Vision Research 154 (2019) 85–96

Contents lists available at ScienceDirect

Vision Research

journal homepage: www.elsevier.com/locate/visres

Motion prediction at low contrast

Claudio de'Sperati[a,b,*], Ian M. Thornton[c]

[a] Faculty of Psychology, Laboratory of Action, Perception and Cognition, Vita-Salute San Raffaele University, via Olgettina 58, 20132 Milano, Italy
[b] Experimental Psychology Unit, Division of Neuroscience, San Raffaele Scientific Institute, via Olgettina 60, 20132 Milano, Italy
[c] Department of Cognitive Science, Faculty of Media and Knowledge Sciences, University of Malta, Msida MSD 2080, Malta

ARTICLE INFO

No of reviewers = 2

Keywords:
Human-computer interaction
Motion extrapolation
Motion prediction
Speed
Contrast
Action-perception dissociation

ABSTRACT

Accurate motion prediction is fundamental for survival. How does this reconcile with the well-known speed underestimation of low-contrast stimuli? Here we asked whether this contrast-dependent perceptual bias is retained in motion prediction under two different saccadic planning conditions: making a saccade to an occluded moving target, and real-time gaze interaction with multiple moving targets. In a first experiment, observers made a saccade to the mentally extrapolated position of a moving target (imagery condition). In a second experiment, observers had to prevent collisions among multiple moving targets by glancing at them through a gaze-contingent display or by hitting them with the touchpad cursor (interaction condition). In both experiments, target contrast was manipulated. We found that, whereas saccades to the imagined moving target were systematically biased by contrast, the gaze interaction performance, as measured by missed collisions, was generally unaffected – even though low-contrast targets looked slower. Interceptive actions increased at low contrast, but only when the gaze was used for interaction. Thus, perceptual speed underestimation transfers to saccades made to imagined low-contrast targets, without however necessarily being detrimental to effective performance when real-time interaction with multiple targets is required. This differential effect of stimulus contrast suggests that in complex dynamic conditions saccades are rather tolerant to visual speed biases.

1. Introduction

Estimating object motion is fundamental for survival. Whether it is a matter of hunting prey or crossing a busy street, being wrong about the future course of events can have a high cost. However, it appears that we are not too accurate in estimating visual speed, as with both real-life and laboratory stimuli speed cay be largely underestimated (Burr & Thompson, 2011; de'Sperati & Baud Bovy, 2017; Gegenfurtner, Mayser, & Sharpe, 1999; Rossi, Montanaro, & de'Sperati, 2018; Snowden, Stimpson, & Ruddle, 1998; Thompson, 1982; Thompson, Brooks, & Hammett, 2006; Zuliani, Caputi, & Scaini, in press). Contrast is one of the factors responsible for a poor sense of speed.

It is well known that contrast affects motion perception, especially at low speed. Low-contrast stimuli are judged to be slower than high-contrast stimuli in a variety of experimental conditions (Senna, Parise, & Ernst, 2015; Stone & Thompson, 1992; Thompson, 1982; Vintch & Gardner, 2014; Weiss, Simoncelli, & Adelson, 2002). This observation has been extended to real-life contexts, and for example contrast-dependent speed underestimation has been attributed a role in car accidents under foggy conditions (Snowden et al., 1998 – but see Pretto, Bresciani, Rainer, & Bulthoff, 2012).

How contrast affects speed perception is still a matter of debate. According to one account, speed underestimation depends on a Bayesian prior for low speed that would come into play when uncertainty increases, for example at low contrast. The prior would reflect the statistics of exposure to natural motions, which would be biased towards low speeds (Senna et al., 2015; Stocker & Simoncelli, 2006; Weiss et al., 2002). According to an alternative account, however, temporal filters in early visual areas are sufficient to produce speed underestimation, without the need to invoke additional mechanisms. Indeed, quantitative models that incorporate tuning properties of magnocellular and parvocellular systems (ratio models) predict this perceptual effect (Hammett, Champion, Thompson, & Morland, 2007; Hassan & Hammett, 2015; Thompson et al., 2006).

To gain a further insight into contrast-dependent speed underestimation, here we asked whether this perceptual bias extends to other visually-based processes. In particular, we chose to examine two very different contexts, asking whether (i) saccadic eye movements based on extrapolated motion are also biased by speed underestimation, and (ii) contrast has any impact in a more complex context of visuo-motor

* Corresponding author at: Faculty of Psychology, Laboratory of Action, Perception and Cognition, Vita-Salute San Raffaele University, via Olgettina 58, 20132 Milano, Italy.
E-mail address: desperati.claudio@unisr.it (C. de'Sperati).

https://doi.org/10.1016/j.visres.2018.11.004
Received 5 May 2018; Received in revised form 26 October 2018; Accepted 6 November 2018
Available online 27 November 2018
0042-6989/

interaction with dynamic displays. On the theoretical side, finding that contrast has a different effect in different tasks – the other conditions being the same – may point to the existence of parallel speed processing, specific to how motion signals are treated in the brain – e.g., vision for action vs. vision for perception (Goodale, 2011), or fast vs. slow visuo-motor decisions (de'Sperati & Baud-Bovy, 2008; Rossetti, 1998; Zimmermann, Morrone, & Burr, 2012).

In Experiment 1 we took advantage of a task previously used to investigate motion imagery (de'Sperati, 1999) and asked observers to make a saccade to a mentally imagined moving target. Because motion imagery retains several features of motion perception (Battaglini, Campana, & Casco, 2013; de'Sperati & Santandrea, 2005; de'Sperati, 2003b; Jonikaitis, Deubel, & de'Sperati, 2009; Makin & Poliakoff, 2011; Makin, Stewart, & Poliakoff, 2009; Pearson, Naselaris, Holmes, & Kosslyn, 2015), saccades based on such mental representation of motion are expected to be subject to similar effects as visual perception. Therefore, when the trajectory of a low-contrast target is mentally extrapolated in imagery, saccades directed to its imagined position should fall short of the objective (invisible) target position more than if a high-contrast target is imagined. The alternative hypothesis is that saccades access a dedicated motion representation, which might not be affected by contrast-dependent speed biases. Because dissociations between saccades and visual perception are found in fast, real-time contexts (de'Sperati & Baud-Bovy, 2008; Gregori-Grgič, Balderi, & de'Sperati, 2011; Zimmermann et al., 2012), we predicted that saccades made to a single, imaginary slowly moving target would show a contrast-dependent visual speed bias.

Experiment 2 tested whether contrast affects saccadic planning in a more complex motion prediction task. Building upon a recently developed active tracking task (Thornton, Bulthoff, Horowitz, Rynning, & Lee, 2014), observers were engaged in real-time interaction with multiple moving targets with the goal of avoiding collisions by looking at the targets through a gaze-contingent display or by hitting them with the touchpad cursor. Particularly in demanding conditions, where impending collisions prompt quick action decisions, visual speed processing may be dominated by a fast feed-forward mode (VanRullen, 2007), thus escaping perceptual biases (Burr & Santoro, 2001; de'Sperati & Baud-Bovy, 2008; Gregori-Grgič et al., 2011; Pearson et al., 2015). A second aim of Experiment 2 was to compare gaze and finger interaction. Indeed, while many studies have shown a tight relation between visual attention and manual actions (Baldauf & Deubel, 2008; Bekkering & Neggers, 2002; Hesse & Deubel, 2010, 2011), these two modalities may not be fully equivalent in complex visual search tasks with dynamic displays (Johannesson, Thornton, Smith, Chetverikov, & Kristjansson, 2016; Jonikaitis & Deubel, 2011).

Thus, while both tasks involve motion prediction, they differ in several respects, mostly that in the former case a single planned saccade is made to the currently imagined position of a single (vanished) target, while in the latter case saccades (or touchpad movements) are continuously made to moving targets selected among several identical targets. The conditions for motion prediction are therefore different in the two tasks, as in the former case the target trajectory is entirely predictable while in the latter case the target trajectories must be continuously updated due to multiple collisions among targets and bounces on the display borders, which restrict the temporal window available to predict target motion.

2. Experiment 1

In this experiment we tested the effects of target contrast on the performance in a visual motion imagery task derived from previous experiments (de'Sperati, 1999, 2003a, 2003b). Observers had to mentally extrapolate target motion along a circular trajectory after its disappearance from sight, and to make a saccade to its imagined position upon an unpredictable auditory cue (Fig. 1). While in classical mental rotation experiments observers respond by pressing a key and thus response time is the dependent variable (Battaglini et al., 2013; Shepard & Cooper, 1986), here we exploited the spatial information provided by the saccade end-point to measure directly the spatial coding of imagery process in each trial, which in turn was used to estimate the speed of the mental process driving saccades with different target contrasts. We expected that saccades would be affected by target contrast.

2.1. Methods

2.1.1. Participants

Twelve adult observers aged between 21 and 26 (10 females) took part in this experiment on a voluntary basis, and gave informed consent prior to the beginning of the experiments. The study was conducted in accordance to the principles of the Declaration of Helsinki and the San Raffaele Ethical Committee.

2.1.2. Stimuli and tasks

Observers were seated 57 cm in front of a laptop screen (15 in., 1366 × 768 pixels resolution, 60 Hz refresh rate), with their head stabilized by means of a chin rest. The visual stimulus consisted of a grey circular target (diameter = 2 deg of subtended visual angle, with either 0.54 or 0.02 Weber contrast) moving on a grey background (luminance = ~20 cd/m^2) along a circular trajectory (eccentricity = 5 deg) at constant velocity (either 1, 2, or 3 deg/s, clockwise). The target started to move at a random position along the circular trajectory and disappeared after 3 s. After a further variable time (range, 0–10 s, randomly extracted from a uniform distribution), a beep was presented. Observers had to keep the gaze on the central fixation dot until beep presentation. They were instructed to carefully follow the moving target with spatial attention, mentally continuing its motion after its disappearance, and finally making a saccade to the imagined target position upon beep presentation, as if they had to hit it with the gaze. No feed-back was provided. The experimental session consisted of 60 trials (2 contrasts × 3 speeds × 10 repetitions). A familiarization session was given before the beginning of the experimental session.

2.1.3. Eye movement recordings and data analyses

Binocular two-dimensional eye movements were recorded through video-oculography (Tobii Eyex, 60 Hz sampling frequency), preceded by a 9-points calibration session. Gaze position signals were low-pass filtered at 30 Hz and oversampled at 240 Hz. Instantaneous tangential velocity, which was computed through first time derivative of individual components, identified the onset of saccadic eye movements (threshold, 50 deg/s). Saccade offset was defined as the moment saccade tangential velocity dropped below 25 deg/s.

For each trial, we measured both the saccadic latency, computed as the time interval between beep presentation and saccadic onset, and the angular position of the saccade end-point, computed from the median eye position over an interval of 300 ms after saccade offset, and expressed in arcdeg. Extrapolation speed, our main dependent measure, was taken as the slope of the linear fit between saccade end-point and extrapolation duration (i.e., the time interval from target vanishing to beep presentation), computed for each observer over the ten trials at each target speed and contrast.

Each measure was analyzed using the same repeated-measures ANOVA design, with the Greenhouse-Geisser correction whenever required, with target Speed (1, 2, 3 deg/s) and Contrast (high vs. low) as factors. Normality was checked with the Shapiro-Wilk test.

Stimulus generation, eye movement recordings and data analyses were performed with custom programs written in Matlab, using the Psychophysics Toolbox extensions (Kleiner, Brainard, Pelli, Murray, & Broussard, 2007). For statistical analyses, the statistical package SPSS (v.24) was used.

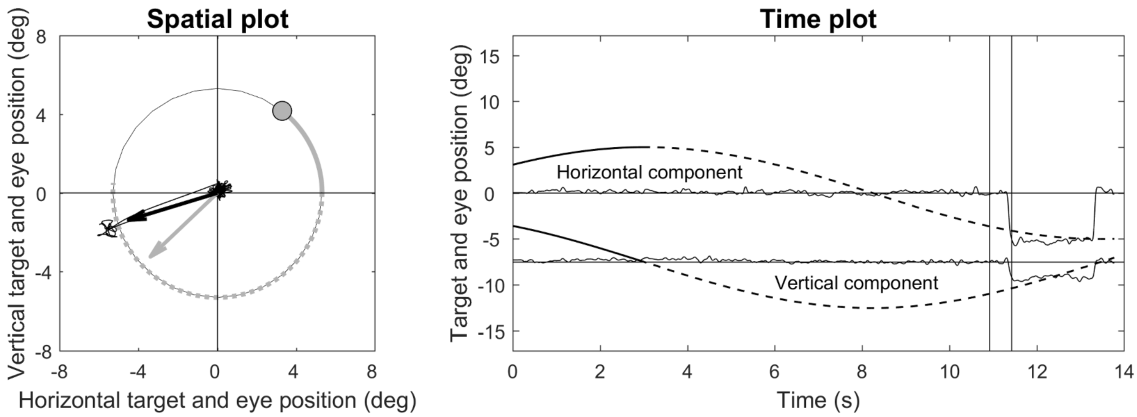

Fig. 1. A representative trial of the motion imagery task. Left panel. The target (grey disk, dimension is arbitrary) moved clockwise along a circular trajectory for 3 s (continuous grey trajectory) and then disappeared. Observers had to extrapolate target motion in imagery (grey dotted trajectory). After an unpredictable time, a beep indicated to make a saccade (black trace, symbolized by the thick black arrow) from the central fixation dot to the currently imagined target position. In this example, the saccade end-point was ahead the virtual target position at the time of the beep (grey arrow), indicating imagery lead. Right panel. Time plot of the horizontal and vertical components of both eye position and target position. The motion extrapolation phase, starting upon target vanishing, is indicated by the dashed target trajectory. Vertical leftward and rightward lines mark beep presentation and saccade offset, respectively. Horizontal continuous lines indicate the central horizontal and vertical coordinates, respectively. For graphical clarity, a vertical offset was introduced in the traces representing the vertical component.

2.2. Results

Observers responded readily to the beep presentation. The saccadic latency was on average 492 ms (22 SEM), and did not vary as a function of task conditions (main effect of Contrast, $F(1,11) = 0.038$, $p = 0.848$; main effect of Speed, $F(1,14) = 0.663$, $p = 0.464$; interaction Contrast × Speed, $F(2,22) = 0.209$, $p = 0.813$). Because this result is not central to the main issues of the study, we will not further comment it.

As expected, the longer the imagined trajectory, the further away was the saccadic end-point from the target vanishing point, a finding that reflects the unfolding of the imagery process in space and time. Saccades landed on average slightly ahead the position of the invisible target at the time of saccade offset (on average 10.423 arcdeg, with 95% confidence interval crossing zero, −3.485 to 24.332 arcdeg), although this positional error depended on both contrast and speed (main effect of Contrast, $F(1,11) = 19.002$, $p = 0.001$; main effect of Speed, $F(2,22) = 46.512$, $p < 0.001$; interaction Contrast × Speed, $F(2,22) = 0.094$, $p = 0.911$).

To assess extrapolation speed, we computed the regression line between the (mentally) covered trajectory, as measured by the phase angle of saccade end-point relative to the target vanishing point, and extrapolation duration, which was controlled experimentally by presenting the go-signal for the saccade (the beep) at various time-points from target vanishing (Fig. 2). The slope of the regression line provided an estimate of motion extrapolation speed for each observer and for each combination of target contrast and target speed.

Motion extrapolation speed increased with increasing target speed (Fig. 3; main effect of Speed, $F(2,22) = 30.045$, $p < 0.001$), although the slope was less than 1 (0.792, with 95% confidence interval from 0.675 to 0.909). This general tendency (extrapolation speed higher than target speed at lower speeds but lower at higher speeds) was not apparent when considering the six conditions individually. In fact, only in the high-contrast, low-speed condition did the extrapolation speed depart significantly from the actual target speed, as evaluated from confidence intervals.

Crucially, extrapolation speed was lower at low target contrast than at high target contrast (main effect of Contrast, $F(1,11) = 6.075$, $p = 0.031$), with a quite constant difference across target speeds (interaction Contrast × Speed, $F(2,22) = 0.017$, $p = 0.983$).

2.3. Discussion

Besides generally confirming previous findings on visuo-motor mental rotation and motion imagery (de'Sperati, 1999, 2003a, 2003b; Heath, Colino, Chan, & Krigolson, 2018), Experiment 1 showed an effect of contrast on extrapolation speed.

Observers turned out to be rather good in mentally imagining target speed, as extrapolation speed increased orderly with the objective target speed. Overall, the mean extrapolation speed was almost identical to the mean target speed over the entire experiment (grand average, 2.031 deg/s, 0.113 SEM, with a grand average of 2.0 deg/s of the target). However, motion extrapolation showed an opposite tendency at lower and higher target speeds. In the former case, observers tended to overestimate target speed, while in the latter case they tended to underestimate it, possibly because the 3 speeds were not blocked and observers tended to average them in the course of the experiment (central tendency effect, Hollingworth, 1910).

Note that in our experiment motion extrapolation was a truly gradual process, as shown by the tight proportionality between saccade end-point and motion extrapolation duration. Because the latter was randomly specified trial-wise, it is unlikely that the lower extrapolation speed with low contrast targets derived simply from a cognitive bias.

The fact that a perceptual signature such as contrast-dependent speed underestimation was observed in a task in which observers had to produce a saccade further confirms that motion extrapolation is based on visual mechanisms (e.g., motion imagery and attention, (de'Sperati & Deubel, 2006), the oculomotor output being just one of the many possible outcomes (e.g., a manual response, a perceptual localization task, a time-to contact estimation). Indeed, a contrast-dependent speed bias in motion extrapolation has been described also with a purely perceptual task (Battaglini et al., 2013).

3. Experiment 2

In Experiment 1 the target trajectory was fixed and (single) target motion entirely predictable. Does the contrast-dependent speed bias extend to more complex and less predictable contexts where several targets are continuously moving and observers interact with them in real-time? Experiment 2 addressed this question by testing the effects of contrast in a task in which making a saccade to a moving target would

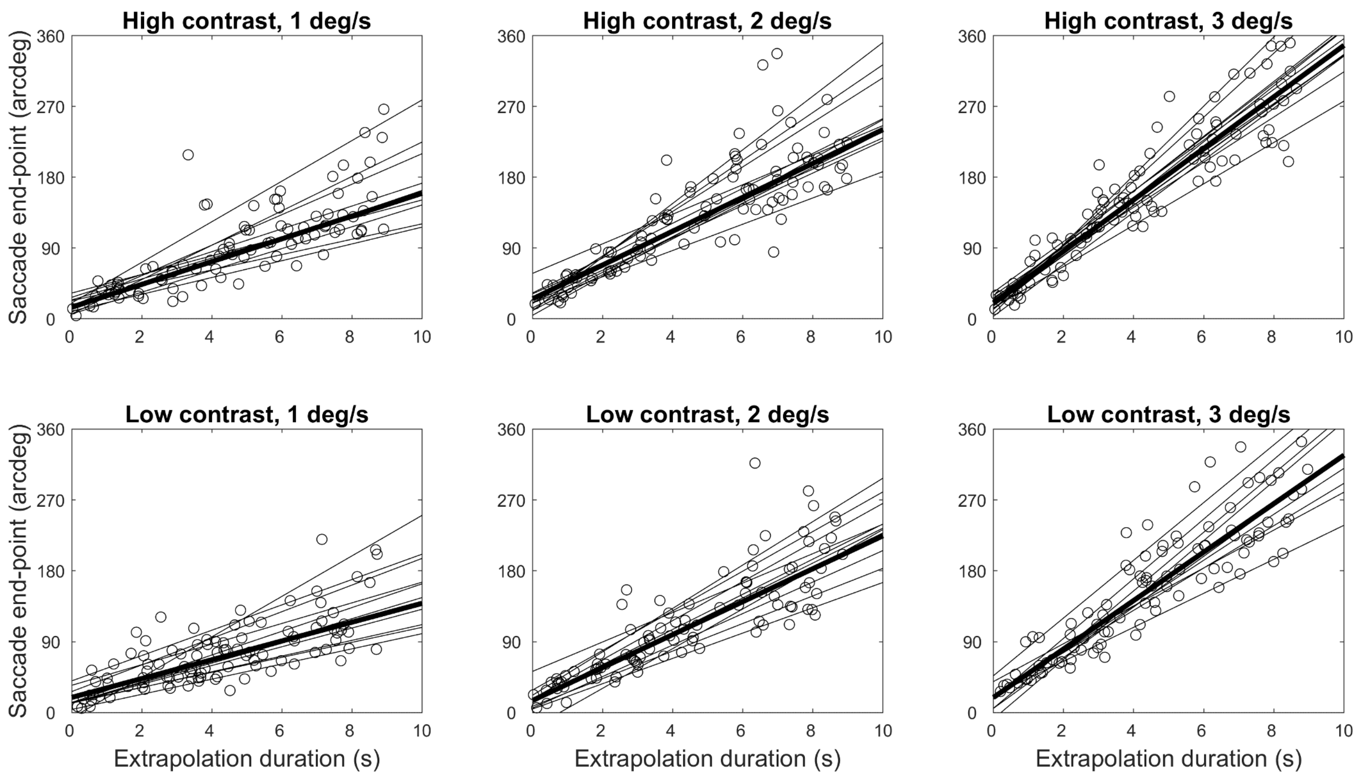

Fig. 2. The linear relationship between saccade end-point (relative to target vanishing point) and motion extrapolation duration, for each contrast and target speed. In each panel, the thin lines represent individual fit for each observer, while the thick line represents the overall fit.

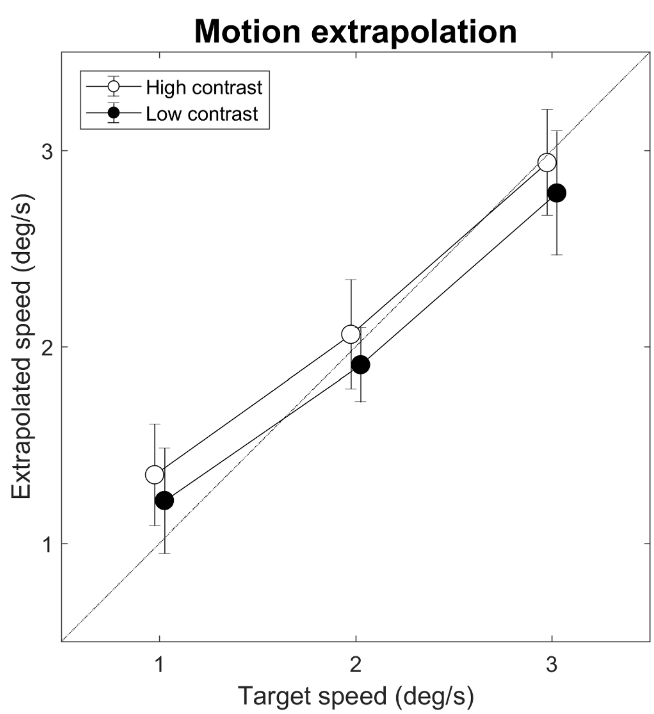

Fig. 3. Estimated motion extrapolation speed for each contrast and target speed. The diagonal line indicates the equivalence between objective and imagined target speed. Error bars are 95% confidence intervals.

invert its direction, thus allowing observers to actively control the display. Although our primary interest was the effect of contrast in the context of saccade planning, for comparison, a second version of the task was administered, in which the interaction effector was the finger (through the computer touchpad).

3.1. Methods

3.1.1. Participants

Twelve adult observers aged between 22 and 28 (9 females) took part in this experiment on a voluntary basis, and gave informed consent prior to the beginning of the experiments. They did not participate in Experiment 1. The study was conducted in accordance to the principles of the Declaration of Helsinki and the San Raffaele Ethical Committee.

3.1.2. Stimuli and tasks

The visual stimulus consisted of a number of white circular targets (between 3 and 6, diameter = 2 deg of subtended visual angle), moving on a grey background (luminance = ~20 cd/m^2) along random rectilinear trajectories at constant velocity (2 deg/s) for 30 s. They bounced upon collisions against each other and upon reaching the borders of a 20 × 15 deg screen area delimited by white lines. The moving targets could have either high or low contrast, in different trials (Weber contrast 0.54 and 0.02, respectively). The initial positions and trajectories of the targets were randomly chosen, with the constraint that inter-target distance was at least 2 deg. The individual targets were identical to the target used in the first experiment.

Observers were seated 57 cm in front of a laptop screen (15 in., 1366 × 768 pixels resolution, 60 Hz refresh rate), with the head stabilized by means of a chin rest. They had to prevent collisions among the targets – irrespective of bounces on the display region borders. In one task, hitting the touchpad cursor on a target by sweeping the finger on the touchpad had the effect of inverting its motion (Touchpad task). The motion of the other targets was not affected. In a second task, target motion was inverted when observers glanced at it (Gaze task). Details of the interactions are given below. In a third, control task (Counting task), observers had simply to count the collisions among the targets in free-viewing condition, without taking any action to avoid collisions. Each task consisted of 16 trials (4 target numerosities × 2 contrasts × 2 repetitions, randomly interleaved). At the end of each task, observers reported which of the two target types (high-contrast vs. low-contrast) appeared to move faster (2-alternative forced choice), followed by a confidence rating (range 0–9). The Counting task was always administered first, followed by the Touchpad and the Gaze tasks, counterbalanced across subjects. A familiarization session with both types of trials was given before the beginning of the experimental session.

3.1.3. Movement recordings, real-time interaction and data analyses

Binocular two-dimensional eye movements were recorded through video-oculography (Tobii Eyex, 60 Hz sampling frequency), preceded by a 9-points calibration session. Fingertip movements were recorded through the computer touchpad at 60 Hz through a dedicated software function. For simplicity, throughout the text the term 'touchpad' will refer to touchpad finger movements. Touchpad and gaze position signals were low-pass filtered at 30 Hz and oversampled at 240 Hz. Instantaneous tangential velocity, which was computed through first time derivative of individual components, identified the onset of both saccadic eye movements and saccadic-like touchpad movements, though with a different threshold to reflect the noisier ocular signal (5 deg/s and 30 deg/s for touchpad and eye movements, respectively). Additional common criteria to identify ocular and touchpad saccades were duration (30–750 ms), amplitude (1–25 deg) and inter-saccadic interval (min 100 ms).

For both gaze and touchpad interaction, target motion was inverted if cursor or gaze remained over a target (i.e., within target's border) for at least 50 ms. In order to inhibit continuous motion inversions, a 500 ms refractory period was added during which touchpad or gaze fixation could not further invert target motion. Successful target interceptions (not necessarily successful collision avoidance) were signaled by a brief target flashing, which served as feed-back to the observer that his/her action inverted target motion.

Task performance was quantified by means of two indexes, the number of residual collisions, i.e., the number of collisions that observers did not prevent, and the number of performative actions, i.e., the number of touchpad or gaze movements that were effective in inverting target direction. While the first index measures how well did observers achieve the task goal, the second index quantifies observers' interactive behavior, regardless of its efficacy in reducing collisions. For example, two observers with quite different interaction "styles" (for example with many or few performative actions) may result in a similar number of residual collisions. Conversely, two observers with a similar interaction "style" (for example with many performative actions) may end up with a quite different number of residual collisions. In the text, the average number of missed collisions and of performative actions is rounded.

For the statistical analyses, we used repeated-measures ANOVAs, with the Greenhouse-Geisser correction whenever required. A full factorial model was used with Task (Touchpad vs. Gaze), Contrast (high vs. low) and Target numerosity (3, 4, 5, 6) as factors. Normality was checked with the Shapiro-Wilk test. The α level was set to 0.05.

3.1.4. Interaction simulation

The interaction task requires frequent, rapid visuo-motor decisions, and thus there is likely to be a very short time available for programming consecutive performative actions, especially when several targets are moving in the display. Intuitively, then, underestimating target speed should entail an increase in the number of missed collisions. This stems from the consideration that a speed bias should lead to wrong collision prediction, with real collisions occurring earlier than collisions predicted on the basis of perceived target speed: if interceptive movements are guided by a biased speed signal, they may miss the target. In order to evaluate the effective impact of speed underestimation on missed collisions, we performed a simple simulation of the interaction behavior under conditions as close as possible to the present experimental conditions.

To this end, we used the same computer program used to run the real experiment, but in which the observer's interaction movements were replaced by the movements of a virtual pointer driven by a look-ahead function. The look-ahead function checks for future target collisions based on the speed (either real or underestimated) and trajectory of all targets, and programs an interaction movement directed to the computed position of one of the two next colliding targets. The simulation was general enough to adapt to both saccadic and finger movements.

Movement onset was taken to reflect uncertainty of the sensorimotor decision, under the assumption that programming a pointing movement should incorporate the movement temporal variability – mostly latency variability – to optimize the time to contact. In demanding interaction conditions this means that the decision is delayed as much as possible to maximize the accrual of sensory evidence until the moment beyond which the movement would occur too late. To estimate latency variability we took the standard deviation of saccadic response times measured in Experiment 1 (~ 100 ms), which was then added as random component to the movement onset time. Spatial variability was further added to the horizontal and vertical end-point movement coordinates (taken as the standard deviation of fixational stability in Experiment 1, ~ 0.25 deg). We do not have equivalent measures for touchpad movements, but we can assume they are not much different. Crucially, in half of the trials we injected a controlled amount of target speed underestimation (5%, which is approximately the speed underestimation bias found in Experiment 1 with low contrast targets moving at 2 deg/s). The simulation was run 10,000 times, and produced a distribution of differences of missed collisions between biased and unbiased trials, that is, an estimate of the expected effect of a 5% speed underestimation.

Stimulus generation, movement recordings and data analyses, including the simulation, were performed with custom programs written in Matlab, using the Psychophysics Toolbox extensions (Kleiner et al., 2007). Cross-correlation between eye and touchpad movements was computed by means of the *xcorr.m* Matlab function. For statistical analyses, the statistical package SPSS (v.24) was used.

3.2. Results

In general, observers reported to feel quite comfortable with the tasks, despite the rather unnatural use of the gaze as an interaction device, and also despite the difficulty when the number of targets was high and contrast low.

We first verified that stimulus visibility was sufficient for observers to adequately perform the task, especially at low contrast with several targets. In the Counting task, in which observers had simply to count the number of collisions, neither target contrast nor target numerosity worsened performance, as assessed through missed collisions. Indeed, performance was always almost perfect (Table 1). This confirmed that observers were capable of detecting practically all collisions, at least

Table 1
Number of total and missed collisions in the Counting task as a function of target contrast and target numerosity. Values are the rounded averages over a 30-s trial and across all observers.

Target contrast	Target numerosity	Total collisions	Missed collisions
High	3	2	0
	4	7	0
	5	11	0
	6	16	2
Low	3	3	0
	4	5	0
	5	11	0
	6	17	0

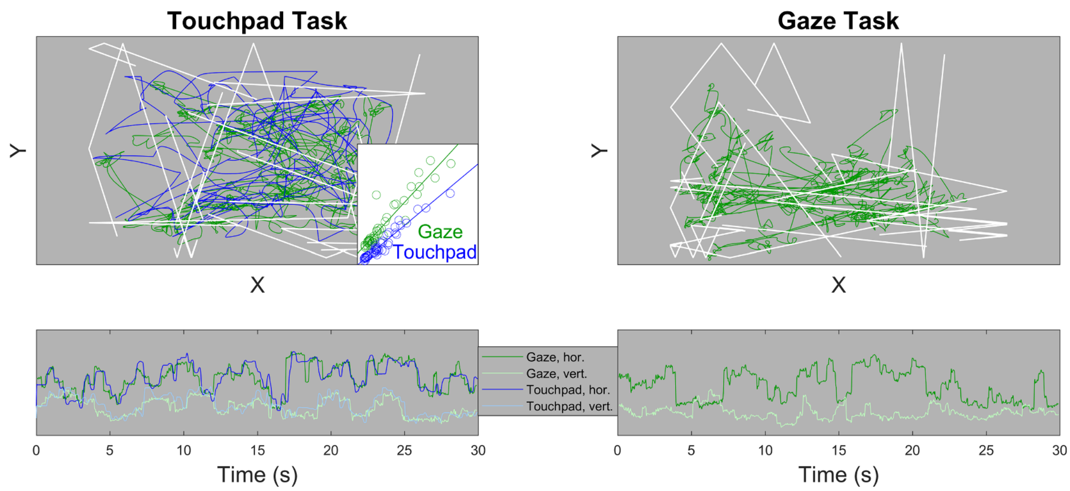

Fig. 4. Examples of single-trial recordings of touchpad (blue/bluish traces) and eye (green/greenish traces) movements in the Touchpad and Gaze tasks. Targets moved along rectilinear trajectories at constant velocity for 30 s (white traces, top panels), bouncing upon collisions against each other and upon reaching the display border. The time plots (bottom panels) show the horizontal and vertical components of eye and touchpad movements. Observers had to avoid collisions by hitting the targets with the touchpad cursor (not shown) in the Touchpad task, or by gazing at targets in the Gaze task: these interceptive actions had the effect of inverting target motion. Inset, amplitude-velocity relationship of touchpad and gaze movements in a single trial (main sequence). Each dot represents a saccadic eye movement or a saccadic-like touchpad movements. Continuous lines are the fitted linear curves. Although ocular saccades are faster, touchpad movements retained the signature of the proportionality between movement extent and peak velocity. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

when no interaction was required.

When interaction was required, with either the touchpad (Touchpad task) or the gaze (Gaze task), the task was clearly more challenging. In the Touchpad task, finger movements looked strikingly similar to eye movements (Fig. 4). Firstly, finger movements on the touchpad showed a saccadic-like shape, to the extent that a main sequence, i.e., the well-known characteristic relationship between saccade amplitude and velocity (Bahill, Adler, & Stark, 1975), applied not only to eye movements but also to finger movements, though in the latter case with a less steep slope (Fig. 4, inset). Secondly, a trial-wise cross-correlation analysis on the Touchpad task data showed a very tight relationship between eye and finger movements. Cross-correlation strength increased with target numerosity ($F(1.306,14.370) = 9.698$, $p = 0.005$) but not with target contrast, and a similar though not statistically significant tendency was present for gaze lead, indicating that task difficulty strengthened eye-hand synergy (Fig. 5). Clearly, the cross-correlation analysis could be performed only in those trials in which both gaze and finger movements were performed, i.e., in the Touchpad task.

The interaction performance, as measured through the number of missed collisions (Fig. 6, top panels), varied as a function of task. Specifically, using the gaze instead of the touchpad to avoid collisions resulted in a slightly but significantly worse performance (missed collisions, 5 ± 1 SEM vs. 4 ± 1 SEM, respectively; main effect of Task, $F(1,11) = 18.008$, $p = 0.001$).

Target numerosity impacted strongly on performance: as the number of targets increased from 3 to 6, the number of missed collisions over a 30-seconds trial increased from less than 1 to more than 10 on average (main effect of Target numerosity, $F(1.254,13.789) = 66.311$, $p < 0.001$), without appreciable differences in the two tasks (interaction Task × Target numerosity, $F(3,33) = 0.697$, $p = 0.560$). Although we do not know how many collisions would have occurred had observers not prevented them, by using the number of total collisions in the Counting task as a reasonable estimate (Table 1) it can be inferred that missed collisions increased from about 25% with 3 targets to about 65% with 6 targets.

Conversely, there was no evidence that contrast affected task performance (main effect of Contrast on missed collisions, $F(1,11) = 1.475$, $p = 0.250$; interaction Contrast × Task, $F(1,11) = 0.119$, $p = 0.736$; interaction Contrast × Target numerosity, $F(2.028,22.308) = 0.697$, $p = 0.510$). The only significant effect was the second-order interaction (interaction Contrast × Task × Target numerosity, $F(3,33) = 3.798$, $p = 0.018$), a hint that the interaction

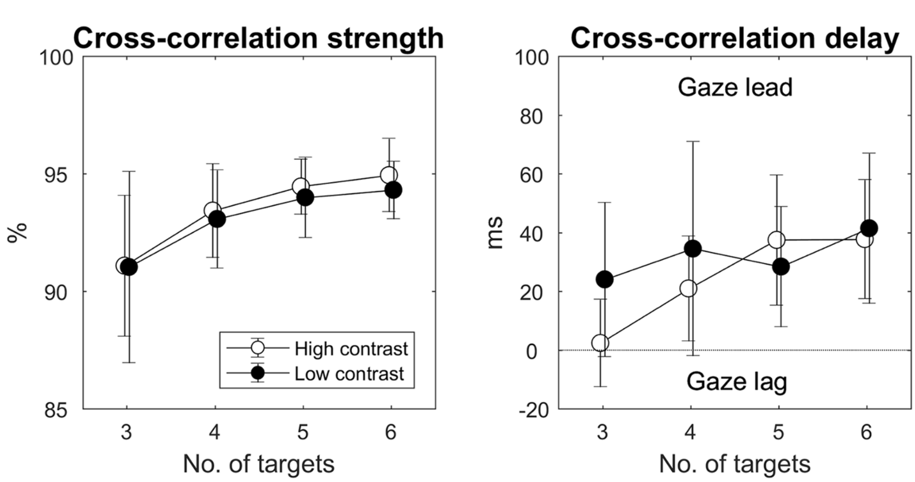

Fig. 5. Cross-correlation between eye movements and touchpad movements when the touchpad was used as interaction device (Touchpad task). Both cross-correlation strength and delay denoted a tight relationship between them, and tended to increase with target numerosity but not target contrast. Bars are 95% confidence intervals.

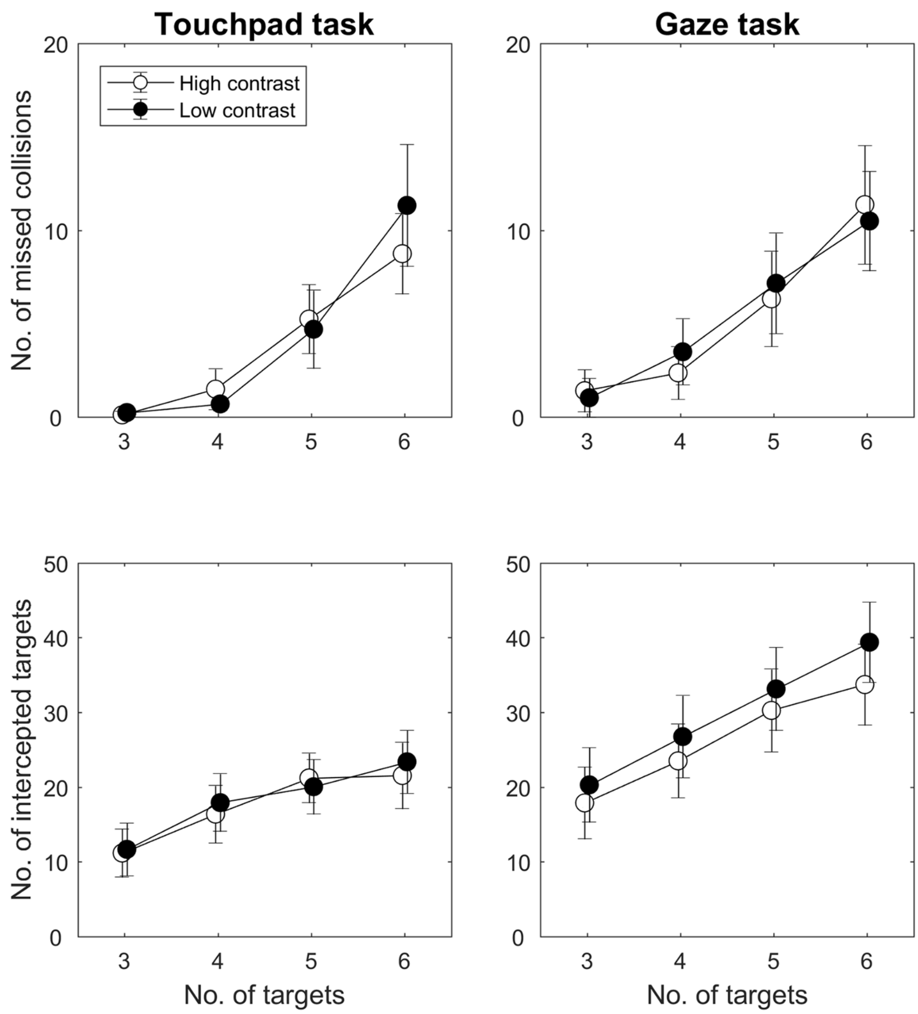

Fig. 6. Task performance (mean number of missed collisions over a 30-s trial) and performative actions (mean number of intercepted targets over a 30-s trial) as a function of task, target contrast and target numerosity. Error bars are 95% confidence intervals.

Contrast × Target numerosity depended on the task.

About one third of missed collisions were "unavoidable", that is, not depending on observers' strategy or rapidity: these were defined as collisions that occurred at an interval of less than 500 ms from each other, such that observers could not reasonably prevent them. While part of these collisions may have occurred by chance, some may have been determined by observers' wrong target interceptions resulting in unintended additional collisions, especially when several targets happened to be spatially close to each other. These "unavoidable" collisions may be a confounding variable when considering the pattern of missed collisions. By removing them from missed collisions, which clearly decreased the overall number of missed collisions, the pattern of results remained the same, except that the second-order interaction disappeared (main effect of Contrast, $F(1,11) = 1.115$, $p = 0.741$; main effect of Task, $F(1,11) = 14.827$, $p = 0.003$; main effect of Target numerosity, $F(3,33) = 67.331$, $p < 0.001$; interaction Contrast × Task, $F(1,11) = 0.01$, $p = 0.979$; interaction Contrast × Target numerosity, $F(3,33) = 0.238$, $p = 0.869$; interaction Task × Target numerosity, $F(3,33) = 1.892$, $p = 0.150$; interaction Contrast × Task × Target numerosity, $F(3,33) = 2.379$, $p = 0.087$). In other words, only the main effects of Task and Target numerosity were robust effects.

Although the above results suggested that contrast generally did not influence the number of missed collisions, to further test this claim we compared the results of the simulations with the experimental data. A first finding is that injecting a 5% target speed underestimation indeed introduces an increase in missed collisions, and such an effect depends on target numerosity (passing from 0% with the 3-target display to ~17% the 6-target display, blue[1] distributions in Fig. 7). This effect of target numerosity is expected, because a demanding interaction condition leaves little time to plan the next performative movement. Thus, even a slight speed underestimation can increase the chance to miss the target. Conversely, a relaxed interaction condition allows observers to more accurately plan the next performative movement. We then compared the expected distribution of the missed collision difference between high-contrast and low-contrast trials obtained from the simulation against the same distribution obtained by bootstrapping the real data collected in the gaze and the touchpad tasks (reddish and greenish distributions in Fig. 7).

From these distributions, it would seem that there is an opposite trend in sensitivity to contrast (mean differences of missed collisions between low-contrast and high-contrast trials, ΔN) of gaze interaction and finger interaction as target numerosity increases. That is, for gaze, the effect of contrast tended to decrease with target numerosity, while for finger it tended to increase. This pattern is even clearer when excluding the easy 3-targets condition, which is the only condition where the simulation does not predict a significant increase of missed collisions with speed underestimation ($\Delta N = 0.02$, 95% confidence intervals for $\Delta N = -0.30$ to 0.32). However, despite the opposite trend for

[1] For interpretation of color in Fig. 7, the reader is referred to the web version of this article.

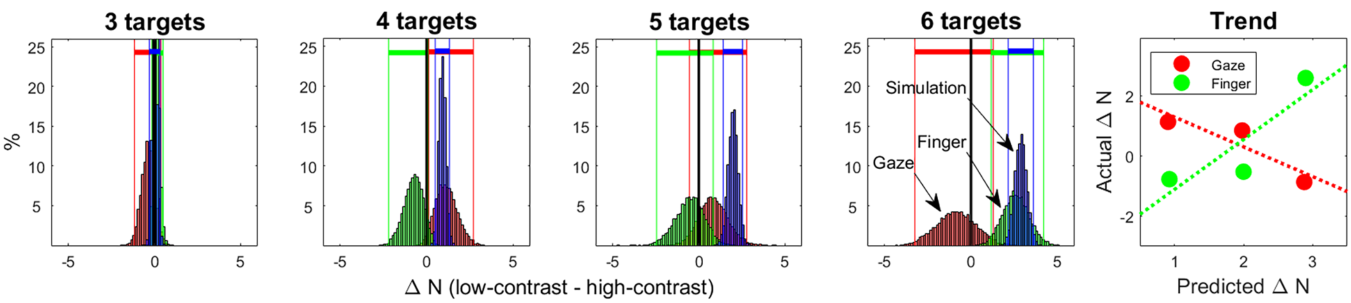

Fig. 7. Effect of contrast on missed collisions for real and simulated data. The histograms are the distributions of the differences of missed collisions (ΔN) between low-contrast and high-contrast trials with each of the target numerosities. Positive values indicate more missed collisions in low-contrast than in high-contrast trials. The expected effect of a 5% speed underestimation is clearly visible in the simulations (rightward-shifted from zero, except for the 3-targets condition, where no effect is predicted). The gaze and finger distributions are obtained through bootstrap from real data. All distributions have the same number of observations (N = 10,000). Vertical lines represent the lower and upper bounds of 95% confidence intervals, emphasized by the horizontal thick lines on the top. Rightmost panel, gaze and finger interaction performance expressed in terms of effective missed collision differences between low-contrast and high-contrast trials (Actual ΔN) as a function of the difference of missed collisions predicted by the simulation, when present (Predicted ΔN).

gaze and touchpad interaction (Fig. 7, right panel), the confidence intervals of the two slopes are largely overlapping (−6.95 to 4.96 and −10.10 to 13.42). This also holds true when the data-points corresponding to the null predicted ΔN are included (data not shown).

We also analyzed the interaction activity by counting observers' performative actions, i.e., touchpad or gaze movements that actually intercepted the targets – regardless of their efficacy in reducing collisions. Observers made more performative actions (Fig. 6, bottom panels) when contrast was low, an effect that depended on task but not target numerosity (main effect of Contrast, $F(1,11) = 12.786$, $p = 0.004$; interaction Contrast × Task, $F(1,11) = 5.921$, $p = 0.033$; interaction Contrast × Target numerosity, $F(3,33) = 1.892$, $p = 0.150$). Indeed, the main effect of contrast was statistically significant in the Gaze task ($F(1,11) = 12.341$, $p = 0.005$), where low-contrast targets were slightly but systematically associated to an increased number of performative actions (on average in each trial from 26 to 30 for high and low contrast, respectively), but not in the Touchpad task ($F(1,11) = 1.222$, $p = 0.293$), where low- and high-contrast targets did not yield any systematic difference in the number of performative actions.

As for Target numerosity and Task, performative actions showed the same pattern as missed collisions (main effect of Target numerosity, $F(1.577,17.343) = 62.201$, $p < 0.001$; main effect of Task, $F(1,11) = 43.820$, $p < 0.001$), although here the effect of task is even more visible, with observers making many more target interceptions with the gaze than with the touchpad, increasing on average from 18 to 28, which corresponds to almost one interception per second. Yet, as seen above, such an increase in interaction activity did not yield a performance improvement.

Finally, observers were unanimous in reporting, at the end of each task, which of the two target types appeared to move faster: For all observers, high-contrast targets looked faster (100% in all tasks), with a fairly good confidence level (6.2, 5.7, 6.3 for the Counting, Touchpad and Gaze tasks, respectively).

3.3. Discussion

The most evident result of Experiment 2 was the similarity of interaction performance with high-contrast and low-contrast moving targets, despite the very limited visibility of low-contrast targets and in spite of the fact that observers unanimously reported low-contrast targets to be slower than high-contrast targets. That is, low contrast was generally not detrimental to the interaction performance, measured through the number of missed collisions. However, low target contrast increased the number of performative actions in the Gaze task – but not in the Touchpad task.

We have no evidence of different strategies for gaze and finger interaction. Yet, a hint that a strategy difference may exist is the apparently opposite trend with target numerosity, where at low contrast demanding interaction conditions might penalize finger but not gaze interaction. However, this hypothesis is currently unsupported by the slope data, which are opposite in sign but largely overlapping for the two interaction modalities. Therefore, whether or not this pattern of results is an indication of a genuine strategy difference between gaze and finger interaction remains to be tested with higher target numerosities.

The overall lack of contrast effect on missed collision is in stark contrast with the reported impression of lower speed for low-contrast targets. Admittedly, the simple and quick way of assessing speed perception that we have used here is rather crude, and may be subject to response bias. Yet, it provides at least a gross indication of the subjective impression of target speed while observers were trying to avoid collisions. Given that observers were unanimous in judging low-contrast targets to be slower – and with good confidence – and given that speed underestimation at low contrast is repeatedly reported in the literature (Senna et al., 2015; Snowden et al., 1998; Stone & Thompson, 1992; Thompson, 1982; Weiss et al., 2002), we deemed it to be unnecessary to administer observers an additional, more structured psychophysical task. Importantly, while perception is usually assessed with dedicated perceptual tasks, here the perceptual assessment was performed in the context of a motor task, thus with the advantage of probing "background" speed perception concomitant with "foreground" speed processing for visuo-motor interaction: low-contrast targets looked slower even though observers were not explicitly instructed to report target speed but to interact with them.

As for the lack of contrast effect in the control task (Counting task), we note that in that case performance was not expected to be affected by poor speed perception at low contrast, as counting did not involve motion processing to anticipate collisions but only to take note of actual collisions. The almost perfect performance found in the Counting task confirmed that low stimulus visibility did not hinder the capability of passively monitoring the visual display in our experimental conditions. Clearly, this does not amount to saying that gaze accuracy remains necessarily the same at low contrast, but only that collisions are still perfectly detected.

4. General discussion

The main findings of this study were that (i) contrast affected saccades directed to an imagined moving target, revealing reduced motion extrapolation speed with low target contrast (Experiment 1), (ii) the same low target contrast did not decrease the capability of preventing target collisions when gaze was used to interact, although low contrast intensified gaze interceptions (Experiment 2), (iii) there was some evidence that low contrast targets led to greater collisions during touchpad interactions (Experiment 2).

Experiment 1 was performed to verify whether the well-known effect of contrast on speed perception (Senna et al., 2015; Snowden et al., 1998; Stone & Thompson, 1992; Thompson, 1982; Weiss et al., 2002) extends to visuo-motor imagery. A large body of evidence indicates that mental motion imagery shares several functional properties with visual motion perception (Crespi, Robino, Silva, & de'Sperati, 2012; de'Sperati & Santandrea, 2005; de'Sperati, 1999, 2003a; Gregori Grgic, Calore, & de'Sperati, 2016; Makin & Bertamini, 2014; Makin & Poliakoff, 2011; Makin et al., 2009; Thomas, 2018). Moreover, a previous study showed that motion extrapolation through an occluder was slowed with low-contrast targets, as compared to high-contrast targets (Battaglini et al., 2013). These findings suggest that a common, perceptual-like representation – thus containing possible contrast-dependent speed biases – is used also to plan a saccade to an imaginary target. However, it is not entirely obvious that speed underestimation at low contrast should automatically transfer to saccadic planning. Indeed, if the contrast-dependent speed bias is introduced at late processing stages of speed decoding and not during early speed encoding, in principle it might not manifest when target speed, even when only mentally represented, is accessed by the saccadic system. For example, the fronto-parietal structures responsible for visuo-motor mental rotation (Heath et al., 2018) may rely on their own visual dynamic representation, perhaps at least partly dissociated from the visual dynamic representation underlying purely perceptual sensations in visual imagery. This may partially explain the differences in mental rotation speed found in visuo-motor mental rotation and purely visual rotation (de'Sperati, 1999). Yet, in the present experiment we documented speed underestimation when making a saccade to the extrapolated position of a low-contrast target, thus further suggesting that the same internal motion representation is available for motion perception and various forms of imagined motion extrapolation.

While in Experiment 1 we have shown that visuo-motor prediction based on a perceptual-like speed representation clearly retains contrast-dependent speed bias, the contrast effect on performance in Experiment 2, when observers had to interact with moving targets, was less straightforward. How can these patterns of results shed light on speed processing? In the following, we will discuss three scenarios for the interaction task. In the first scenario, target speed is simply not relevant for predicting collisions. In the second scenario, speed is underestimated at low contrast but is compensated. In the third scenario, speed processing for visuo-motor interaction is immune to the contrast-dependent bias.

4.1. Scenario 1. Speed is not relevant

That target speed is a relevant stimulus feature for predicting collisions among moving targets may seem trivial. However, whether or not motion prediction is in fact used when observers have to concurrently attend to several moving targets (Multiple Object Tracking, MOT) is a debated issue (Fencsik, Klieger, & Horowitz, 2007; Franconeri, Lin, Pylyshyn, Fisher, & Enns, 2008; Keane & Pylyshyn, 2006). According to some authors, MOT relies on position memory (Intriligator & Cavanagh, 2001; Keane & Pylyshyn, 2006), thus undermining the role of motion prediction, which is based on speed monitoring. A study by Iordanescu, Grabowecky, and Suzuki (2009) showed instead that target speed is in fact monitored in a MOT task, although not necessarily used. In that study, a proportionality was found between target speed and forward shift in target localization, which indicated that speed is effectively taken into account when multiple targets are concurrently moving. More recently, Meyerhoff, Papenmeier, and Huff (2013) provided further evidence that target motion in a MOT task is coded object-wise. It is remarkable that speed encoding was found in tasks where motion prediction was not required to observers: in Iordanescu et al.'s study the task consisted in recovering target position upon their disappearance, and in Meyerhoff et al.'s study the task consisted in identifying pre-tagged targets after a period of motion, suggesting that speed is inherently encoded in MOT, even when no explicit motion prediction is needed. When, as in the present study, observers are required to actively avoid collisions in a MOT display – which amounts to add an interactive motor component to an otherwise purely attentive tracking task – real-time monitoring of target speed to predict impending collisions seems to be even more ineludible (Atmaca et al., 2013; Thornton et al., 2014). Thus, available evidence points to an effective use of visual speed information when actively interacting with multiple moving targets. Under this hypothesis, the contrast-dependent increase of missed collisions with finger interaction and demanding display would not be mediated by any speed processing mechanism.

4.2. Scenario 2. Speed bias is present but compensated

If speed is relevant, and subject to the same processing biases reported in perceptual and perceptual-like tasks, in principle it should be expected that a wrong estimation of target speed yields more interception errors in the interaction task due to the delayed prediction of the time to collision, hence leading to a worse performance (more missed collisions). This expectation was confirmed by the simple simulation that we performed, in which the same speed underestimation that in Experiment 1 was found to affect saccadic planning predicted a clear increase in missed collisions in Experiment 2, except in the easiest interaction condition (3-target display), where the predicted effect of speed underestimation was null. Yet, actual observers' performance in Experiment 2 was generally unaffected by contrast.

A possible explanation is that observers compensated the effects of target speed underestimation by increasing the gaze interceptive effort. This may have even lead to overcompensation, as performative actions increased at low contrast, even though they were not accompanied by a change in the missed collisions rate. The latter result suggests that observers also made more accidental gaze contacts with the targets – the "Midas Touch" effect (Jacob, 1991). As long as the number of unintended collisions is counterbalanced by an equal number of prevented collisions, increasing the interception rate does not impact on the overall number of missed collisions. Thus, it is entirely possible that speed underestimation, despite being ultimately ineffective in terms of missed collisions, was in fact present also in this context of real-time visuo-motor interactions but masked by augmented interceptive oculomotor effort.

4.3. Scenario 3. Parallel speed processing

This scenario suggests a dissociation between veridical visual speed processing in visuo-motor interaction (Gaze task, Experiment 2), and contrast-dependent, biased speed processing in both perceptual (Experiment 2, perception assessment, see also Senna et al., 2015; Snowden et al., 1998; Stone & Thompson, 1992; Thompson, 1982; Weiss et al., 2002) and perceptual-like tasks (Experiment 1, motion extrapolation, see also Battaglini et al., 2013; Fu, Shen, & Dan, 2001).

How could veridical speed processing co-exist with illusory speed processing? A hint may come by comparing the temporal aspects of the extrapolation task and the visuo-motor interaction task. As noted above, in the former task the trajectory of the single target is fixed throughout the trial, and observers can easily predict the position of the imagined target and plan a saccade. On the other hand, interacting with a continuously changing world requires incessant, real-time sensory monitoring and prompt decisions. In this demanding condition, there might be no time for the (biased) speed perception to overcome veridical speed processing running in fast feed-forward mode (VanRullen, 2007). In this view, rapid visuo-motor actions functional to accurately respond to sudden and rapid changes in the environment, typically, saccadic eye movements, would by-pass the slow buildup of perception, which may include illusory phenomena (Burr & Santoro, 2001; de'Sperati & Baud-Bovy, 2008; Gregori-Grgič et al., 2011; Pearson et al., 2015; Rossetti, 1998).

The view of a dissociation between action and perception is highly controversial, though. For example, there are several studies in the literature which have failed to find dissociations (Bruno & Franz, 2009), and others that suggest multiple dissociations (Pisella, Binkofski, Lasek, Toni, & Rossetti, 2006). To remain close to the present study, it is known that the steady-state velocity gain of smooth pursuit eye movements – but not initial velocity – is influenced by perceived speed (Spering, Kerzel, Braun, Hawken, & Gegenfurtner, 2005), which indicates that closed-loop visuo-motor responses involving a single attended target moving at constant velocity may not escape perceptual biases. Also, in a visuo-motor interaction task in which observers had to adjust the trajectory of an illusorily drifting target (De Valois & De Valois, 1991) by tilting the tablet on which the task was run, the trajectory continued to be biased in the direction of the target's apparent drift (Caniard, Bulthoff, & Thornton, 2014). In fact, the error was larger than in a comparison perceptual task in which observers had to visually estimate the target's trajectory. Here we just wish to remark that temporal constraints on visual processing could be the key to understand speed processing differences between the motion extrapolation task and the visuo-motor interaction task.

If fast motor interactions can by-pass sluggish speed perception, then why did target contrast not affect the number of missed collisions when task conditions were less demanding and target trajectory more easily predictable, that is, in trials with a small number of targets? There is one crucial difference, however, namely, that to prevent collisions among three slowly moving targets there is no need to accurately decode their speed, as it is enough to intercept them well in advance of any possible collision, even when collision is a just a remote possibility. When there are many targets – a condition in which the number of potential collisions increases multiplicatively – interception cannot occur too early, for it would be almost impossible to predict the evolution of targets' trajectories. In this condition, target trajectories should be continuously predicted, and interception decisions often taken in a quite short time window. Being very fast, saccades may be specially suited to accommodate this mechanism. Here is where veridical real-time speed processing may have by-passed the illusory impression of slow motion in our gaze interaction tasks.

4.4. Parallel speed processing: filters and priors

The hypothesis of parallel speed processing would suggest that current computational models based on the ratio between low-pass and band-pass filters (Burr & Thompson, 2011; Hammett et al., 2007; Perrone, 2005; Thompson et al., 2006) cannot be the entire story, for they produce a single output at a time, i.e., a single speed. While these models do predict lower speed at low contrast, a phenomenon repeatedly found in several perceptual tasks at low stimulus speeds, they cannot be at the same time insensitive to contrast in driving fast motor responses. Indeed, in Experiment 2 observers were asked for their perceptual impression about the speed of the very same targets they were interacting with, which suggests that truly parallel speed processing was taking place – i.e., parallel processing streams working concurrently within a single task, not different processing in different tasks. Similarly, a single gain control mechanism cannot account for truly parallel speed processing, but only for adjustable, task-dependent speed tuning (Simoncini, Perrinet, Montagnini, Mamassian, & Masson, 2012). Thus, under this view a speed decoding mechanism based on ratio models should at least coexist with another speed decoding mechanism, insensitive to contrast effect. These two mechanisms could be independently and concurrently accessed by distinct downstream circuits in the visual system.

The explanation that speed underestimation depends on a low speed Bayesian prior deriving from the implicit assumption that the visual world contains more frequently low-speed than high-speed motion (Senna et al., 2015; Weiss et al., 2002) seems also problematic, though possible. Of course, one should posit that the prior applies only to perceptual systems. However, limiting the prior to perceptual systems, while beneficial for real-time visuo-motor behaviour, would amount to say that a "Bayesian epi-phenomenon" is implemented in the brain, which sounds somewhat at odds with the idea of optimization that Bayesian mechanisms are supposed to bring about under uncertainty conditions.

The two accounts – filters and priors – may not be mutually exclusive after all. Indeed, it was suggested that speed priors may be encoded in relatively early cortical areas (Vintch & Gardner, 2014), thus suggesting that speed processing, including the low-speed bias, is implemented through a rather upstream, generalized mechanism. A similar point was made for orientation processing (Girshick, Landy, & Simoncelli, 2011).

4.5. Differences between touchpad and gaze interaction

Despite some similarities between touchpad and gaze movements, preventing collisions with the gaze or the touchpad was not entirely equivalent. Firstly, we found a general worsening of the interaction performance (more missed collisions) when the gaze was used to prevent collisions, as compared to using the touchpad. Secondly, the apparently different ΔN slope in the two interaction modalities may be a clue that the oculomotor system, but not necessarily the more sluggish eye-hand-finger system, can overcome the tricks of dynamic visual perception (speed underestimation) under demanding interaction conditions, although as already noted, this remains to be verified. Thirdly, gaze interceptive actions were much more frequent (more performative actions) than touchpad interceptive actions. Such interception increase was not matched by a decrease of missed collisions – and, almost paradoxically, in the case of gaze interaction even by a slight increase. Evidently, the unnatural way of using the eyes as a performative device (i.e., with causal physical power, Giuliani et al., 2017; Gregori Grgic, Crespi, & de'Sperati, 2016), coupled with imperfect real-time gaze measurement, as compared to the straightforward reading of touchpad coordinates, could have augmented both false positives (unintended interceptions) and false negatives (missed interceptions). Future investigation may help to better understand how gaze interaction can be improved through appropriate ocular training and/or improvement of real-time measurement accuracy. In this regard, we should also note that gaze pointing in complex visual environments sometimes leads to better performance than finger pointing. During foraging tasks, where targets are collected with a finger movement, increasing attentional load (i.e., search for targets defined by a single feature vs. conjunction of features) typically switches observers from a random to a systematic foraging strategy (Kristjansson, Johannesson, & Thornton, 2014). By contrast, during visual foraging, in which the gaze is used to collect targets, switching to a systematic strategy is much less common, as if eye movements could easily deal with the more difficult conjunction search condition (Johannesson et al., 2016).

5. Conclusion

In conclusion, while contrast systematically biased saccades made to a single imagined moving target, it did not generally affect performance in a gaze interaction task involving rapid, continuously changing motion predictions with several targets. The only visible effect of low contrast in the interaction task was an increase of gaze interceptive actions, and possibly also a tendency for finger interaction to be penalized by low contrast more than gaze interaction when many targets are present. We surmise that the present results may indicate the existence of parallel visual speed processing, a possibility that is not encompassed by current models of cortical motion processing. However, we remain cautious in this respect, for a simpler dissociation in the way visual dynamic signals are exploited by downstream motor systems may explain our results: fast saccadic eye movements could strategically compensate contrast-dependent interaction errors due to speed underestimation. The difference between these two accounts is that in the former case saccades are guided by an unbiased signal, thus there is no error, while in the latter case saccades may be biased but errors are corrected. Further investigation is required to clarify this point. Whatever the case, our study suggests that designers of gaze-contingent consoles and videogames may not need to compensate for speed underestimation of low-contrast stimuli (though they may wish to compensate for other, content-specific speed biases, Zuliani et al., in press; Rossi et al., 2018).

References

Atmaca, S., Stadler, W., Keitel, A., Ott, D. V., Lepsien, J., & Prinz, W. (2013). Prediction processes during multiple object tracking (MOT): Involvement of dorsal and ventral premotor cortices. *Brain and Behavior, 3*(6), 683–700.

Bahill, A. T., Adler, D., & Stark, L. (1975). Most naturally occurring human saccades have magnitudes of 15 degrees or less. *Investigative Ophthalmology, 14*(6), 468–469.

Baldauf, D., & Deubel, H. (2008). Visual attention during the preparation of bimanual movements. *Vision Research, 48*(4), 549–563.

Battaglini, L., Campana, G., & Casco, C. (2013). Illusory speed is retained in memory during invisible motion. *i-Perception, 4*(3), 180–191.

Bekkering, H., & Neggers, S. F. (2002). Visual search is modulated by action intentions. *Psychological Science, 13*(4), 370–374.

Bruno, N., & Franz, V. H. (2009). When is grasping affected by the Muller-Lyer illusion? A quantitative review. *Neuropsychologia, 47*(6), 1421–1433.

Burr, D. C., & Santoro, L. (2001). Temporal integration of optic flow, measured by contrast and coherence thresholds. *Vision Research, 41*(15), 1891–1899.

Burr, D. C., & Thompson, P. (2011). Motion psychophysics: 1985–2010. *Vision Research, 51*(13), 1431–1456.

Caniard, F., Bulthoff, H. H., & Thornton, I. M. (2014). Action can amplify motion-induced illusory displacement. *Frontiers in Human Neuroscience, 8*, 1058.

Crespi, S., Robino, C., Silva, O., & de'Sperati, C. (2012). Spotting expertise in the eyes: billiards knowledge as revealed by gaze shifts in a dynamic visual prediction task. *Journal of Vision, 12*(11).

De Valois, R. L., & De Valois, K. K. (1991). Vernier acuity with stationary moving Gabors. *Vision Research, 31*(9), 1619–1626.

de'Sperati, C. (1999). Saccades to mentally rotated targets. *Experimental Brain Research, 126*(4), 563–577.

de'Sperati, C. (2003b). Precise oculomotor correlates of visuospatial mental rotation and circular motion imagery. *Journal of Cognitive Neuroscience, 15*(8), 1244–1259.

de'Sperati, C. (2003a). The inner working of dynamic visuo-spatial imagery as revealed by spontaneous eye movements. In J. Hyona, R. Radach, & H. Deubel (Eds.). *The mind's eye. Cognitive and applied aspects of eye movements research*. Elsevier Science BV.

de'Sperati, C., & Baud Bovy, G. (2017). Low perceptual sensitivity to altered video speed in viewing a soccer match. *Scientific Reports, 7*(1), 15379.

de'Sperati, C., & Baud-Bovy, G. (2008). Blind saccades: An asynchrony between seeing and looking. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience, 28*(17), 4317–4321.

de'Sperati, C., & Deubel, H. (2006). Mental extrapolation of motion modulates responsiveness to visual stimuli. *Vision Research, 46*(16), 2593–2601.

de'Sperati, C., & Santandrea, E. (2005). Smooth pursuit-like eye movements during mental extrapolation of motion: The facilitatory effect of drowsiness. *Brain Research. Cognitive Brain Research, 25*(1), 328–338.

Fencsik, D. E., Klieger, S. B., & Horowitz, T. S. (2007). The role of location and motion information in the tracking and recovery of moving objects. *Perception & Psychophysics, 69*(4), 567–577.

Franconeri, S. L., Lin, J. Y., Pylyshyn, Z. W., Fisher, B., & Enns, J. T. (2008). Evidence against a speed limit in multiple-object tracking. *Psychonomic Bulletin & Review, 15*(4), 802–808.

Fu, Y. X., Shen, Y., & Dan, Y. (2001). Motion-induced perceptual extrapolation of blurred visual targets. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience, 21*(20), RC172.

Gegenfurtner, K. R., Mayser, H., & Sharpe, L. T. (1999). Seeing movement in the dark. *Nature, 398*(6727), 475–476.

Girshick, A. R., Landy, M. S., & Simoncelli, E. P. (2011). Cardinal rules: Visual orientation perception reflects knowledge of environmental statistics. *Nature Neuroscience, 14*(7), 926–932.

Giuliani, M., Martoni, R. M., Gregori Grgic, R., Crespi, S. A., Cavallini, M. C., & de'Sperati, C. (2017). Who has done it? Exploring gaze agency in obsessive-compulsive checkers. *Frontiers in Integrative Neuroscience, 11*, 39.

Goodale, M. A. (2011). Transforming vision into action. *Vision Research, 51*(13), 1567–1587.

Gregori Grgic, R., Calore, E., & de'Sperati, C. (2016). Covert enaction at work: Recording the continuous movements of visuospatial attention to visible or imagined targets by means of Steady-State Visual Evoked Potentials (SSVEPs). *Cortex, 74*, 31–52.

Gregori Grgic, R., Crespi, S. A., & de'Sperati, C. (2016). Assessing self-awareness through gaze agency. *PloS one, 11*(11), e0164682.

Gregori-Grgič, R., Balderi, M., & de'Sperati, C. (2011). Delayed perceptual awareness in rapid perceptual decisions. *PLoS One, 6*(2), e17079.

Hammett, S. T., Champion, R. A., Thompson, P. G., & Morland, A. B. (2007). Perceptual distortions of speed at low luminance: Evidence inconsistent with a Bayesian account of speed encoding. *Vision Research, 47*(4), 564–568.

Hassan, O., & Hammett, S. T. (2015). Perceptual biases are inconsistent with Bayesian encoding of speed in the human visual system. *Journal of Vision, 15*(2).

Heath, M., Colino, F. L., Chan, J., & Krigolson, O. E. (2018). Visuomotor mental rotation of a saccade: The contingent negative variation scales to the angle of rotation. *Vision Research, 143*, 82–88.

Hesse, C., & Deubel, H. (2010). Advance planning in sequential pick-and-place tasks. *Journal of Neurophysiology, 104*(1), 508–516.

Hesse, C., & Deubel, H. (2011). Efficient grasping requires attentional resources. *Vision Research, 51*(11), 1223–1231.

Hollingworth, H. L. (1910). Central tendency of judgment. *Journal of Philosophy, Psychology and Scientific Methods, 7*, 461.

Intriligator, J., & Cavanagh, P. (2001). The spatial resolution of visual attention. *Cognitive Psychology, 43*(3), 171–216.

Iordanescu, L., Grabowecky, M., & Suzuki, S. (2009). Demand-based dynamic distribution of attention and monitoring of velocities during multiple-object tracking. *Journal of Vision, 9*(4) 1 1-12.

Jacob, R. J. K. (1991). The use of eye movements in human-computer interaction techniques: What you look at is what you get. *ACM Transactions on Information Systems, 9*(3), 152–169.

Johannesson, O. I., Thornton, I. M., Smith, I. J., Chetverikov, A., & Kristjansson, A. (2016). Visual foraging with fingers and eye gaze. *i-Perception, 7*(2) 2041669516637279.

Jonikaitis, D., & Deubel, H. (2011). Independent allocation of attention to eye and hand targets in coordinated eye-hand movements. *Psychological Science, 22*(3), 339–347.

Jonikaitis, D., Deubel, H., & de'Sperati, C. (2009). Time gaps in mental imagery introduced by competing saccadic tasks. *Vision Research, 49*(17), 2164–2175.

Keane, B. P., & Pylyshyn, Z. W. (2006). Is motion extrapolation employed in multiple object tracking? Tracking as a low-level, non-predictive function. *Cognitive Psychology, 52*(4), 346–368.

Kleiner, M., Brainard, D., Pelli, D., Murray, R., & Broussard, C. (2007). What's new in psychtoolbox-3. *Perception, 36*(14), 1–16.

Kristjansson, A., Johannesson, O. I., & Thornton, I. M. (2014). Common attentional constraints in visual foraging. *PloS one, 9*(6), e100752.

Makin, A. D., & Bertamini, M. (2014). Do different types of dynamic extrapolation rely on the same mechanism? *Journal of Experimental Psychology: Human Perception and Performance, 40*(4), 1566–1579.

Makin, A. D., & Poliakoff, E. (2011). Do common systems control eye movements and motion extrapolation? *Quarterly Journal of Experimental Psychology (Hove), 64*(7), 1327–1343.

Makin, A. D., Stewart, A. J., & Poliakoff, E. (2009). Typical object velocity influences motion extrapolation. *Experimental Brain Research, 193*(1), 137–142.

Meyerhoff, H. S., Papenmeier, F., & Huff, M. (2013). Object-based integration of motion information during attentive tracking. *Perception, 42*(1), 119–121.

Pearson, J., Naselaris, T., Holmes, E. A., & Kosslyn, S. M. (2015). Mental imagery: Functional mechanisms and clinical applications. *Trends in Cognitive Sciences, 19*(10), 590–602.

Perrone, J. A. (2005). Economy of scale: A motion sensor with variable speed tuning. *Journal of Vision, 5*(1), 28–33.

Pisella, L., Binkofski, F., Lasek, K., Toni, I., & Rossetti, Y. (2006). No double-dissociation between optic ataxia and visual agnosia: Multiple sub-streams for multiple visuo-manual integrations. *Neuropsychologia, 44*(13), 2734–2748.

Pretto, P., Bresciani, J. P., Rainer, G., & Bulthoff, H. H. (2012). Foggy perception slows us down. *Elife, 1*, e00031.

Rossetti, Y. (1998). Implicit short-lived motor representations of space in brain damaged and healthy subjects. *Consciousness and Cognition, 7*(3), 520–558.

Rossi, F., Montanaro, E., & de'Sperati, C. (2018). Speed biases with real-life video clips. *Frontiers in Integrative Neuroscience, 12*, 11.

Senna, I., Parise, C. V., & Ernst, M. O. (2015). Hearing in slow-motion: Humans underestimate the speed of moving sounds. *Scientific Reports, 5*, 14054.

Shepard, R., & Cooper, L. (1986). *Mental images and their transformations.* MIT Press.

Simoncini, C., Perrinet, L. U., Montagnini, A., Mamassian, P., & Masson, G. S. (2012). More is not always better: Adaptive gain control explains dissociation between perception and action. *Nature Neuroscience, 15*(11), 1596–1603.

Snowden, R. J., Stimpson, N., & Ruddle, R. A. (1998). Speed perception fogs up as visibility drops. *Nature, 392*(6675), 450.

Spering, M., Kerzel, D., Braun, D. I., Hawken, M. J., & Gegenfurtner, K. R. (2005). Effects

of contrast on smooth pursuit eye movements. *Journal of Vision, 5*(5), 455–465.
Stocker, A. A., & Simoncelli, E. P. (2006). Noise characteristics and prior expectations in human visual speed perception. *Nature Neuroscience, 9*(4), 578–585.
Stone, L. S., & Thompson, P. (1992). Human speed perception is contrast dependent. *Vision Research, 32*(8), 1535–1549.
Thomas, N. J. T. (Ed.). (2018). *The Stanford encyclopedia of philosophy*(Spring 2018 ed.). Stanford Univ..
Thompson, P. (1982). Perceived rate of movement depends on contrast. *Vision Research, 22*(3), 377–380.
Thompson, P., Brooks, K., & Hammett, S. T. (2006). Speed can go up as well as down at low contrast: Implications for models of motion perception. *Vision Research, 46*(6–7), 782–786.
Thornton, I. M., Bulthoff, H. H., Horowitz, T. S., Rynning, A., & Lee, S. W. (2014). Interactive multiple object tracking (iMOT). *PloS one, 9*(2), e86974.
VanRullen, R. (2007). The power of the feed-forward sweep. *Advances in Cognitive Psychology, 3*(1–2), 167–176.
Vintch, B., & Gardner, J. L. (2014). Cortical correlates of human motion perception biases. *Journal of Neuroscience, 34*(7), 2592–2604.
Weiss, Y., Simoncelli, E. P., & Adelson, E. H. (2002). Motion illusions as optimal percepts. *Nature Neuroscience, 5*(6), 598–604.
Zimmermann, E., Morrone, M. C., & Burr, D. (2012). Visual motion distorts visual and motor space. *Journal of Vision, 12*(2).
Zuliani, E., Caputi, M., Scaini, S., & de'Sperati, C. (in press). Videos look faster as children grow up: sense of speed and impulsivity throughout primary school. *Journal of Experimental Child Psychology*.