond-

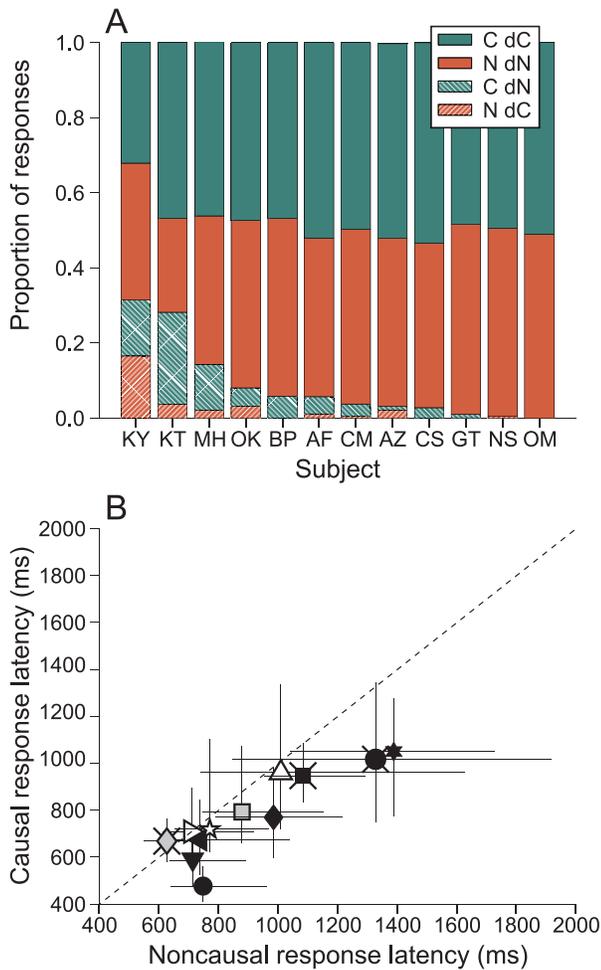


Figure 3. Psychophysical results, [Experiment 1](#). (A) Response fractions for all subjects, sorted by incorrect response rate. Most subjects classified the stimuli without difficulty. For legend, C = causal, N = noncausal, d = stimulus direction; thus C dN denotes a response of ‘Causal’ to a stimulus where the reaction direction was noncausal (90° angle). See text for a more detailed explanation. (B) Median latency of responses “causal” versus latency of responses “noncausal” for all subjects. Symbols and other details as in [Figure 2B](#). Note that causal responses tended to have shorter latencies.

onds; Friedman $\chi^2 = 8.3$, $df = 23$, $p < 0.005$; [Figure 3B](#)). This was consistent with previous studies (e.g., Straube & Chatterjee, 2010), and was also consistent with the oculomotor latency differences.

[Figures 2](#) and [3](#) show that overall, responses of “causal” were preferred for both the oculomotor and psychophysical tasks. However, if a common cognitive process is driving both tasks, correlations should be evident across subjects. In other words, those subjects that strongly identify causality in the oculomotor task, for example, by having a large direction bias or latency difference, would be expected to show a large difference in the psychophysical task. In fact, little correlation was found. A regression between the causal/noncausal

latency difference for psychophysical responses and initial pursuit direction was not significant ($R^2 = 0.01$, $p = 0.8$), and there was only a marginal correlation between the psychophysical latency difference and pursuit latency difference ($R^2 = 0.35$, $p = 0.0415$). Neither of the motor metrics was significantly correlated with the psychophysical response error rate ($R^2 < 0.02$, $p > 0.7$ for both).

Experiment 2

The weak correlations observed from [Experiment 1](#) do not necessarily rule out a connection between the oculomotor and psychophysical tasks. They could also be due to a ceiling effect—if subjects had found the psychophysical task too easy, their responses would not have had sufficient variation to yield a meaningful regression. Thus, a more complex set of stimuli was designed and [Experiment 2](#) was performed. Roughly half of the subjects were experienced, having participated in [Experiment 1](#), while the other half were naïve (see [Methods](#)). The protocol was identical to [Experiment 1](#), except that in 50% of trials a 300-millisecond time delay was present between the collision and the reaction motion onset.

For the oculomotor trials, the interleaved delays had very little effect on the overall response pattern. [Figure 4A](#) shows the predictive pursuit direction for all subjects. As before, the predictive zone was defined as ± 100 milliseconds around the time of launcher collision. No-delay and delay trials were pooled. The strong causal direction bias is evident (signed rank sum = 1, $df = 17$, $p < 0.001$), though interestingly, it was less pronounced for experienced subjects (rank sum = 107, $p < 0.005$). Examining only predictive zone saccades did not qualitatively alter these trends, nor did separating the data into no-delay and delay trials (not shown). For the history analysis, tests were run using prior trials grouped by stimulus direction (dC/dN) and delay (tC/tN). There was no significant effect of either attribute on movement direction for any subject.

As in the previous experiment, smooth pursuit relative to the onset of reaction target motion tended to occur earlier in the causal direction (median difference 26 milliseconds; Friedman $\chi^2 = 18$, $df = 35$, $p < 0.0001$; [Figure 4B](#)). The magnitude of the latency difference did not depend on the experience of the subject (rank sum = 82, $df = 17$, $p > 0.6$). There was no significant effect of stimulus history in any subject, with the exception of prior delay for AK (rank sum = 8,621, $df = 206$, $p < 0.0005$). Compared with [Experiment 1](#), both causal and noncausal movement latencies were significantly later across the population (rank sum ≤ 109 , $df = 29$, $p < 0.002$ for both).

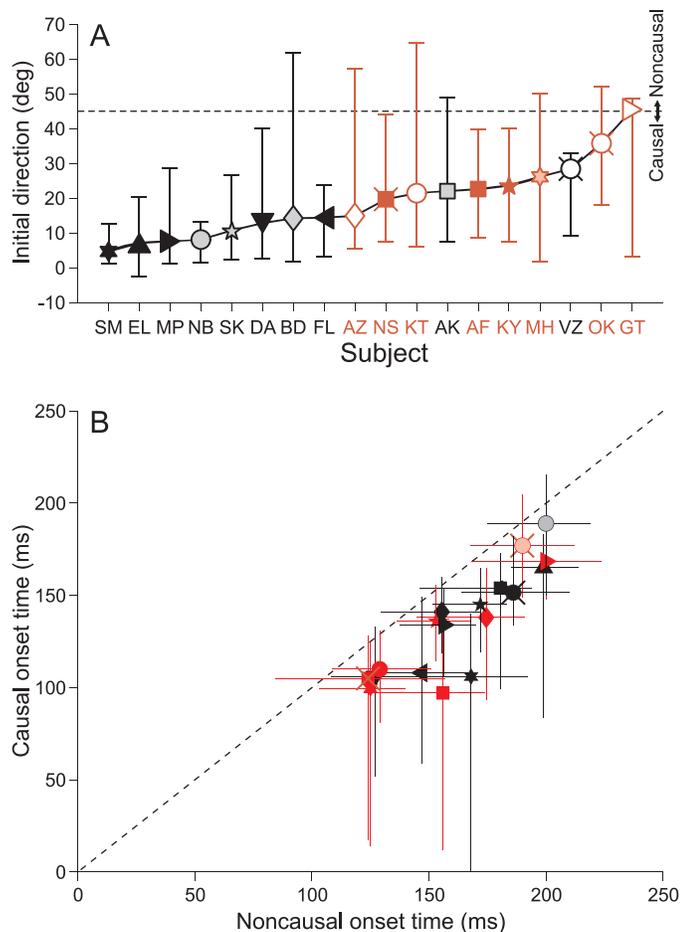


Figure 4. Oculomotor results, Experiment 2. For all plots, symbols in red indicate subjects that participated in Experiment 1; naïve subjects are plotted in black. Filled symbols indicate significance ($p \leq 0.0028$); shaded symbols indicate marginal significance ($p \leq 0.05$). (A) Predictive pursuit direction. No-delay and delay trials were combined and aligned on the time of collision. Other details as per Figure 2A. Note that the direction bias was maintained, and was greater for naïve subjects than for experienced ones. (B) Median difference of causal versus noncausal smooth pursuit movements. No-delay and delay trials were combined and aligned on the time of reaction target motion (time zero). Symbols as in panel A, other details as in Figure 2B. Note that in all cases, movements in the causal direction tended to occur earlier. There was no effect of subject experience.

In contrast to the oculomotor data, the psychophysical data for Experiment 2 were more variable. The additional stimulus conditions provoked different responses from different subjects, summarized as a matrix in Figure 5A. The four columns of the matrix represent each possible stimulus condition (see Methods). The rows of the matrix represent the different subjects, plus three “ideal” exemplars. Shading indicates the proportion of “causal” responses, from red (100%) to blue (0%). Experienced subjects (i.e., those

who had participated in Experiment 1) are labeled in red and naïve subjects in black.

The key result of Figure 5A is that the subjects could be partitioned into three groups, based on their classification strategy. From the top, subject GT accounted for both time and direction in his responses; i.e., he responded “causal” only for stimuli in the causal direction with no time delay (**dC tC**). The next seven subjects (five experienced) accounted only for direction; they responded predominantly “causal” for any causal direction (**dC**) stimulus, whether it had a time delay (**tN**) or not (**tC**). The final 10 subjects (eight naïve) accounted only for time; they responded “causal” for any no delay (**tC**) stimulus regardless of direction (**dC** or **dN**). Not only were the categories themselves evident, but they largely overlapped with the amount of training subjects had received: naïve subjects tended to classify based on time delay only and experienced subjects tended to classify based on direction. Despite the small sample size, the trend was borderline significant (Fisher’s exact test, $p = 0.0536$). Thus, prior training seemed to bias subjects to take into account the reaction target angle, just as it tended to reduce their predictive movement direction bias (see Figure 4A). More interestingly, naïve subjects seemed to ignore the reaction target direction in the psychophysical task, even though their eye movements had been clearly biased towards it!

The different classification preferences complicated the task of comparing causal and noncausal response latencies. Specifically, for subjects that classified based only on time, the relevant information (presence or absence of a time delay) was available immediately following the collision in every trial. For subjects that classified based only on direction, the information (reaction target direction) was available 300 milliseconds earlier in no-delay trials as compared to delay trials. Subject GT had to cope with both sets of contingencies. Thus, the following system was adopted: the time-using subjects had their latencies aligned on the moment of collision and stimuli of both directions (**dC** and **dN**) were pooled, yielding the comparison causal response, no-delay stimulus versus noncausal response, stimulus with delay (**C d* tC** versus **N d* tN**). For direction-using subjects the latencies were aligned on the moment of reaction target motion and no-delay and delay stimuli (**tC** and **tN**) were pooled, yielding the comparison causal response, causal direction stimulus versus noncausal response, noncausal direction stimulus (**C dC t*** versus **N dN t***). For subject GT the direction scheme was used, but with no-delay trials only; thus the comparison was causal response, causal direction no-delay stimulus versus noncausal response, noncausal direction no-delay stimulus (**C dC tC** versus **N dN tC**). Note that in general, it was impossible to completely separate responses from stimuli due to the

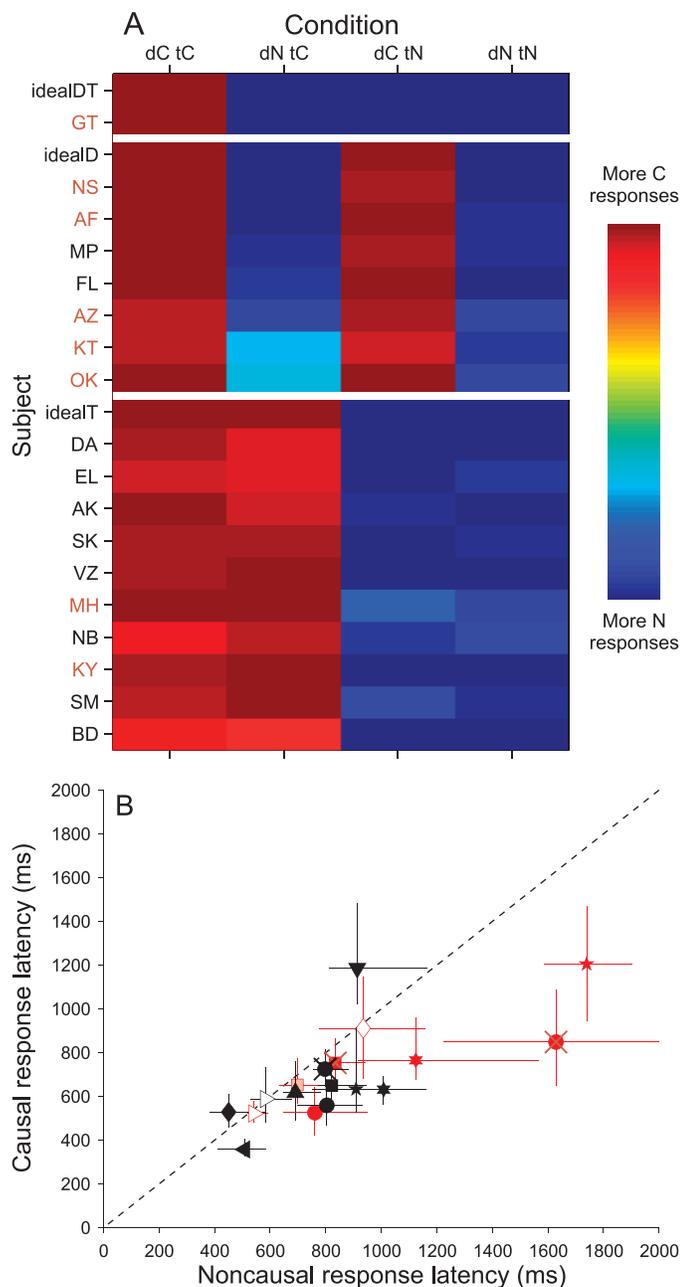


Figure 5. Psychophysics results, Experiment 2. (A) Matrix of response fractions for each possible stimulus combination. Column codes are *d* = direction, *t* = time, *C* = causal, *N* = noncausal. Thus for example, the label “*dN tC*” represents stimuli in the noncausal direction (90° angle) but with the causal timing (0 milliseconds delay). Red shading indicates a higher fraction of causal responses; blue indicates more noncausal responses. Row labels indicate subject, except for the three model classifiers: *idealDT* = classify by direction and time, *idealD* = classify by direction only, *idealT* = classify by time only. White lines group subjects based on their strategy. From the top, *GT* classified stimuli according to both time and direction, the next 7 subjects (5 experienced) accounted only for direction, and the next 10 subjects (2 experienced) accounted only for time. For more details see text. (B) Causal versus noncausal response time.

lack of data for certain conditions (e.g., noncausal responses to a causal direction no-delay stimulus).

The resultant latency data is shown in Figure 5B. As in the previous experiment, subject causal responses tended to be earlier than noncausal responses (median difference 116 milliseconds; Friedman $\chi^2 = 8.0$, $df = 35$, $p < 0.005$). There was no difference between naïve and experienced subjects (rank sum = 66, $df = 17$, $p > 0.4$). As in Experiment 1, there were no correlations across subjects between median direction bias and psychophysical causal/noncausal latency difference, nor between oculomotor latency difference and psychophysical latency difference ($R^2 < 0.16$, $p > 0.1$ for both).

Experiment 3

An apparent divergence between oculomotor and perceptual responses to causality was observed in Experiment 2. Subjects’ eye movements were predisposed to be in the causal direction, regardless of the classification scheme those subjects adopted for the psychophysical task. Furthermore, oculomotor and psychophysical metrics were not correlated across subjects. Despite the previous results, it could be argued that the instructions and experimental conditions were sufficiently different that it would be unfair to compare the two tasks.

To enable a more direct comparison between the oculomotor and psychophysical behavior, Experiment 3 was performed. It required subjects to track the reaction target and make a psychophysical rating of it in the same trial. We were particularly interested in whether the direction of predictive eye movements could also predict some aspect of the subsequent psychophysical response. However, the paradigm design also enabled us to examine to what degree the state of the subject (i.e., informed or uninformed) influenced the oculomotor response.

The oculomotor data during the dual-task trials resembled the single-task data from the previous experiments. As shown in Figure 6A, there was still a strong bias for predictive movements to begin in the causal direction (signed rank sum = 0, $df = 13$, $p < 0.001$), although the difference between naïve and experienced subjects was no longer present (rank sum

Subjects that classified by time had their responses aligned on the launcher collision; all other subjects were aligned on reaction target motion. Stimulus conditions that produced the same response (*C* or *N*) for a given subject were pooled; see text for exact groupings. As in Experiment 1, the subjects tended to make earlier causal responses. Note that the right side of the error bar for subject *OK* has been clipped for clarity; it actually extends to 2,358 milliseconds. Symbols and other details as in Figure 4B.

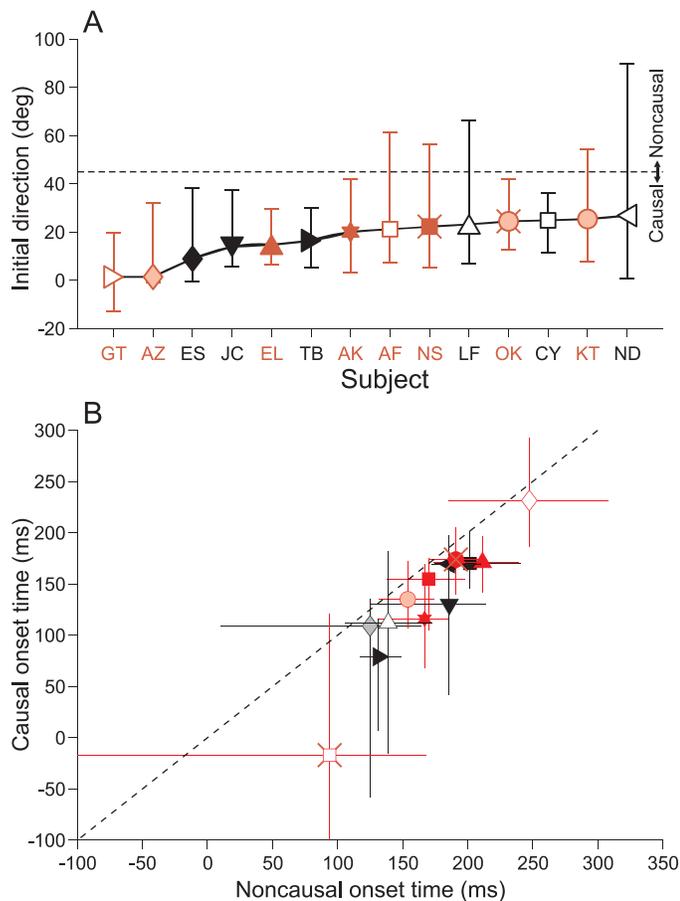


Figure 6. Oculomotor results, Experiment 3. For all plots, symbols in red indicate subjects that participated in Experiment 2; naïve subjects are plotted in black. Filled symbols indicate significance ($p \leq 0.0036$); shaded symbols indicate marginal significance ($p \leq 0.05$). (A) Predictive pursuit or saccade direction. No-delay and delay trials were combined and aligned on the time of collision. Other details as per Figure 4A. Note that the direction bias was maintained, although there was no longer a difference between naïve and experienced subjects. (B) Median difference of causal versus noncausal pursuit movements. Note that the error bars for subject NS have been clipped for clarity; they actually extend to -268 milliseconds horizontally and -235 milliseconds vertically. Symbols as in panel A, other details as in Figure 4B. Note that movements in the causal direction still tended to occur earlier. There was no effect of subject experience.

$= 49$, $p > 0.6$). Note that combined data from pursuit and saccades are shown. Separating the data yielded the same trend for both movement types, but precluded the use of all subjects due to limited datasets: over all trials, GT made only six pursuit movements and no saccades during the predictive interval, while ND had no pursuit and only four saccades. Even after pooling, for four subjects fewer than 10 data points were available for the analysis; of these GT, CY, and ND were not significant and AZ was only marginally significant (Figure 6A).

For the time analysis, low data counts were not an issue: all subjects made at least 45 smooth pursuit movements in both the causal and the noncausal direction, the usual number being closer to 100. Movements in the noncausal direction still occurred later overall (median difference 24 milliseconds; Friedman $\chi^2 = 14$, $df = 27$, $p < 0.0005$; Figure 6B) with no influence of subject experience (rank sum = 42, $df = 13$, $p > 0.6$). Latencies in Experiment 3 were still longer than those in Experiment 1 ($p < 0.003$, $df = 25$, rank sum ≤ 102 for both causal and noncausal movements), but there was no difference compared with Experiment 2 (rank sum ≥ 252 , $df = 31$, $p > 0.4$ for both).

Before considering the psychophysical results of Experiment 3, we took advantage of the block structure to compare oculomotor performance across three conditions. The single-task pre-instruction condition refers to the initial oculomotor-only trials shown to the subject, before the experimenter mentioned causality. The dual-task blocks were simply those in which the subjects had to make their manual response in addition to tracking the target. Finally, in the single-task post-instruction condition subjects again had to only track the target, though unlike the pre-instruction case they had just completed the manual response blocks and thus had been introduced to the concept of causality. The analysis assessed to what extent oculomotor causality behavior was influenced in the short term by additional information (the instructions) or a competing task (the psychophysical classification). Nonparametric ANOVA showed no significant effect on direction for any subject ($p > 0.1$ for all), and a significant effect on causal/noncausal latency difference only for subject LF. Subjects AZ and EL reached marginal significance for latency.

The psychophysical results (Figure 7) were also similar to those of Experiment 2. Once again, response frequencies to the four possible stimulus conditions are shown as a matrix (Figure 7A). This time there were two subjects that used both direction and time information for their classifications, GT and EL. GT maintained his performance from the previous experiment. EL was a more interesting case, as she participated in Experiment 2 as a naïve subject and used a time-only classification (see Figure 5A). As an experienced subject, she appears to have transitioned into accounting for direction as well. After GT and EL, the next six subjects used primarily direction, and the majority of them (five) were experienced. The five subjects after them favored time, with that majority (four) naïve. Note that the single experienced subject in the time-preference subgroup, AK, was a naïve subject in Experiment 2 and did not change her strategy (unlike her compatriot EL). Subject TB used a predominantly time-based classification as well, but inverted—she consistently classified time delay trials as causal and

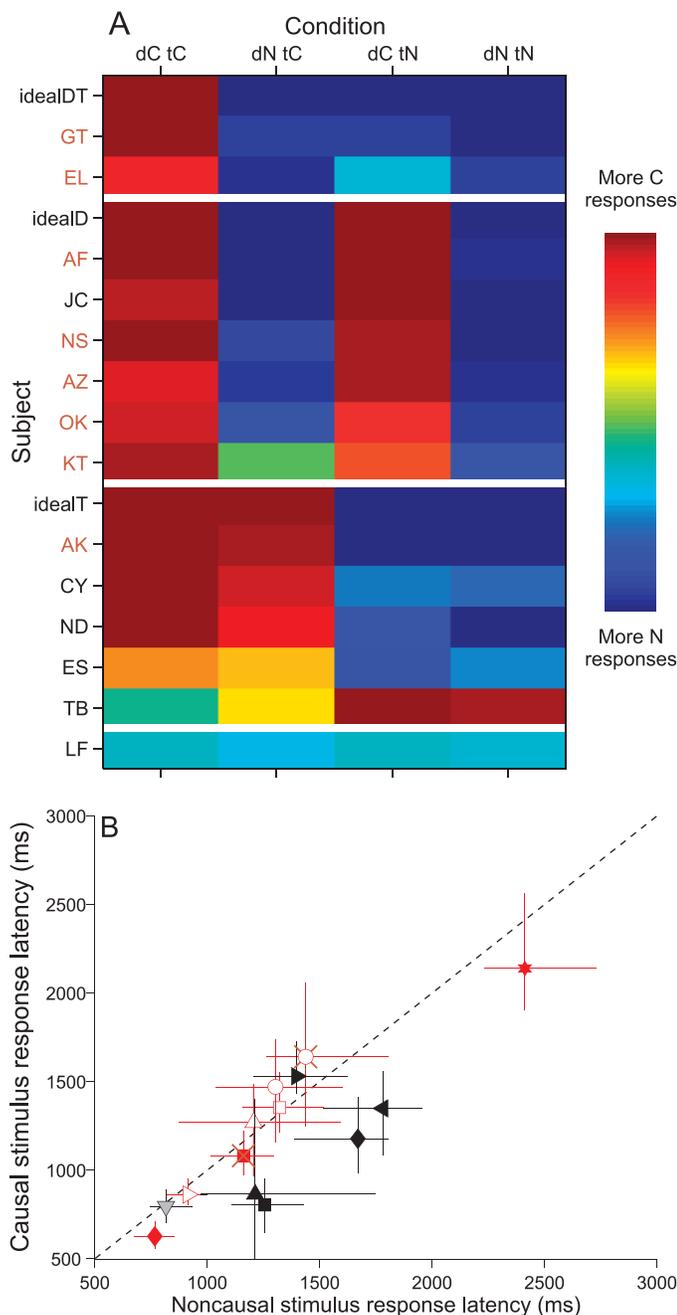


Figure 7. Psychophysics results for Experiment 3. (A) Matrix of response fractions. Organization is the same as in Figure 5A, and the results are comparable to those of Experiment 2. From the top, GT and EL accounted for both time and direction, the next six subjects (five experienced) accounted only for direction, the next five subjects (one experienced) accounted only for time, and LF did not respond to either. Note that subject EL transitioned from a time preference to a direction+time preference between Experiments 2 and 3. (B) Causal versus noncausal response time. Response alignment and pooling was customized for each subject as in Experiment 2, although unlike that experiment, there was little tendency for causal responses to have shorter latencies than noncausal ones. Note that the bottom of the error bar for subject EL has been clipped for clarity; it actually extends to 475 milliseconds. Symbols and other details as in Figure 6B.

no-delay trials as noncausal. Debriefed after the experiment, she reported that she perceived the no-delay collisions as having a negative time delay, i.e., that the reaction target moved before the collision. Finally, subject LF was unable to come up with a consistent classification scheme. Even more so than in Experiment 2, experienced subjects were more likely to include direction in their strategy than naïve ones (Fisher's exact test, $p = 0.0319$).

The psychophysical latency data (Figure 7B) were less striking than the classification results. As was done in Experiment 2, the latency values were aligned and compared according to the classification preference of the subject (the time-preference scheme was used for LF). Unlike the previous experiment, there was no tendency across the population for causal responses to occur earlier (median difference 66 milliseconds; Friedman $\chi^2 = 1.1$, $df = 27$, $p > 0.2$), nor was there a difference between naïve and experienced subjects (rank sum = 31, $df = 13$, $p > 0.08$).

Consistent with the previous experiments, there was no population correlation between either direction bias or pursuit latency and psychophysical response latency ($R^2 < 0.04$, $p > 0.5$ for both). However, the real interest in Experiment 3 was to take advantage of the dual-task to search for correlations within subjects. When the initial movement directions were grouped based on psychophysical response, there was no difference between causal and noncausal trials for any subject save JC and TB, and those only reached marginal significance. Put another way, causal direction bias did not seem to be a predictor of causal classification. Moreover, robust linear regression did not yield a significant correlation between the pursuit movement latency and psychophysical response latency for the majority of the subjects; only GT and ND showed a significant result, and ES was marginally significant. Limiting the regressions to only causal or noncausal trials did not qualitatively change the result. Thus, it appears that causal decision timing is more uncoupled to oculomotor behavior than is, for example, a standard interval reproduction task (Badler, Lefèvre, & Missal, 2008).

Discussion

For relatively simple causal stimuli (i.e., those of Experiment 1), predictive eye movements and perceptual classifications were similar. Predictive movements tended to be biased toward the causal direction, and subjects correspondingly rated that direction as “causal.” Causally directed movements and responses both tended to have shorter latencies. However, beyond the superficial similarities no substantial subject-by-subject

correlations were observed for the two response types. When stimulus complexity was increased by adding a randomly interleaved time delay, the oculomotor and psychophysical responses diverged even more obviously. Oculomotor responses maintained their causal bias, whereas psychophysical responses became much more variable, differing according to the subject and influenced by prior task experience. We begin by considering the two response types separately, then discuss their interaction (or lack thereof) and its implications.

Our first claim is that the oculomotor results are largely driven by context. In all three experiments, there was a predictive direction bias in the causal direction. There was also a latency bias, in which causally directed smooth pursuit movements tended to occur earlier. The results confirm and extend those of the previous study (Badler, Lefèvre, & Missal, 2010), in which the causal bias was consistent given certain conditions: namely, spatial continuity between the launcher and reaction target, and a 50/50 distribution of causal and noncausal reaction motions. The requirement of temporal contiguity is more complex: the previous study showed that the causal bias was lost if a postcollision delay was present in *all* trials, whereas the current study showed that it can be maintained if the delay is present only 50% of the time. A possible explanation is one of optimization: a strategy of waiting for reaction target motion before initiating an eye movement would introduce a large amount of tracking error in the other 50% of trials *without* a time delay. Of course, the delay was not ignored by the oculomotor system but rather formed part of the context because the latencies in [Experiments 2 and 3](#) were significantly later than those in [Experiment 1](#). Lacking any other information about the upcoming direction of a reaction, the system usually initiated a movement in the causal direction instead of guessing randomly, reinforcing the view of causality as a “default” judgment (Choi & Scholl, 2006; Michotte, 1946/1963; Scholl & Tremoulet, 2000; Straube & Chatterjee, 2010).

Other evidence that context largely determines the oculomotor causal bias can be inferred from factors that do *not* influence it. The amount of experience that subjects had with the task had very little effect on their oculomotor measurements. An influence was observed in the direction data of [Experiment 2](#) ([Figure 4A](#)), but importantly it did not affect the direction of the causal bias, only its magnitude. Moreover, the pre-instruction/dual-task/post-instruction comparisons of [Experiment 3](#) overwhelmingly showed no effect—subjects exhibited the same pattern of eye movements regardless of whether they had been specifically instructed to think in terms of causality, and regardless of whether they had to subsequently classify the stimuli they were

tracking. The lack of a stimulus history effect is not evidence against context; rather, it suggests a long-term integration of many trials, possibly even entire trial blocks. Recall also that the stimulus geometry differed greatly from trial to trial, with reaction motion possible in any of the four cardinal directions for both causal and noncausal trials. The resultant tracking differences would overshadow any subtle history effects that existed. Overall, there is abundant evidence that stimulus characteristics are integrated over multiple presentations in the oculomotor domain (Barnes & Asselman, 1991; Heinen, Badler, & Ting, 2005; Kao & Morrow, 1994; Kowler & McKee, 1987), even by nonhuman primates (Badler & Heinen, 2006; de Hemptinne, Lefèvre, & Missal, 2006).

Compared with the oculomotor data, the psychophysical classification results followed very different rules. Perhaps most strikingly, the consistency between subjects observed in the first experiment was thrown completely awry by the introduction of time-delay trials. Instead, subjects sorted themselves according to their preferred classification strategy. Those with prior experience with the task tended to use reaction motion direction to classify stimuli as causal or not, ignoring time delay in most cases. On the other hand, naïve subjects tended to do the opposite, using only the time delay to classify the stimuli while ignoring direction. The latter result is particularly striking given their consistent oculomotor bias in the causal direction—in effect, those subjects’ eyes seemed to be responding to one aspect of the stimuli while their hands responded to a different aspect. Nonetheless, the existence of different classification strategies is not unprecedented; it is known that individuals display variable sensitivities to different types of perceptual causal violations (Schlottmann & Anderson, 1993; Straube & Chatterjee, 2010; Young, Rogers, & Beckmann, 2005). The effect of experience or training is also not unprecedented: simply requiring subjects to think about causality, rather than some other aspect of the stimulus, is sufficient to affect their evaluations (Young, Rogers, & Beckmann, 2005) and may even be associated with specific patterns of brain activity (Fonlupt, 2003, though see Blakemore et al., 2001).

As for why more subjects didn’t use both time and direction information to make their classifications, they may have been using the “take the best” heuristic (Gigerenzer, 2004; Gigerenzer & Goldstein, 1996). After all, there were numerous relevant (time and direction) as well as irrelevant (geometric orientation, reaction target handedness) pieces of information available in each trial, and subjects (especially naïve ones) may not have had time to process them all. Therefore, they could have simply chosen the “best” piece of information to use, i.e., the one that was most salient to them. All of the experienced subjects that

participated in [Experiment 1](#) had practice in categorizing causal/noncausal trials based on trajectory direction, and accordingly all of them used directory (wholly or in part) to make their classifications in [Experiment 3](#). On the other hand, the 300-millisecond time delay may have seemed more salient to most of the naïve subjects—although they could have also based their decisions on the *first* piece of relevant information they perceived, since the presence or absence of the collision delay obviously preceded the reaction target motion.

Given the stark differences between the patterns of oculomotor and psychophysical data, it is unsurprising that few correlations between them were found. Over the population used in the present study, the difference between causal and noncausal classification latencies in a subject was not able to predict the magnitude of their oculomotor direction or latency bias. Even within subjects, the dual-task data of [Experiment 3](#) revealed no relation between the initial movement direction of a subject and their ultimate classification response. Although unsurprising at face value (the former is a prediction based on context, while the latter is based on the actual stimulus), many subjects had sufficient classification variability to reveal a link if it existed. Moreover, there was not even a correlation between oculomotor latency and classification latency, unlike what was observed in our laboratory during a simpler timing task (Badler, Lefèvre, & Missal, 2008).

It is clear that the systems underlying oculomotor behavior and psychophysical classification use the same basic stimulus parameters (here, direction and time), but afterwards they seem to diverge considerably until their outputs have no more than a superficial resemblance. Such an organization is quite different from the encapsulated, general-purpose causality detector envisioned by Michotte (1946/1963), but now increasingly falling out of favor (see e.g., Rips, 2011 for a review). [Figure 8](#) summarizes a possible alternative scheme. At the base are elementary units for evaluating stimulus characteristics pertinent to causality. Angular or direction deviation and time asynchrony were varied in the present study; other possible elements would respond to the spatial distance or speed difference between two putative causal events. In particular, a spatial gap is known to eliminate both the perception of causality (Michotte, 1946/1963; Schlottmann & Anderson, 1993; Young, Rogers, & Beckmann, 2005) and the oculomotor bias (Badler, Lefèvre, & Missal, 2010). Angle-, time-, and spatial gap-specific networks have also been identified using functional magnetic resonance imaging in subjects asked to evaluate the causal nature of launching stimuli (Fugelsang, Roser, Corballis, Gazzaniga, & Dunbar, 2005; Straube & Chatterjee, 2010).

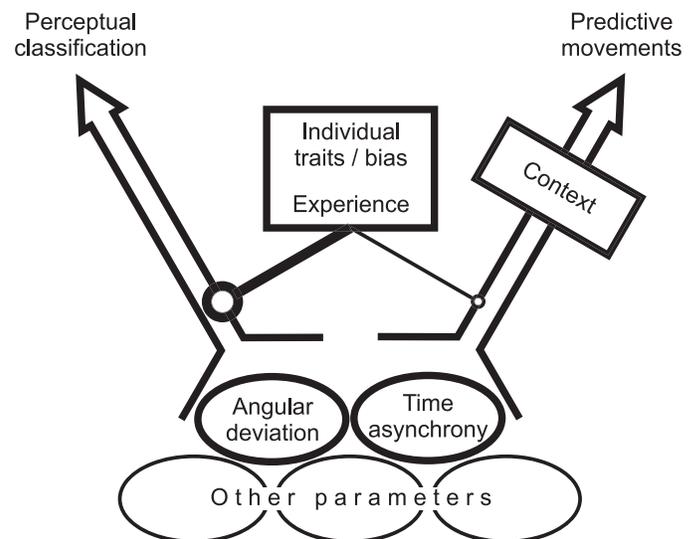


Figure 8. Possible mechanism for processing causal events. Elementary stimulus analyzers (bottom) are sensitive to angular deviation, time asynchrony, or other interaction parameters between potential causal agents. For the classification of perceived stimuli (left branch), the evaluations of each individual parameter are first modulated by factors such as increased individual sensitivity or prior training. The modified evaluations are then combined to make the classification choice. For predictive movements (right branch), the outputs of the elementary analyzers are much less influenced by individual factors. Instead, multiple evaluations are collected over numerous episodes or trials to form a representation of context. The context is then used to generate predictive movements that minimize potential errors overall.

The output from the basic analyzers diverges into two processing branches. The first branch, represented on the left side of the diagram, leads to the perceptual classification. The outputs of the basic analyzers are combined, with their relative contributions modified based on individual bias (Schlottmann & Anderson, 1993) and prior experience. The second processing branch drives predictive movements. As before, the elementary analyzers assess the parameters of each stimulus and combine the information. However, there are two major differences. First, there is much less influence of the traits and experience of the subject. Second, instead of directly evoking a response for each trial individually as is done on the perceptual side, stimulus information is accumulated over the course of a trial block. The aggregate stimulus characteristics are used to build an estimate of the context in which they occur—e.g., whether stimuli that can be interpreted as causal are present. The context information is then used for programming the predictive movements, since by definition they cannot be based on the immediately upcoming stimulus. In practical terms, the context module blurs stimulus information over multiple trials,

and is the proximal reason why the perceptual classification does not necessarily match the oculomotor behavior. Since subjects were not evaluating causality per se in the oculomotor trials, the prediction branch (as revealed by the oculomotor behavior) might reflect how it is processed and used unconsciously.

Conclusions

Subjects consistently maintained an oculomotor bias to causally directed reaction motion following a collision, even in the intermittent presence of a time delay. This relative invariance may reflect holistic processing, in which the oculomotor system uses multiple stimulus presentations to estimate a context and then produces predictive behavior calibrated to that context. On the other hand, perceptual classifications only matched the oculomotor bias for stimuli in which reaction angle was the only causal parameter that varied; when the time delay was introduced, the two measurements diverged according to subject experience and internal preference. There was also little correlation between the characteristics of the oculomotor and classification behavior. Thus causality perception seems to use a separate system, specialized to evaluate each incoming stimulus individually, though it is susceptible to individual bias and sometimes takes heuristic shortcuts that ignore relevant information. The two systems could implement the different optimal strategies necessary for minimizing error in the oculomotor and perceptual domains.

Acknowledgments

This work was supported by the Belgian Fonds National de la Recherche Scientifique, the Fondation pour la Recherche Scientifique Médicale, the Belgian Program on Interuniversity Attraction Poles initiated by the Belgian Federal Science Policy Office, and internal research grants from the Université catholique de Louvain (Fonds Spéciaux de Recherche, Action de Recherche Concertée). The scientific responsibility rests with the authors. We wish to thank Dr. Laetitia Cirilli for assistance.

Commercial relationships: none.

Corresponding author: Marcus Missal.

Email: marcus.missal@uclouvain.be.

Address: Laboratory of Neurophysiology, Center for Systems Engineering and Applied Mechanics and Institute of Neuroscience Université catholique de Louvain, Brussels, Belgium.

References

- Badler, J. B., & Heinen, S. J. (2006). Anticipatory movement timing using prediction and external cues. *Journal of Neuroscience*, 26(17):4519–4525. [[PubMed](#)] [[Article](#)].
- Badler, J., Lefèvre, P., & Missal, M. (2008). Anticipatory pursuit is influenced by a concurrent timing task. *Journal of Vision*, 8(1):1–9, <http://www.journalofvision.org/content/8/16/5>, doi:10.1167/8.16.5. [[PubMed](#)] [[Article](#)].
- Badler, J., Lefèvre, P., & Missal, M. (2010). Causality attribution biases oculomotor responses. *Journal of Neuroscience*, 30(31):10517–10525. [[PubMed](#)] [[Article](#)].
- Barnes, G. R., & Asselman, P. T. (1991). The mechanism of prediction in human smooth pursuit eye movements. *Journal of Physiology*, 439:439–461. [[PubMed](#)].
- Beasley, N. A. (1968). The extent of individual differences in the perception of causality. *Canadian Journal of Psychology*, 22(5):399–407. [[PubMed](#)].
- Blakemore, S. J., Fonlupt, P., Pachot-Clouard, M., Darmon, C., Boyer, P., Meltzoff, A. N., et al. (2001). How the brain perceives causality: an event-related fMRI study. *Neuroreport*, 12(17):3741–3746. [[PubMed](#)].
- Chappell, J. (2006). Avian cognition: understanding tool use. *Current Biology*, 16(7):244–245. [[PubMed](#)].
- Choi, H., & Scholl, B. J. (2006). Perceiving causality after the fact: postdiction in the temporal dynamics of causal perception. *Perception*, 35(3):385–399. [[PubMed](#)].
- de Hemptinne, C., Lefèvre, P., & Missal, M. (2006). Influence of cognitive expectation on the initiation of anticipatory and visual pursuit eye movements in the rhesus monkey. *Journal of Neurophysiology*, 95(6):3770–3782. [[PubMed](#)] [[Article](#)].
- Falmier, O., & Young, M. E. (2008). The impact of object animacy on the appraisal of causality. *American Journal of Psychology*, 121(3):473–500. [[PubMed](#)].
- Fonlupt, P. (2003). Perception and judgement of physical causality involve different brain structures. *Cognitive Brain Research*, 17(2):248–254. [[PubMed](#)].
- Fugelsang, J. A., Roser, M. E., Corballis, P. M., Gazzaniga, M. S., & Dunbar, K. N. (2005). Brain mechanisms underlying perceptual causality. *Cognitive Brain Research*, 24(1):41–47. Epub 2005 Apr 19. [[PubMed](#)].
- Gemelli, A., & Cappellini, A. (1958). The influence of

- the subject's attitude in perception. *Acta Psychologica*, 14:12–23.
- Gigerenzer, G. (2004). Fast and frugal heuristics: The tools of bounded rationality. In D. Koehler & N. Harvey (Eds.), *Blackwell handbook of judgment and decision making* (pp. 62–88). Oxford, UK: Blackwell.
- Gigerenzer, G., & Goldstein, D. G. (1996). Reasoning the fast and frugal way: Models of bounded rationality. *Psychological Review*, 103(4):650–669. [PubMed].
- Gopnik, A., Sobel, D. M., Schulz, L. E., & Glymour, C. (2001). Causal learning mechanisms in very young children: two-, three-, and four-year-olds infer causal relations from patterns of variation and covariation. *Developmental Psychology*, 37(5):620–629. [PubMed].
- Hauser, M., & Spaulding, B. (2006). Wild rhesus monkeys generate causal inferences about possible and impossible physical transformations in the absence of experience. *Proceedings of the National Academy of Sciences U.S.A.*, 103(18):7181–7185. [PubMed] [Article].
- Heinen, S. J., Badler, J. B., & Ting, W. (2005). Timing and velocity randomization similarly affect anticipatory pursuit. *Journal of Vision*, 5(6):493–503, <http://journalofvision.org/5/6/1/>, doi:10.1167/5.6.1. [PubMed] [Article].
- Hindmarch, I. (1973). Eye movements and the perception of phenomenal causality. *Psychologica Belgica*, 13:17–23.
- Kao, G. W., & Morrow, M. J. (1994). The relationship of anticipatory smooth eye movement to smooth pursuit initiation. *Vision Research*, 34(22):3027–3036. [PubMed].
- Kowler, E., & McKee, S. P. (1987). Sensitivity of smooth eye movement to small differences in target velocity. *Vision Research*, 27(6):993–1015. [PubMed].
- Krauzlis, R. J., & Miles, F. A. (1996). Release of fixation for pursuit and saccades in humans: Evidence for shared inputs acting on different neural substrates. *Journal of Neurophysiology*, 76(5):2822–2833. [PubMed].
- Leslie, A. M., & Keeble, S. (1987). Do six-month-old infants perceive causality? *Cognition*, 25(3):265–288. [PubMed].
- Michotte, A. (1946/1963). *The perception of causality*. Translated by T. R. Miles & E. Miles. New York: Basic Books.
- Morris, M. W., & Peng, K. (1994). Culture and cause: American and Chinese attributions for social and physical events. *Journal of Personality and Social Psychology*, 67(6):949–971.
- O'Connell, S., & Dunbar, R. I. (2005). The perception of causality in chimpanzees (*Pan spp.*). *Animal Cognition*, 8(1):60–66. [PubMed].
- Penn, D. C., & Povinelli, D. J. (2007). Causal cognition in human and nonhuman animals: a comparative, critical review. *Annual Review of Psychology*, 58:97–118. [PubMed].
- Ray, E., & Schlottmann, A. (2007). The perception of social and mechanical causality in young children with ASD. *Research in Autism Spectrum Disorders*, 1(3):266–280.
- Rips, L. (2011). Causation from perception. *Perspectives on Psychological Science*, 6(1):77–97.
- Saxe, R., & Carey, S. (2006). The perception of causality in infancy. *Acta Psychologica (Amsterdam)*, 123(1–2):144–165. [PubMed].
- Schlottmann, A., & Anderson, N. H. (1993). An information integration approach to phenomenal causality. *Memory & Cognition*, 21(6):785–801. [PubMed].
- Schlottmann, A., & Shanks, D. R. (1992). Evidence for a distinction between judged and perceived causality. *Quarterly Journal of Experimental Psychology A*, 44(2):321–342. [PubMed].
- Scholl, B. J., & Tremoulet, P. D. (2000). Perceptual causality and animacy. *Trends in Cognitive Sciences*, 4(8):299–309. [PubMed].
- Seed, A. M., Tebbich, S., Emery, N. J., & Clayton, N. S. (2006). Investigating physical cognition in rooks, *Corvus frugilegus*. *Current Biology*, 16(7):697–701. [PubMed].
- Straube, B., & Chatterjee, A. (2010). Space and time in perceptual causality. *Frontiers in Human Neuroscience*, 4:28. [PubMed] [Article].
- Trujillo-Ortiz, A., Hernandez-Walls, R., Castro-Perez, A., Rodriguez-Cardozo, L., Ramos-Delgado, N. A., & Garcia-Sanchez, R. (2004). *Fisherextest: Fisher's Exact Probability Test. A MATLAB file*. Internet site: www.mathworks.com/matlabcentral/fileexchange/loadFile.do?objectId=5957 (Accessed May 19, 2009).
- Tschacher, W., & Kupper, Z. (2006). Perception of causality in schizophrenia spectrum disorder. *Schizophrenia Bulletin*, 32(1):S106–112. Epub 2006 Aug 8. [PubMed] [Article].
- Wagemans, J., van Lier, R., & Scholl, B. J. (2006). Introduction to Michotte's heritage in perception and cognition research. *Acta Psychologica (Amsterdam)*, 123(1–2):1–19. [PubMed].
- Young, M. E., Rogers, E. T., & Beckmann, J. S. (2005). Causal impressions: predicting when, not just whether. *Memory & Cognition*, 33(2):320–331. [PubMed].