

Like a rolling stone: Naturalistic visual kinematics facilitate tracking eye movements

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Newtonian physics constrains object kinematics in the real world. We asked whether eye movements towards tracked objects depend on their compliance with those constraints. In particular, the force of gravity constrains round objects to roll on the ground with a particular rotational and translational motion. We measured tracking eye movements towards rolling objects. We found that objects with rotational and translational motion that was congruent with an object rolling on the ground elicited faster tracking eye movements during pursuit initiation than incongruent stimuli. Relative to a condition without rotational component, we essentially obtained benefits of congruence, and, to a lesser extent, costs from incongruence. Anticipatory pursuit responses showed no congruence effect, suggesting that the effect is based on visually-driven predictions, not on velocity storage. We suggest that the eye movement system incorporates information about object kinematics acquired by a lifetime of experience with visual stimuli obeying the laws of Newtonian physics.

Introduction

The kinematics of objects that we see in the world is constrained by the laws of Newtonian physics. As a consequence, although the kinematics of the virtual objects that we typically use in laboratory settings to study perception can be infinitely varied, the kinematics of physical objects is constrained by those laws, limiting the types of motion that we experience. For instance, car wheels most often adhere to the ground and rotate clockwise relative to the observer when the car is moving rightward. It would be very unlikely to see the wheel rotating counterclockwise and moving rightward without decelerating rapidly—at least for rotation speeds at which the wagon wheel illusion is not experienced (Purves, Paydarfar, & Andrews, 1996).

Yet, we know little about the extent to which visual and motor systems use this type of knowledge about physics in the real world to control action. We used wheels as stimuli because there is no special status attached to them. Observers may have stronger expectations about the behavior of agents (Schutz-Bosbach & Prinz, 2007), such as point-light-walkers, than about inanimate objects, such as wheels. For the latter, however, testing the effect of congruence with known physical constraints appears more straightforward. For instance, an inverted point-light walker defies physical rules, while having equivalent motion energy. But in that case both object processing and the obedience with known physical rules are changed. The inverted stimulus will have a less familiar shape, its motion will appear to be less coherent, and its kinematics will be incongruent with the direction of the force of gravity. Unlike a point-light walker, a rotating wheel has no canonical orientation and equal motion energy in any direction. When we change the rotation direction of a wheel, it is just the congruence with the way objects roll on the ground that changes. Predictions regarding biological motion are also arguably more complex: Although physical constraints *are* relevant to both agents and inanimate objects, we need to incorporate knowledge about intentionality and body dynamics to predict the behavior of agents.

The visuo-motor loop responsible to match the speed and position of our eyes to that of the object of interest can be made more efficient by incorporating predictions about the target kinematics, thus partially compensating for sensori-motor delays (Kerzel & Gegenfurtner, 2003). We hypothesized that the knowledge acquired about the behavior of objects in the physical world is factored in when programming eye movements, as it provides a supplementary source of information about the target trajectory. Prior information can not only be used to give a head start to the

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oculomotor system, allowing anticipatory responses (Barnes, 2008), but also improve on a noisy sensory signal (Weiss, Simoncelli, & Adelson, 2002).

In the context of pursuit eye movements, we know that several target parameters can be anticipated based on past trials, such as onset time, speed and direction of movement (Barnes, 2008). A lifetime of experience with the kinematics of physical objects is also likely to generate predictions about their trajectory. To our knowledge, evidence of this type is restricted to the use of Newton's law of gravity to time interception of free-falling objects (McIntyre, Zago, Berthoz, & Lacquaniti, 2001; Zago, McIntyre, Senot, & Lacquaniti, 2008). To test this idea we used a task in which rotation of the stimulus (as in the car example) is either congruent or incongruent with its translation along the horizontal axis. In this case, gravity has no influence on the horizontal component, but on the combination of rotation direction and translation direction. We show that congruence with physical laws is sufficient to generate predictions that will improve smooth pursuit eye movements, even though a constant speed of translation is always shown.

Material and methods

Stimuli were displayed on a NEC MultiSync CRT screen (1280 × 1024 pixels at 85 Hz) at 66 cm from the observer, whose head was held by a chin and front rest. The right eye position was tracked by an Eyelink 1000 (SR Research Ltd, Kanata, Ontario, Canada). We used the Psychophysics toolbox (Brainard, 1997) in MATLAB (version R2010a, The Mathworks Inc., Natick, MA) to generate the visual stimulation. There were ten to 16 participants in each experiment. They were all students of the University of Geneva (18 to 37 years old), who received course credit for participation. Participants gave informed consent to participate but were naïve regarding the purpose of the experiments. The experiments were carried out in accord with the declaration of Helsinki and were approved by the Ethics Committee of the *Faculté de Psychologie et des Sciences de l'Éducation*.

The analysis of eye movements was based on horizontal and vertical velocity. The position signal was filtered by a low-pass Butterworth second-order filter; with a cutoff frequency of 50 Hz. Velocity was derived by using a two-point central difference method with a 20 ms step-size (Bahill, Kallman, & Lieberman, 1982; Bahill & McDonald, 1983a). The velocity signal was linearly interpolated during a saccadic episode (see Coppe, de Xivry, Missal, & Lefevre, 2010). For detecting saccadic episodes we used the Eyelink 1000 algorithm (acceleration threshold: $5000^\circ/\text{s}^2$, velocity

threshold: $22^\circ/\text{s}$). We subtracted 25 ms from onset estimates and added 40 ms to offset estimates, in order to remove glissadic components after a saccade that could be missed by the algorithm. To make sure that the main results (the effect of congruence) were not due to the interpolation procedure, we also ran the statistics on average de-saccaded traces. Statistical significance was confirmed in the same conditions as with interpolated data, although de-saccaded averages are necessarily noisier.

To obtain estimates of pursuit latency (when using a step-ramp in the experiment testing “costs and benefits”) we used a semi-automatic algorithm (Adler, Bala, & Krauzlis, 2002). We set onsets manually and then fitted a piecewise linear function to the velocity trace. The location of the hinge of the best-fitting function (in the least-squares sense) gives the onset within -20 to 20 ms around a manually set marker. We excluded latencies shorter than 60 ms, likely to be anticipations, and latencies longer than 500 ms.

We applied several selection criteria to improve the quality of the data. Trials were excluded if a blink was found from -100 to 600 ms relative to target motion onset; if root mean square (RMS) of vertical velocity from 80 to 600 ms exceeded RMS of vertical velocity from -100 to 80 ms by three standard deviations; if a saccade was detected from -100 to 80 ms. Finally, visual inspection ensured that no other artifact was present in the velocity traces. Trials were rejected most often due to blinks during the analysis interval and small saccades made around motion onset. Participant were only included when less than 50% of trials were rejected in any condition. Across experiments, after applying those criteria, about 25% (individually 2–42%) of trials were removed. At most 3% (individually 0–8%) of trials were removed after visual inspection in each experiment.

Effect of congruence and speed

We asked participants to track two types of discs that rotated and translated in the horizontal direction: either congruent with an object rolling on the ground without slipping or incongruent with this interpretation. The aim of the first experiment was to test for the existence of an effect of congruence during smooth pursuit initiation.

At the start of the trial, a stationary red dot (0.3°) and a random-dot disk was shown at the centre of the screen for 500 ms (Figure 1b). The disk was composed of 100 randomly positioned dots within a radius of 3° , moving either leftward or rightward with a translational speed v_t of 13.25 or $26.5^\circ/\text{s}$. The stimulus started to translate and rotate simultaneously. In the congruent condition, the rotational speed ω of the disk

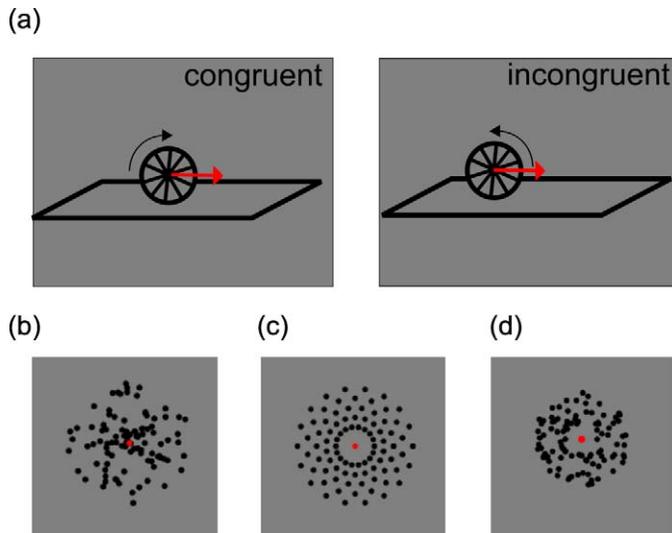


Figure 1. (a) Illustration of the congruent and incongruent condition. Lower panels (b–d) show a static slice of the different stimuli that we used. The task was to track the red dot, and to ignore the surrounding dots’ motion.

approximates the kinematics of a sphere that rolls on the ground without slipping, with constant velocity, meaning that rotational speed ω was obtained by $\omega = v_t/(2\pi r)$, r being the radius of the notional disk. ω was 0.7 and 1.41 c/s for the slow and fast translation speed respectively. In the *congruent condition*, the rotational and linear translation component indicated the same direction as for an object rolling on the ground—ignoring other forces—as shown in Figure 1a. It could also be interpreted as an object rotating in mid-air, i.e., as a tennis ball to which a *topspin* (or forward spin) is imparted by the player. However, observers report a compelling percept of a ball rolling on a surface.

In the *incongruent* condition the rotation was incompatible with the interpretation of an object rolling on the ground without slipping. It could be perceived as an object rotating on a slippery surface, as an object rolling against an upper surface without slipping (a ceiling), or as an object rotating in mid-air. An important point is that, in any case, those interpretations defy the laws of mechanics. If they were to be taken as objects in the real world, the object should either decelerate (due to friction in the first case) or fall (last two cases) due to the force of gravity. When asked to choose between alternative interpretations, observers reported most often the second: “an object rotating in mid-air.”

We started each session by a 5-point calibration of the eyetracker, followed by 10 training trials and then four experimental blocks (2 congruence \times 2 speed) of 80 trials. The stimulus direction of translation was randomized. Block order was balanced across participants using a 2×2 Latin square design. The

instruction was to track the red spot as precisely as possible (Figure 1b) while ignoring the surrounding dots. Trials were self-paced, by pressing a key on a gamepad. At the end, observers completed a questionnaire regarding stimulus interpretation in congruent and incongruent conditions.

For data analysis, leftward and rightward trials were pooled together, after inverting the sign of horizontal eye velocity in leftward trials.

Effect of congruence and blocking

To know whether subject expectations play a role in effects of congruence, we tested the effect of blocking versus interleaving congruent and incongruent trials. If the congruence effect was due to participants’ strategic behavior or to expectations based on previous trials, it should be reduced or absent with interleaved presentations, when stimulus congruence of the next stimulus is unpredictable. The interleaved and blocked versions were tested in two different groups of participants. Also, we used a stimulus resembling a wheel, which might afford a stronger impression of rolling on a ground surface (see Figure 1c). Points were uniformly spaced to form a 2° disk, with a dot-free zone (0.6° radius) around the target to make it easier to ignore the surrounding dots.

Costs or benefits of congruence

In the previous experiments, we were unable to distinguish whether incongruence (backspin) interferes with tracking or if it is rather the case that congruence has a beneficial effect on tracking. For this reason we ran an experiment in which performance was compared to a baseline condition without object rotation ($\omega = 0$; cf. [Supplementary Video](#)). Additionally, we had an *incoherent* condition, in which half of the dots rotated in a congruent direction and half in an incongruent direction. The purpose of this condition was to show a stimulus that equated the rotating speed of individual dots in either congruent or incongruent stimuli, but that did not appear as a “coherent” object—rather as two superimposed surfaces. We expected this condition to yield similar results as the “no rotation condition” while controlling for local motion in the stimulus.

Further, we used a step-ramp paradigm (Rashbass, 1961). With this paradigm, the target steps to one side before reversing direction. This way pursuit is often initiated before a saccade is made to catch-up with the target, allowing us to calculate pursuit latency. The target jumped by 1.8° to one side before moving in the opposite direction, such that the target went past the initial fixation point 140 ms later. The stimulus was a

disk composed of 100 dots, with an empty zone around the target dot of 0.67° radius and an outer radius of 2° (Figure 1d), which allowed us to have an incoherent condition in addition to a congruent and incongruent condition.

The procedure was similar to the other experiments. The four conditions were interleaved within a block. There were 120 trials per condition.

Anticipation of congruent versus incongruent trials

In a last experiment, we tested if anticipatory responses show a congruence effect. Pursuit can be driven by a memory-based signal (velocity storage) (Barnes, 2008). We wanted to know if this signal, rather than a visually-based response, is responsible for the effect of congruence. To generate anticipatory smooth pursuit, we replicated the procedure of the other experiments (with Figure 1d stimulus), but showed a target that was always translating rightward. In that situation a strong anticipatory response is generated after a few trials (e.g., Kao & Morrow, 1994).

Results and discussion

Effect of congruence and speed

Figure 2a–c shows average horizontal velocity ($N = 10$) in congruent and incongruent conditions, with two different target speeds. The slower target speed ($13.25^\circ/s$) yields a congruence effect at around 100 to 300 ms after target motion onset: Over this period congruent stimuli are tracked with a higher gain (ratio of eye velocity to target velocity) than incongruent ones (Figure 2a, b). The highest speed ($26.5^\circ/s$) yields virtually no difference between conditions (Figure 2c). Based on significant (uncorrected) two-tailed t tests, the congruence effect concerned only the slow speed, mainly for a time-window running from 140 to 290 ms after onset of target motion, $t(9) = 3.1$, $p = 0.012$, $d_z = 0.98$.¹ In this interval, pursuit gain was 0.80 in the incongruent condition and of 0.85 in the congruent condition (0.60 in both conditions for the high speed). The t tests indicate a second smaller time-frame from 414 to 443 ms, which is not reliably found in subsequent experiments.

The latency of the first saccade after target motion onset was analyzed to know whether the saccadic system contributes, or even explains entirely, the congruency effect. A catch-up saccade was systematically triggered at the beginning of tracking. It could

therefore be that a delay in saccade latency was responsible for the effects observed on velocity traces, because we interpolated velocity across saccades. However, with the slow speed, the difference in saccade latency was not statistically significant (congruent: 189 ms, incongruent: 191 ms), $t(9) = 0.48$, $p = 0.643$, $d_z = 0.15$. Latencies were also very similar with the high speed (171 and 172 ms, respectively).

To sum up, we found a congruence effect at the beginning of closed-loop pursuit initiation, but limited to the lower target speed. The higher target speed of $26.5^\circ/s$ was far from the stimulus velocity at which smooth pursuit responses saturate—about $90^\circ/s$ (Meyer, Lasker, & Robinson, 1985)—but it nonetheless abolished the congruence effect. Although it is unclear why, it can be noted in Figure 2b–c that subjects never reached the same steady-state pursuit gain that was reached with the lower speed. Thus, the absence of a steady-state tracking phase may have abolished the effect. Another interpretation is that information about the real rotation direction is less reliable with this rotation speed, due to ‘aliasing’ in the visual system (Purves et al., 1996). We did not follow up on this issue and used only the slow target speed in the following experiments.

Effect of congruence and blocking

In further experiments we compared the gain during the temporal interval defined in the first experiment: 140 to 290 post motion onset.

As shown in Figure 3, blocked and interleaved presentations led to higher gains in the congruent condition compared to the incongruent condition [blocked: 0.86 vs. 0.81, $t(15) = 2.71$, $p = 0.016$, $d_z = 1.07$; interleaved: 0.83 vs. 0.79; $t(13) = 2.75$, $p = 0.017$, $d_z = 1.18$]. In the blocked version, latency was significantly longer in the incongruent compared to the congruent condition (207 vs. 200 ms, respectively), $t(15) = 3.1$, $p = 0.007$, $d_z = 0.77$, but not in the interleaved version (200 and 202 ms), $p = 0.446$, $d_z = 0.21$.

An analysis of variance with presentation type as between-subject factor and congruence as within-subject factor confirmed a significant effect of congruence on gain, $F(1, 28) = 14.52$, $p < 0.001$, $\eta^2 = 0.34$, but no significant effect of presentation type (blocked vs. interleaved) or interaction between presentation type and congruence, $p = 0.992$. Hence, predictability of the next stimulus is not a necessary condition for finding an effect of congruence, nor does it significantly modulate this effect. Therefore, the effect of congruence is likely not due to the anticipation of certain kinematics on the next trial. More likely, it reflects visually-based mechanisms.

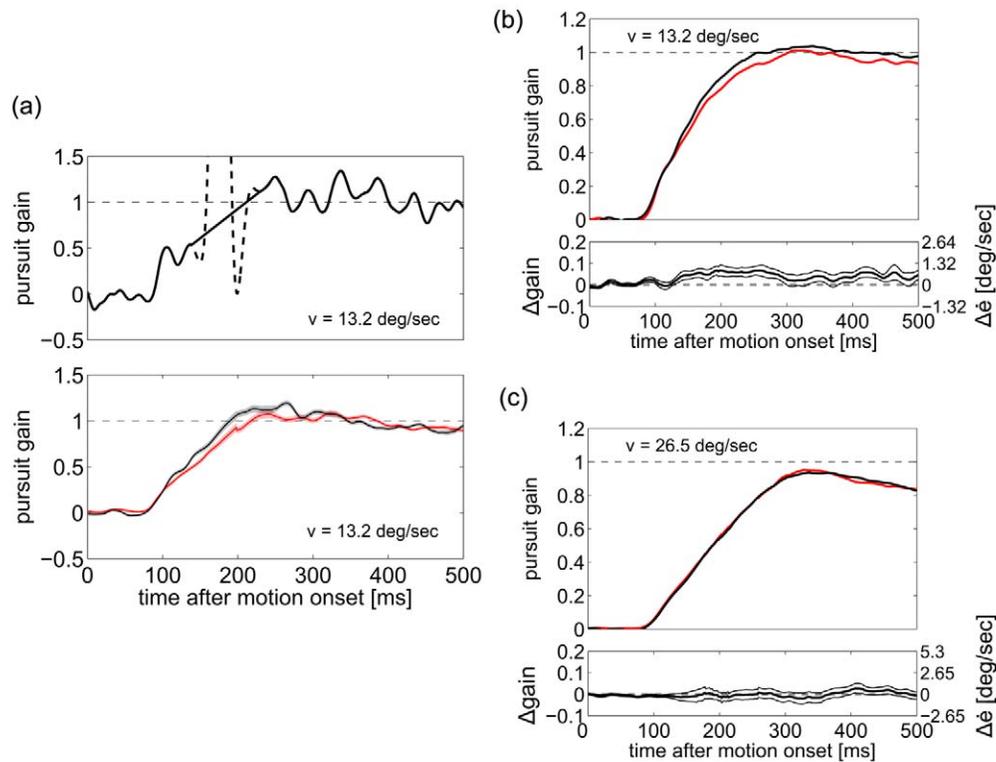


Figure 2. Results from Experiment 1. (a) The upper panel shows horizontal pursuit gain (eye velocity/target velocity) in a typical trial with a saccade occurring after about 150 ms. In our analysis, saccades were removed and the data were interpolated. The original trace is indicated by a dashed line. The lower panel shows a sample subject's average (interpolated data) in incongruent (red) and congruent (black) conditions. (b, c) Shows the average across observers ($N = 10$) for (b) low speed and (c) high speed targets. The lower panels show the difference in average gain (Δgain) and velocity ($\Delta\dot{e}$) between congruent and incongruent conditions (congruent minus incongruent; thick lines) across subjects. The thin lines in the lower panels of (b, c) represent the between-subjects \pm standard error of the mean. The shaded areas in (a) represent \pm standard error of the mean across trials.

The first catch-up saccade was significantly delayed by 7 ms in the incongruent compared to the congruent condition with blocked presentation, but not with interleaved presentation. However, there was no effect of congruence in the first experiment where presentation was also blocked. Therefore, we refrain from drawing any strong conclusions from the observed latency difference.

Costs and benefits (step-ramp)

In the congruent condition pursuit was faster than in the no rotation condition during pursuit initiation—about 100 to 250 ms post target motion onset. We asked whether this difference was due to a benefit of congruence over a simple translation condition, to costs due to incongruence, or both.

We compared gain in incongruent and congruent conditions (see Figure 4a, c) within the aforementioned temporal window (140 to 290 ms) and observed a similar effect as in previous experiments using a ramp

paradigm (Figure 3, “Exp. 4: Step-ramp”). Most relevant is the comparison with the no rotation condition, as we wanted to know which condition led to a benefit or a cost. Only the congruent condition led to a significantly higher gain compared to the no rotation condition (0.78 vs. 0.72), $t(14) = 3.89$, $p < 0.001$, $d_z = 1.00$. In contrast, gain was very similar in no rotation and incongruent conditions over the same time-window (0.71 vs. 0.72), $t(14) = 0.48$, $p = 0.637$, $d_z = 0.12$, indicating no costs of incongruence. Further, the gain in the congruent condition was not significantly different from the gain in the incoherent condition (0.78 vs. 0.76), $t(14) = 0.79$, $p = 0.442$, $d_z = 0.20$.

With the step-ramp paradigm smooth pursuit onset becomes a better indicator of the latency of the tracking response than the first saccade. As with catch-up saccade latency in previous experiments, there was very little difference in pursuit latency between incongruent and congruent conditions (101 vs. 103 ms), and both conditions led to only slightly faster pursuit latencies compared to the no rotation condition (107 ms). A one-way ANOVA showed a significant effect of condition on pursuit latency, $F(3, 42) = 3.93$, $p = 0.015$, $\eta^2 = 0.41$.

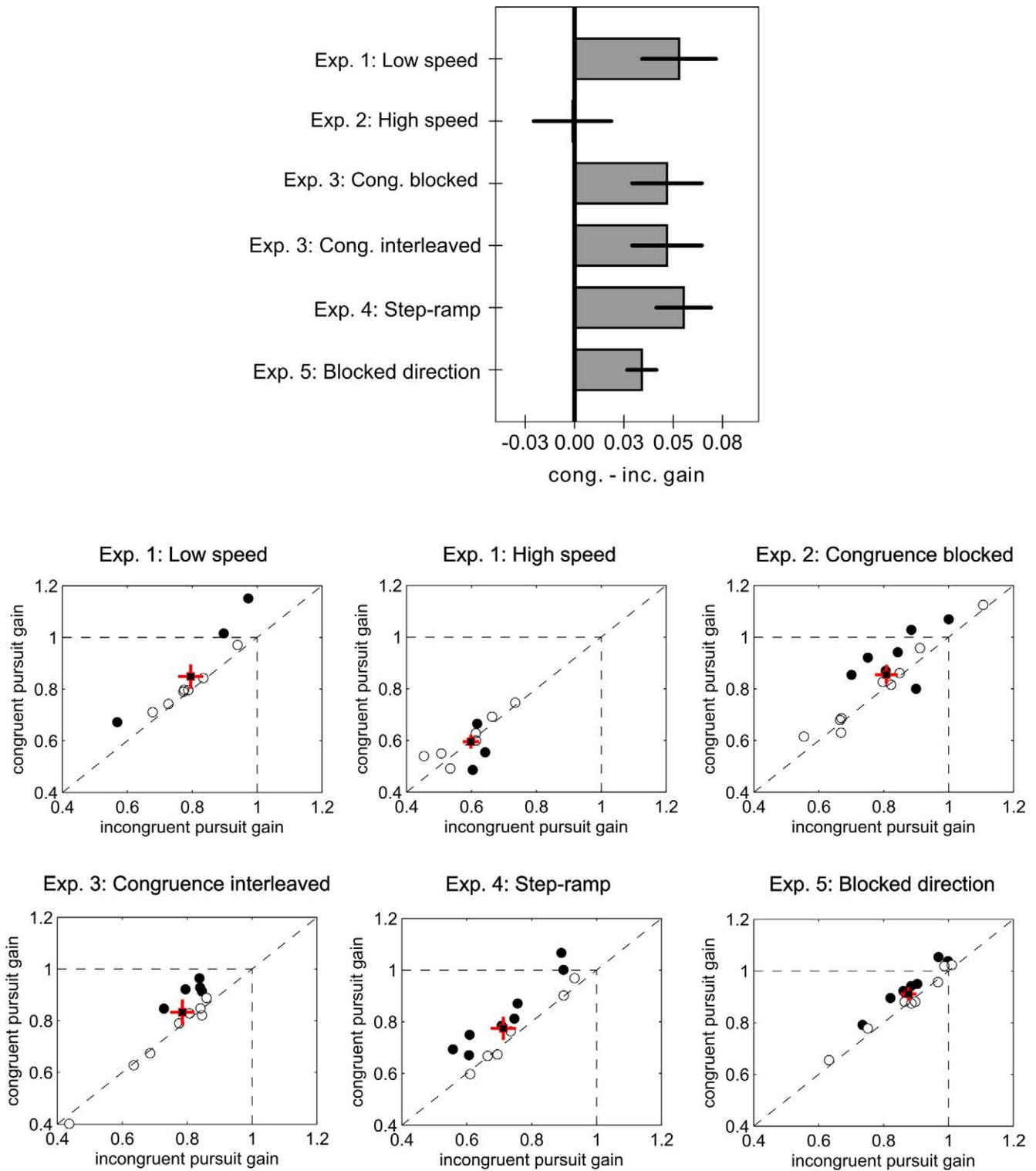


Figure 3. Effects of congruence in all experiments over the same averaging interval, i.e., 140 to 290 ms after target motion onset. The first panel shows the average congruence effect across subjects (congruent – incongruent pursuit gain), while the bottom panels show individual data. Filled dots indicate statistical significance ($p < 0.05$) of the congruence effect for a given individual (two-tailed t tests). The error bars represent between-subjects \pm standard error of the mean.

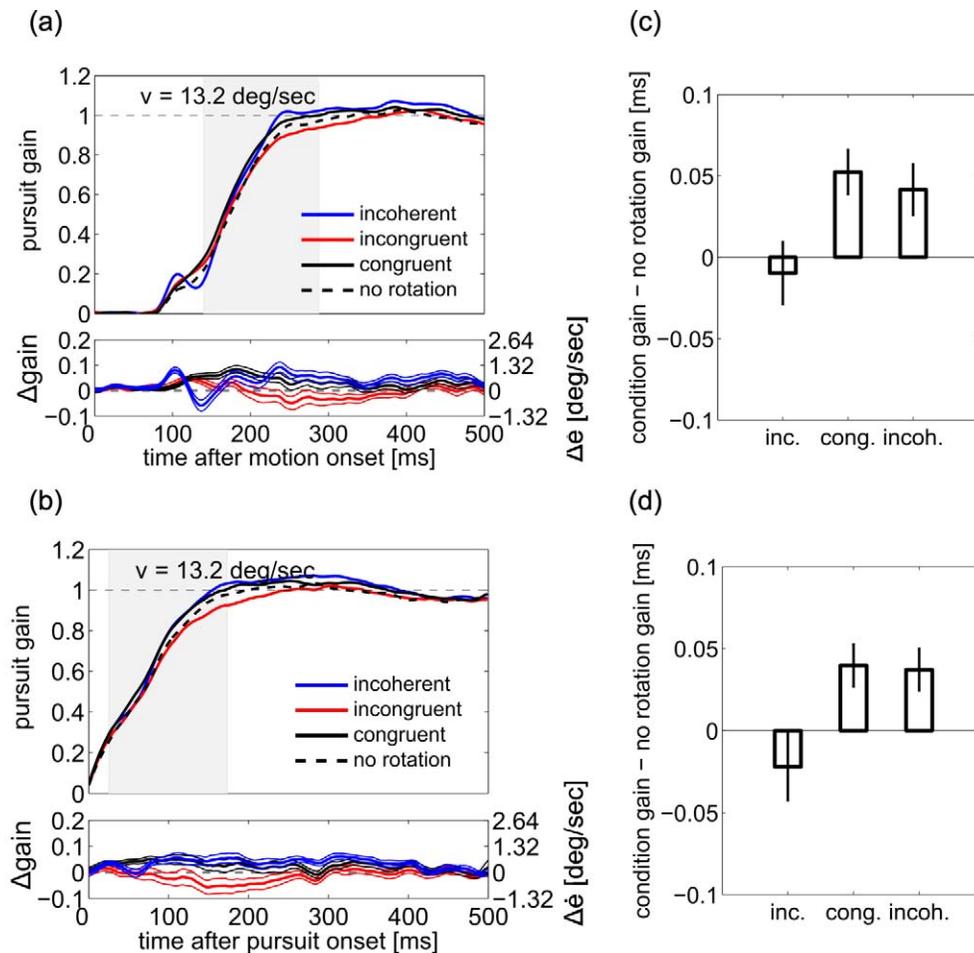


Figure 4. Results from Experiment 4. (a) The upper panel shows pursuit gain, and the lower panel shows the difference between the no rotation condition and the incongruent (red), congruent (black), and incoherent (blue) conditions. The data were locked to the onset of stimulus motion. (b) As in (a), but the data were locked to pursuit onset. (c) Difference between no-rotation condition and incongruent, congruent, and incoherent condition (inc., cong., and incoh., respectively) in a time-window indicated by the shaded area in (a); (d) As in (c), but the data were locked to pursuit onset.

Multiple comparisons, after applying the Bonferroni correction, showed that latencies in congruent and incongruent conditions were significantly shorter compared to no rotation condition (5 and 4 ms), $t(14) = 3.19$, corrected- $p < 0.018$, $d_z = 0.82$; $t(14) = 2.97$, corrected- $p = 0.030$, $d_z = 0.84$.

Earlier studies have distinguished different phases during open-loop pursuit initiation: a 0–20 ms period and a 20–80 ms period post pursuit onset (Tychsen & Lisberger, 1986). In the first period the response is independent of stimulus velocity, but scales with velocity during the later period. To examine at which period the congruence effect takes place, the analysis needs to be locked to pursuit onset. Traces locked to pursuit onset show a similar pattern as traces locked to motion onset (see Figure 4b, d). The close alignment of the different traces during the first 40 ms indicates that the differences in traces locked to motion onset are not due to a delay to respond to the target but to an

enhanced response in the congruent condition. We ran statistics on the same averaging interval as for data locked to motion onset, but subtracted the average pursuit onset. Thus, the time-window became 31 to 180 ms post pursuit onset. Congruent stimuli led to 9% higher gain compared to incongruent stimuli (0.72 vs. 0.66), $t(14) = 3.99$, corrected- $p = 0.004$, $d_z = 1.05$ (see Figure 4b). Both the congruent, $t(14) = 3.09$, corrected- $p = 0.032$, $d_z = 0.81$, and incoherent condition (0.72), $t(14) = 2.93$, corrected- $p = 0.044$, $d_z = 0.78$, led to significantly higher gains compared to the no rotation condition (0.68), consistent with the analysis locked to motion onset.

The data shows an unexpected feature in the incoherent condition. The Figure 4a (blue line) shows a systematic double inflexion at the start of the response. The inflexion is less clearly found on traces locked to pursuit onset. We have no good explanation for this

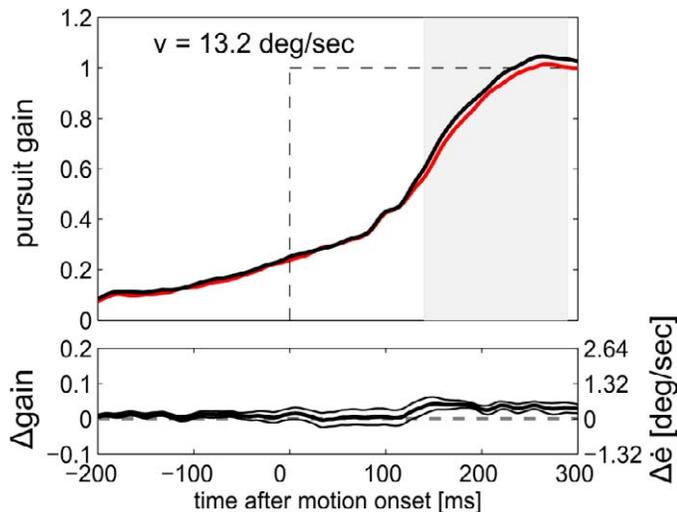


Figure 5. Pursuit gain for incongruent (red) and congruent (black) conditions in Experiment 5, with blocked motion direction. Same graphical conventions as in Figure 2b, c.

double-inflexion, except that it might reflect the ambiguity of the incoherent target.

Further, the incoherent target yielded about the same gain as in the congruent condition in the usual time window. Because we did not believe the stimulus to be either congruent or incongruent, we were expecting an intermediate effect. The results might indicate that observers paid attention to the layers that are most congruent with the behavior of the ball. Given the tracking direction, it seems plausible that after pursuit initiation, observers selected the layer of dots that was most congruent. In an analogue fashion, the depth ordering of two layers of moving dots is shown to depend on which layer is pursued, after being initially independent (Schütz, 2011).

To sum up, this experiment shows an enhancement of pursuit gain during initiation in the congruent condition, relative to no rotation and incongruent conditions. The incoherent stimulus elicited similar responses as the congruent condition, which could indicate a prevalence of the congruent component after movement initiation.

Anticipatory pursuit and congruence

In the last experiment, stimulus direction was blocked. Because we were interested in anticipatory responses, the analysis interval was extended from -300 ms to 600 ms, relative to target motion onset. Small saccades were often made in the direction of the anticipated movement direction, although the anticipatory response was typically characterized by a smooth pursuit eye movement of a smaller acceleration

than the initial visually-driven response (Kao & Morrow, 1994), as shown in Figure 5. Therefore, unlike in previous experiments, we accepted traces with saccades around the time of stimulus motion onset if their amplitude was less than 1° . Overall, 15.6% of trials were found to be invalid (2–34% per subject), less than 1% after visual inspection (0–11% per subject).

For comparison with previous experiments, eye velocity is divided by $13.25^\circ/\text{s}$, even before the target starts to move (Figure 5). Pursuit gain (visually-driven) was higher by only 3% in the congruent condition (0.91) compared to the incongruent condition (0.88) during the aforementioned time-window (140 to 290 ms), but significantly so, $t(16) = 4.88$, $p < 0.001$, $d_z = 1.18$. The latency of the first catch-up saccade was of 234 ms in the incongruent condition and of 238 in the congruent condition, but this difference did not reach significance, $p = 0.17$, $d_z = 0.34$. Saccade latencies were necessarily longer than in previous experiments due to the large anticipatory component.

It is apparent in Figure 5 that the anticipatory response is very similar in the incongruent and congruent condition and only deviates during the visually-driven period. Average gain for the -200 to 0 ms time-window was of 0.15 and 0.16, respectively, $p = 0.19$, $d_z = 0.34$.

The results suggest that velocity storage (Barnes, Grealy, & Collins, 1997) does not cause the effect of congruence but that it depends on the availability of visual information. The possibility remains that memory-driven eye movements of a higher velocity would generate a compatibility effect, such as the memory-driven responses that can be generated by making the target disappear during maintained pursuit.

In all other experiments, congruence had the effect of reducing the velocity error (gain was nearer to 1 in the congruent condition). However, with blocked motion direction, the velocity error is sometimes larger, due to a slight overshoot in the congruent condition at the beginning of maintained pursuit at around 200 ms after motion onset (cf. Figure 5), perhaps due to the addition of the anticipatory component.

Finally, we asked whether the congruence effect is the same at the beginning and at the end of the experimental session by comparing the first 20 trials to the last 20 trials of each condition. This question is of special interest in this experiment because anticipation builds up across time. An ANOVA (congruence by trial bin) replicated the effect of congruence, $F(1, 16) = 20.29$, $p < 0.001$, $\eta^2 = 0.56$. Pursuit gain was larger at the end than at the beginning of the session (0.83 vs. 0.92), $F(1, 16) = 15.07$, $p < 0.001$, $\eta^2 = 0.48$. Most interestingly, an interaction between trial bin and congruence occurred, $F(1, 16) = 10.39$, $p = 0.004$, $\eta^2 = 0.39$, indicating that the effect of congruence was larger at the beginning (incongruent: 0.77, congruent: 0.88)

than at the end (incongruent: 0.82; congruent: 0.83) of the experimental session. This analysis supports the idea that the congruence effect is not memory driven, as it tends to vanish when anticipation builds up.

We ran the same analysis on the other experiments, but failed to find a significant interaction between trial bin and congruence in any of them.

General discussion

We have shown in several experiments that congruence between object motion and prior knowledge of the behavior of physical objects can enhance tracking, even when this information is not useful in the laboratory task. In most experiments, congruence had the effect of reducing the velocity error. Across experiments, we observed a relatively small but robust increase (at the group level) in gain of about 5% during pursuit initiation. This effect appears to be visually-driven, since it is absent from purely anticipatory responses and is equally present in blocked and interleaved conditions. We can also say that it is essentially due to a higher smooth pursuit gain in congruent conditions compared to a simple translation condition.

We also showed that with a higher target speed the congruency effect vanished. Perhaps at higher rotation speeds the visual system has learned to “distrust” the perceived rotation direction, due to ‘aliasing’ in the visual system, as shown with the wagon wheel illusion in reality and in movies (Purves et al., 1996).

Significant enhancements of tracking were observed in a congruent condition relative to a “pure” translation condition, but no significant decrements in the incongruent condition. We may therefore conclude that the effect of congruence is essentially a positive one and not, or not only, the result of a predicted slowing due to the backspin—e.g., imparting a backspin to a billiard ball will slow down its movement.

Mechanisms

The congruence-effect was absent from anticipatory eye movements, suggesting that it is a visually driven effect. It is also mostly confined to the initiation of the steady-state phase of pursuit, but does not occur in the very first visually-driven response, as shown by small effects on pursuit latency and the first catch-up saccade latency. A related dissociation between anticipatory pursuit, and object motion was shown by anticipatory responses to slanted diamonds. The initial eye movement is perpendicular to the image contour (normal vector) and only subsequently directed towards the true direction of object motion. However, anticipatory

pursuit, which is generated when the direction of motion is made predictable, follows the true direction of object motion (Montagnini, Spering, & Masson, 2006).

In the context of smooth pursuit eye movements, some authors proposed that long-term implicit learning could also improve pursuit of some classes of stimuli (Bahill & McDonald, 1983b). For instance, extensive experience with tracking sinusoidal motion could improve tracking specifically for sinusoids by improving the predictive signal. In the model of Bahill and McDonald (1983b), this knowledge takes the form of a “target-selective adaptive controller” which adapts the default prediction about the target trajectory. This controller can also generate an initial estimate of the target trajectory, which can be done in different ways, one of them being to select from a database of learned trajectories according to contextual cues. Our experiments might then suggest that we incidentally learn to track a special kind of visual stimulus in its natural environment and that this pervades into artificial situations in the laboratory. This notion is in accord with evidence that the visual system can use prior information to improve on a noisy measurement of velocity or position, by combining independent sources of information (Soechting, Juveli, & Rao, 2009; Soechting, Rao, & Juveli, 2010; Tassinari, Hudson, & Landy, 2006).

An alternative to stimulus-specific sensori-motor learning is the idea that we possess implicit knowledge about what constrains the trajectory of physical stimuli: the *internalization* of classical mechanical laws (McIntyre et al., 2001; Zago et al., 2008). In this vein, recent studies have shown that complex acceleration patterns that are generated by objects sliding on a slanted surface can be learned to generate adaptive interceptive action (de Rugy, Marinovic, & Wallis, 2012). It is important in the context of our study that even objects which appear to be virtual are expected to behave according to rules of the physical world, such as those imposed by gravity (Baures, Benguigui, Amorim, & Hecht, 2009; Samuel & Kerzel, 2011; Zago et al., 2004). This finding could as well reflect reliance on prior information in combination with actual measurements to generate the best possible prediction of target kinematics (Weiss et al., 2002; Zago et al., 2004).

Recent research has underscored the importance of internal models in sensorimotor learning and adaptation (Kawato, 1999; Wolpert, Diedrichsen, & Flanagan, 2011). It has been proposed that we use a forward model to generate accurate saccades (Chen-Harris, Joiner, Ethier, Zee, & Shadmehr, 2008). Forward models would predict the sensory consequences of an eye movement as well as the eye state from the actual state of the eye and the motor command (Wolpert,

Ghahramani, & Jordan, 1995). Such predictive signals may also be used during pursuit to allow accurate pursuit across blanks or to drive adaptation to the artificial introduction of position errors (Schütz & Souto, 2011). The forward model may incorporate knowledge about object kinematics in order to generate accurate predictions of the target position during the eye movement. When object kinematics is consistent with prior experience, those predictions may have caused the benefit induced by congruence.

On the other hand, we cannot exclude an explanation of the congruence effect based on a very crude model of object kinematics. It is plausible that through experience a given rotation direction becomes associated with linear motion in a given direction, facilitating pursuit in congruent conditions. Facilitation in that case could arise after the repeated co-activation of rotation sensitive cells (Lagae, Maes, Raiguel, Xiao, & Orban, 1994; Orban et al., 1992) and translation-sensitive cells that drive pursuit. Rotation sensitive cells that appear to be implicated in self-motion perception from optic flow can be found in MST (Orban et al., 1992), which also furnishes motion information to the pursuit system (Komatsu & Wurtz, 1989; Pack, Grossberg, & Mingolla, 2001). Moreover, successful parsing of optic flow requires that eye movements are taken into account (Shenoy, Crowell, & Andersen, 2002). However, if background rotation may be important for the estimation of heading or self-motion, target rotation is not and therefore may be processed in a very different way.

Finally, congruence effects were observed at the group level. Only a fraction of individuals showed a significant effect, which could be due to the lack of context specifying the environment in which objects behave. Further studies are needed to know whether this effect is relevant to real-life situations, by testing tracking, for instance, in dynamic, realistic 3D scenes, where multiple cues indicate congruence or incongruence with physical laws.

Conclusion

We showed that pursuit initiation is not only determined by sensory motion information, but that it is influenced by the congruence of target behavior with ecological stimulation. Congruent stimulation speeds up pursuit initiation, perhaps because an internal model of target kinematics overrides the actual input (Zago et al., 2004). Pursuit initiation therefore reflects not only a response to a visual signal, but also the prior information acquired about object kinematics outside the lab.

Keywords: visual kinematics, smooth pursuit, internal model, prediction, catch-up saccade

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Footnote

¹ We report two different measures of effect size, facilitating the comparison of effects across experiments: d_z for paired t tests (table 3, Faul, Erdfelder, Lang, & Buchner, 2007), and partial eta-square (η^2) for F tests resulting from an analysis of variance, obtained with IBM SPSS 19.

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