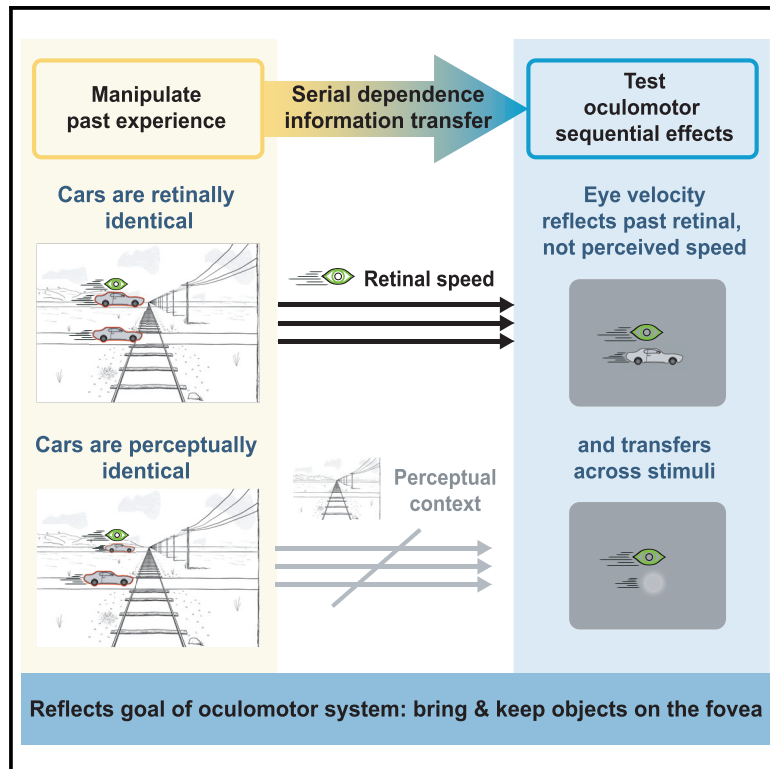# Current Biology

Serial dependence for oculomotor control depends on early sensory signals

Graphical abstract

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In brief

Oculomotor behavior can be affected by past history. Goettker and Stewart show that such serial-dependence effects are mediated by retinal error signals and ignore size and velocity constancy mechanisms based on spatial context. This might seem suboptimal but directly reflects the goal of the oculomotor system: bring and keep objects on the fovea.

Highlights

- Oculomotor control is directly influenced by past experiences

- Sequential effects for oculomotor behavior can transfer across different visual stimuli

- Sequential effects for oculomotor behavior are mediated by retinal velocity errors ignoring spatial context

- Reflects the goal of the oculomotor system: bring and keep objects on the fovea

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Serial dependence for oculomotor control depends on early sensory signals

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SUMMARY

To create an accurate percept of the world, the visual system relies on past experience and prior assumptions.[1] For example, although the retinal projection of an object moving in depth changes drastically, we still perceive the object at a constant size and velocity.[2,3] Consequently, if we see the same object with a constant retinal size at two different depth levels, the perceived size differs (illustrated by the Ponzo illusion). Past experience also directly influences perceptual judgments, an effect known as serial dependence.[4,5] Such sequential effects have also been reported for oculomotor behavior, even on the trial-by-trial level.[6–10] An integration of past experiences seems like a smart and sophisticated mechanism to reduce uncertainty and improve behavior in a world full of statistical regularities. By leveraging the Ponzo illusion to dissociate perceived size and speed from retinal signals, we show that serial-dependence effects for oculomotor control are mediated by retinal error signals. These sequential effects likely take place in early sensory processing because they transfer to different visual stimuli. In contrast to recently reported history effects for perceptual decisions,[11] sequential effects for oculomotor control deviate from perceptual mechanisms by not integrating spatial context and by ignoring size and velocity constancy. Although this dissociation might appear suboptimal, we argue that this effect reveals the different goals of the oculomotor and perceptual systems. The oculomotor system tries to reduce retinal error signals to bring and keep the target close to the fovea, whereas the visual system interprets retinal input to achieve an accurate representation of the world.[12]

RESULTS

We assessed serial dependence for oculomotor behavior by testing 16 participants in a well-established paradigm designed to elicit the effects of previous experience.[6–8] Each trial consisted of two movements, each lasting for one second. First, the prior, varied from trial to trial to manipulate recent experience. Second, the probe, was always the same across all trials. Since the sensory input in the probe is the same, differences in the oculomotor response to the probe can be directly attributed to the influence of the prior. To disentangle the role of retinal and perceptual information on subsequent oculomotor behavior, we used the Ponzo illusion. Stimuli used for the prior were a cartoon car moving across a custom-drawn scene that used linear perspective, such that the car appeared to be at different perceived depth levels (foreground or background; Figure 1), which in turn changed the perceived size and speed of the car despite the same retinal input (see STAR Methods for more details). To establish the basic effect of serial dependence with our new stimuli, the car presented as the prior could vary not only in perceived depth level but also in its speed. For this analysis, we used the two prior conditions where the car moved at either 5 deg/s (slow) or 15 deg/s (fast) for the prior stimulus, whereas the probe stimulus always moved at 10 deg/s (Figure 2A). Across different sessions,

the probe stimulus could either be the same car or an unrelated Gaussian blob, both moving in front of a gray background.

In line with previous findings,[6–8] the oculomotor response during the probe was faster following the fast prior than following the slow prior (Figure 2B). We quantified this effect for each condition by computing the average velocity between 100 and 400 ms after motion onset (see Goettker[8]), which allowed us to quantify the speed of the initial oculomotor response, based on potential differences in latency, acceleration, or peak speed. Across all comparisons, we found a significant difference in probe pursuit velocity based on the velocity of the prior (fast versus slow prior; all t_{15} values > 6.84, all p values < 0.001). We visualized this by plotting the difference between the fast and slow velocities prior for each condition (Figure 2C). However, there were two unexpected results, as the magnitude of this difference, and therefore the magnitude of the sequential effect, did not differ across conditions. First, for the foreground as well as the background conditions, the sequential effect for oculomotor behavior transferred to a different target object. Sequential effects were not statistically different between conditions where the car or the Gaussian blob was used as probe stimuli (both t_{15} values < 2.02, p values > 0.06, BF_{01} values > 0.78). Descriptively, the effect was even stronger when the target was switched from a prior car to the blob. Second, despite the illusory
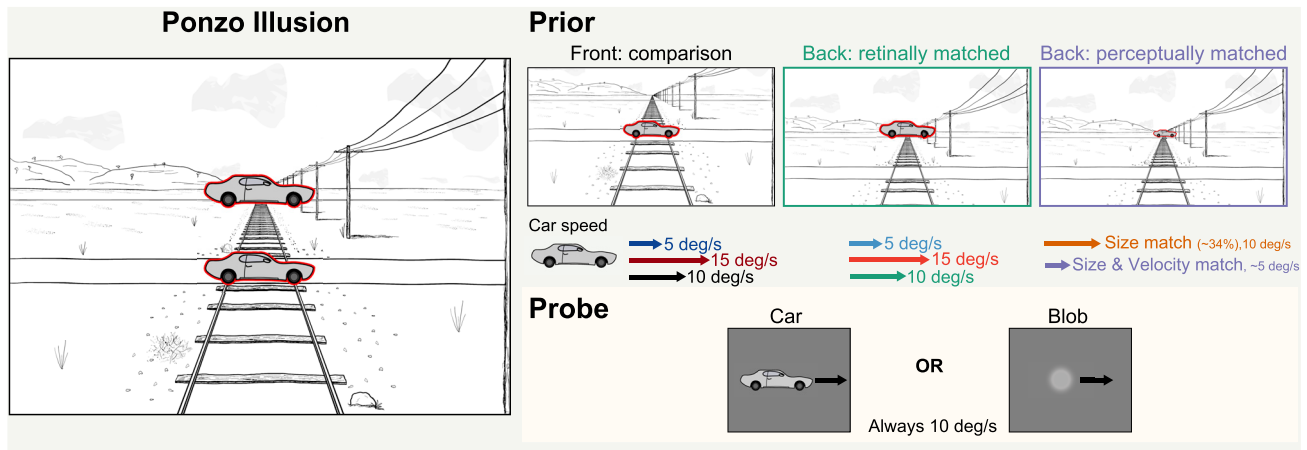
Figure 1. Paradigm

The Ponzo illusion was used to induce perceived differences in the depth of a car in a scene. Prior: a car moved across the scene at different perceived depths or speeds (depicted by arrows colored by condition). The "front: comparison" condition served as a control condition, where perceived and retinal size were always congruent. In the "back: retinally matched" condition, the retinal size of the car was matched with the comparison condition, but the perceived size differed due to the position of the car on the illusory perspective background. In the "back: perceptually matched" condition, the car in the back was adjusted by the observer to match either only the perceived size or the perceived size and velocity for a full perceptual match of the car in the foreground (as in "front: comparison"). Please note that we shifted the background scene to keep the car at the same spatial location in the center of the screen. Average size and velocity settings across observers are given in the figure and reflect the expected effect of the Ponzo illusion. Probe: either a car or a Gaussian blob moved across a gray screen at a constant velocity of 10 deg/s.

differences in perceived depth leading to differences in the perception of the car's size and movement speed, the sequential effect was comparable whether the probe was presented in the foreground or background (all t_{15} values < 0.91, all p values > 0.38, all BF_{01} values > 2.74), for both probe stimuli. Bayes factor analysis showed that the data were more than 2.74 times more likely under the null hypothesis of no difference between the foreground and background conditions than the alternative hypothesis of a difference between conditions.

To directly contrast the influence of perceptual and retinal speed, we used adaptive staircases for each participant to first adjust the size and then the velocity of a car in the background to match the perceived size and velocity of a car moving in the foreground at 10 deg/s. Average adjustment results of participants reflected the Ponzo illusion. The retinal size of the car in the background was set to 34% of the size of the car in the foreground; speed was set to 52%. In this way, we could directly compare the influence on the probe trial between the car moving in the foreground of the scene (front: comparison, 10 deg/s), with either a perceptually matched car (adjusted size and speed to be congruent with the perspective illusion) or a retinally matched car (same retinal size and speed) in the background.

The oculomotor response to the prior (Figure 3A) demonstrates that the oculomotor system follows the retinal and not the perceived motion of the target; although the initial oculomotor response is similar for the retinally matched prior (despite the different *perceived* speed and size caused by the depth illusion), it is much slower for the perceptually matched condition matching the correct retinal target speed. This focus on retinal signals also transfers to the influence on the probe trial (Figure 3B): the perceptually matched car in the back led to a significantly different effect on the oculomotor behavior (t_{15} values > 3.64, all p values < 0.002), whereas the retinally matched prior led to a

similar influence on the probe trial as the comparison moving in the foreground (all t_{15} values < 1.73, all p values > 0.10, all BF_{01} values > 1.16). The magnitude of the effect matches the predictions of a simple model based on the measured differences in retinal speed during the prior, which also captures the individual differences across participants (see Figure S1), but not the predictions of a model based on perceived speed (Figure 3C; see STAR Methods section for more details about the model).

Given the eye movements already follow the retinal speed in the prior trial, one could argue that the sequential effect for oculomotor behavior in the perceptually matched condition might be explained purely by differences in eye velocity. We therefore added a condition, where instead of the full perceptual match (speed and size), the prior car was only matched in perceived size and moved with the same retinal speed as the foreground comparison (10 deg/s; Figure 3D). Interestingly, although this reduced retinal size led to a slightly weaker motion signal and therefore a slower and delayed eye movement response in the prior trial, the oculomotor response was faster in the probe trial. This effect cannot be explained by a model that accounts only for the eye speed signal (Figure 3E). It must be based on the related increase in retinal velocity. Please note that in addition to this empirical result, there is also a strong theoretical argument against the use of eye velocity as a prior; the weighted integration of past information and current sensory input that depends on visual reliability cannot be explained by extraretinal eye velocity information.[8] This again supports the idea that sequential effects are based only on the retinal speed in the prior trial.

DISCUSSION

Many researchers have investigated sequential effects for oculomotor behavior,[6–8] but none of the previous studies could
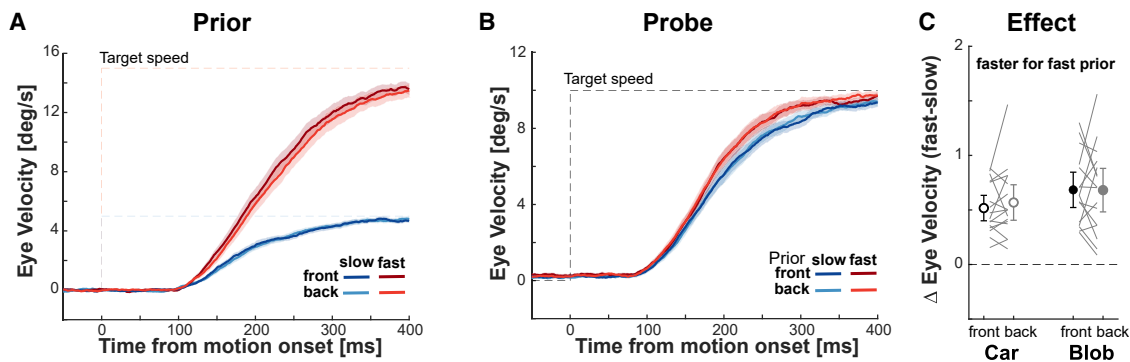
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Figure 2. Influence of prior velocity

(A and B) Initial oculomotor response to the prior (A) and probe trial (B) for priors moving at different speeds and different perceived depths. Different colors depict different prior trials (refer to speed condition arrows in Figure 1). Lighter colors depict the target moving in the background, darker in the foreground: note these are hard to differentiate due to overlap of the data.

(C) Effect shows the difference between the velocity profiles in the probe trial for fast versus slow priors. Positive values depict a faster oculomotor response in the probe trial after the fast prior. Left data points show the effect for a moving car as the probe target, right data points show the effect for a Gaussian blob as the probe target. Light gray lines depict the individual subjects. All shaded areas reflect the standard error; error bars, the 95% CI.

disentangle the contributions of early sensory signals from the changes in the perceived speed of the target. By leveraging the Ponzo illusion to dissociate these signals, our results reveal that the relevant signals mediating sequential effects on oculomotor behavior are not affected by contextual depth cues and seem therefore to be based on purely retinal information. These prior signals also seem to interact with new incoming sensory information at an early level of visual processing, as they transfer from one target object to another and are therefore independent of later processing for object recognition. Our results reveal fundamentally different uses of retinal signals for sequential effects for perceptual decisions and oculomotor control in three key aspects.

First, although the exact signals that underlie sequential effects are still a matter of debate, a recent study elegantly demonstrated that priors for perceptual decisions are based on high-level visual information. Cicchini and colleagues[11] used the "surround tilt illusion" to dissociate the perceptual from the physical orientation of a stimulus. They leveraged the illusion to show that priors for these perceptual decisions are high-level constructs incorporating contextual information (the priors are based on the perceived rather than physical orientation). However, this higher level prior influenced the subsequent decision at the level of early sensory signals (Figure 4; perceptual decision). The authors interpreted their finding in accordance with a predictive coding framework, where higher level priors based on perceptual experience are tested against early sensory signals, to create a correction signal.[13] Our results for sequential effects on oculomotor behavior agree with the idea of the prior acting at an early level of sensory input but differ in a major point: The mediating signal for oculomotor behavior is based on early level sensory input (Figure 4; oculomotor control). Within the framework of predictive coding, this suggests that the nature of the correction signals differs for perception and oculomotor control. The correction signal for perceptional decisions is used for efficient coding of high-level perceptual information, whereas the correction signals for oculomotor control act on low levels of visual processing. In a broader context, this idea of serial dependence working on different levels of processing

depending on the necessary task is consistent with research into sequential effects across attention, memory, action, and perception.[14] For example, although serial dependence for shape judgments occurs mostly at the feature level, serial dependence of emotional expression occurs on a higher object-level representation.[15] Moreover, the strength and even the direction (attraction versus repulsion) of the integration can be modulated by the changeability of a feature in the natural world,[16] which suggests that serial dependence is a general processing principle helping us to maintain a continuous percept of the world.

Second, not only the origin of the relevant signals but also the integration and grouping mechanisms for the prior signal seem to differ between perceptual decisions and oculomotor control. Intuitively, if you want to use past experience to improve your tracking performance, you should learn about the behavior of the object of interest, but this knowledge should not transfer to another object, since that might behave differently. For perceptual decisions, multiple studies have reported a decreased influence of past information when the past and current sensory inputs visually differ by too large an extent, indicating that information is only integrated when the prior and current are grouped together (e.g., Fischer and Whitney[4] and Cicchini et al.[11]). In our paradigm, the strength of the serial-dependence effect stayed comparable, even when switching the target objects from a car to a blob. This switch is substantial compared with the typical intertrial stimulus changes that have been shown to reduce the serial-dependence effect for perceptual decisions (e.g., when the same oriented grating differs by more than 30 degrees between prior and probe[4]). This strongly suggests that the critical factor for the integration of past information for oculomotor control seems to be a single feature: similarity in retinal speed. Since the car and the blob are similar in this feature space, differences in other visual characteristics of the target object are ignored. Although the strength of the sequential effect was comparable for the car and blob probe, there was a trend for an even bigger effect for the blob. This is not necessarily surprising: given the blob was relatively low in contrast and therefore the sensory input about the target motion less reliable,
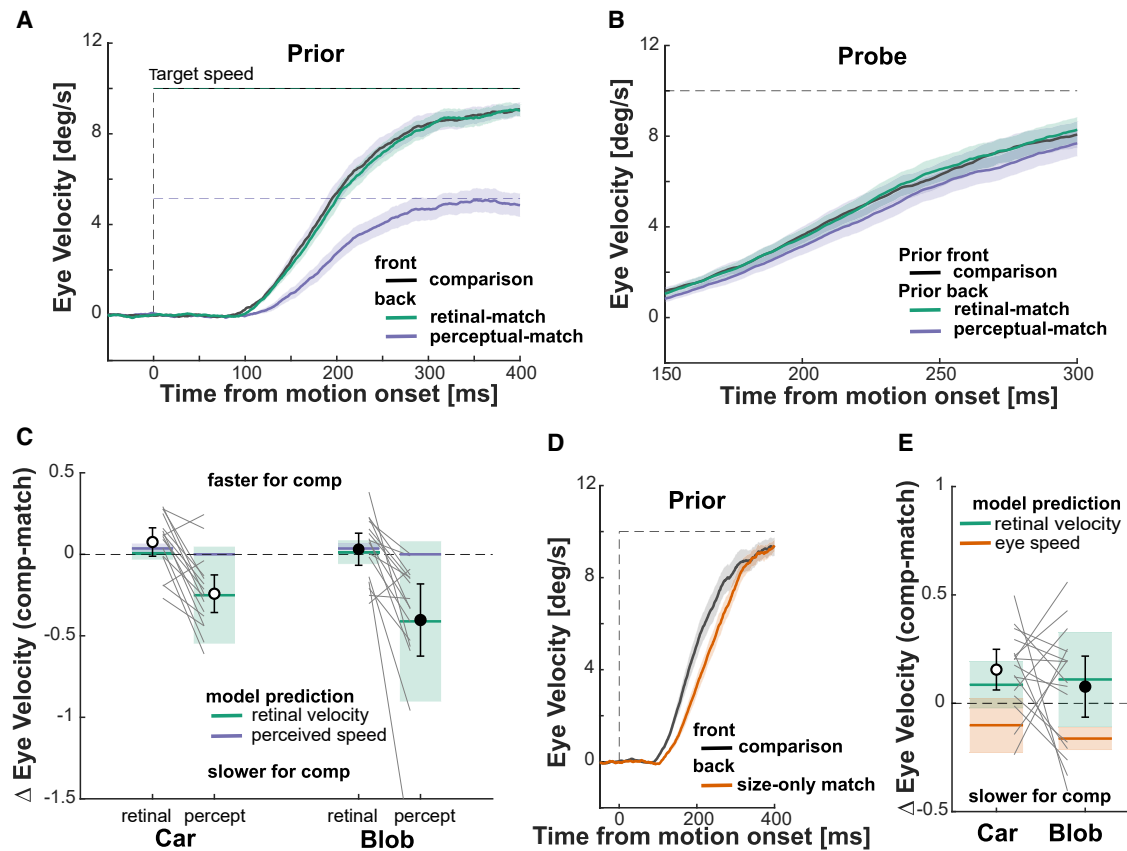
Figure 3. Retinal versus perceived speed versus eye speed

(A and B) Initial oculomotor response to the prior (A) and probe (B) trial, colored lines are a retinal or perceptual match to the comparison target movement (10 deg/s) in the foreground depicted in black.

(C) The effect of the prior on the probe shows the differences in eye velocity in the probe trial after the prior target movement was in the foreground compared with retinally or perceptually matched stimuli (retinal versus percept) in the background. Shaded areas show model predictions based on retinal or perceptual information.

(D) Prior eye velocity for comparison movement in foreground plotted against the prior matched in size only moving in the background with the same retinal velocity.

(E) This shows the effect of the prior on the probe trial, with model predictions based on retinal velocity (green) and eye speed (orange). For more results with respect to model performance, please see Figure S1. Shaded areas represent the standard error; error bars, the 95% CI.

one could and should even expect a larger effect due to reliability-weighted integration of current and past sensory input.[6–8] Similar generalizations across task irrelevant object features for sequential behavior can also be found for perceptual decisions but again are mainly based on higher level representations. For example, serial-dependence effects for numerosity judgments generalize across different visual presentation formats, suggesting grouping by an abstract representation of numerosity.[17] This points again to the differential focus on early versus late stages of visual processing for serial-dependence effects for oculomotor control and perceptual decisions.

Third, the temporal integration of information is different for oculomotor control and perceptual decisions. Although a recent study elegantly demonstrated this difference for single behavioral trials,[18] similar claims have been also made for serial dependence.[19,20] When repeatedly seeing the same movement sequence, perceptual decisions tend to be based on adaptation and integration of information across a longer time period. In

contrast, oculomotor behavior only uses very recent information as priming to update sequential oculomotor responses and to allow better tracking responses.[19] Together, this focus on recent low-level retinal error signals suggests that the goal of the oculomotor system is to adjust subsequent oculomotor behavior to allow faster foveation of relevant objects. This focus on retinal signals can lead to a deviation from common perceptual mechanisms such as velocity constancy but enables the faster foveation of objects which in turn allows for more accurate processing of targeted objects due to higher quality of the visual information.[21]

The focus on retinal error signals in the early levels of sensory analysis fits well with the proposed neural implementation of the serial-dependence effect for oculomotor control, which takes motion signals from the middle temporal area (MT) as input and integrates them in the frontal eye field.[6] It also raises the interesting question as to the spatial specificity of serial dependence for oculomotor control: the perceptual continuity field for serial dependence in perceptual decisions extends beyond
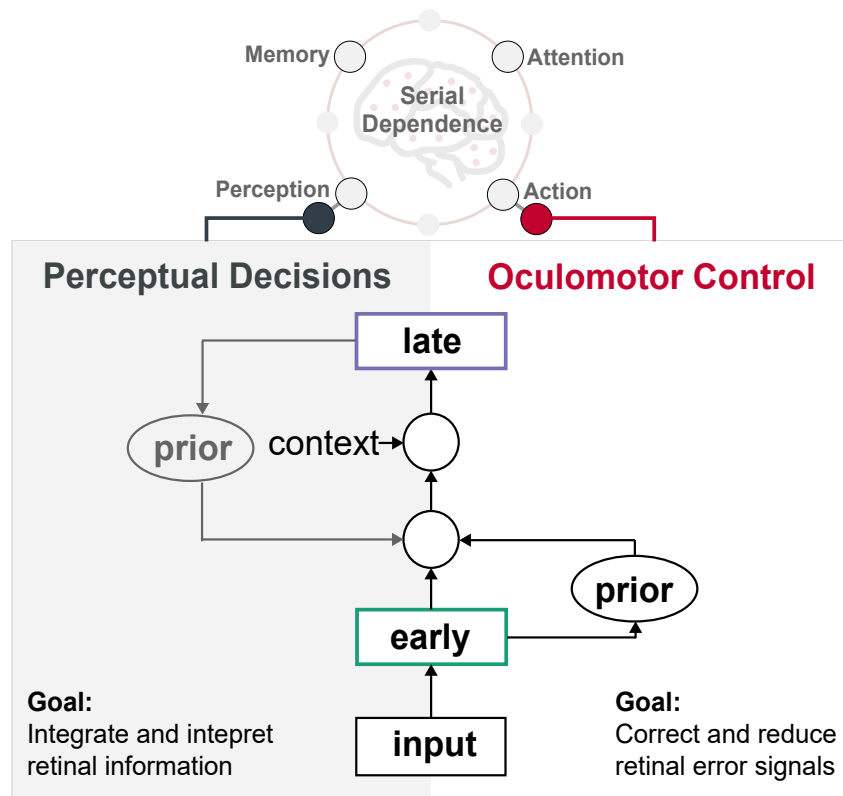
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Figure 4. Framework for serial dependence for oculomotor control and perceptual decisions

The framework is adapted from Cicchini et al.[11] Serial dependency operates across many domains, but here, we focus on contrasting perceptual decisions and oculomotor control. The visual processing hierarchy is shown in the center, with color codes indicating the levels probed by different conditions in our experiment. Early matches the retinal prediction, whereas late would match the perceptual prediction where context in integrated. The pathway for the perceptual decision prior (left) is based on the results of Cicchini paper. Crucially, the pathway for the prior for oculomotor behavior based on our results differs: the mediating signal for sequential effects in oculomotor behavior is based on the early retinal error signals. The level at which the prior is integrated reflects and realizes the substantially different goals of the perceptual and oculomotor systems.

central vision,[4] and this window seems to operate in retinotopic coordinates for saccades.[22] Since in our paradigm prior and probe always moved in the same direction and started at the same spatial location, further research that varies these factors is needed to gain deeper insights into the spatial extent of the observed effect. Closely related and also with respect to processing in MT, it is debated whether encoding in MT is spatiotopic or retinotopic.[23–25] An experiment on sequential behavior with pursuit eye movements that varies factors such as direction and spatial location could provide insight into the reference frame of the MT-encoded motion priors.

Our results directly uncover the substantially different goals of the oculomotor and perceptual systems; however, their significance goes beyond only showing another perception-action dissociation.[26–29] The perceptual system integrates and interprets retinal information to accomplish size and velocity constancy across perceived depths. In contrast, the oculomotor system ignores these constancy mechanisms and simply tries to bring and keep any object of interest close to the fovea. When these goals are in conflict, dissociations can and should be expected and are not an exception.[30–33] Relying on early retinal error signals for sequential behavior is a logical predictive mechanism for an oculomotor control system whose main goal is to keep items of interest on the fovea. Therefore, as with the Ponzo illusion, it is a matter of perspective: The sequential effect for the oculomotor system might look suboptimal when taking a perceptual point of view, but an accurate and vivid percept of the world would not be possible if the oculomotor system would not follow its own goals.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.cub.2022.05.011.

Science, Research and Art. All stimuli, gaze data, and parts of the applied analysis code will be made available online upon acceptance of the manuscript.

REFERENCES

1. Kersten, D., Mamassian, P., and Yuille, A. (2004). Object perception as Bayesian inference. Annu. Rev. Psychol. 55, 271–304.
2. Wallach, H. (1939). On constancy of visual speed. Psychol. Rev. 46, 541–552.
3. Brown, J.F. (1931). The visual perception of velocity. Psychol. Forsch. 14, 199–232.
4. Fischer, J., and Whitney, D. (2014). Serial dependence in visual perception. Nat. Neurosci. 17, 738–743.
5. Cicchini, G.M., Mikellidou, K., and Burr, D.C. (2018). The functional role of serial dependence. Proc. Biol. Sci. 285, 20181722.
6. Darlington, T.R., Beck, J.M., and Lisberger, S.G. (2018). Neural implementation of Bayesian inference in a sensorimotor behavior. Nat. Neurosci. 21, 1442–1451.
7. Deravet, N., Blohm, G., de Xivry, J.-J.O., and Lefèvre, P. (2018). Weighted integration of short-term memory and sensory signals in the oculomotor system. J. Vis. 18, 16.
8. Goettker, A. (2021). Retinal error signals and fluctuations in eye velocity influence oculomotor behavior in subsequent trials. J. Vision 21, 28.
9. Collins, T. (2014). Trade-off between spatiotopy and saccadic plasticity. J. Vision 14, 28.
10. Cont, C., and Zimmermann, E. (2021). The motor representation of sensory experience. Curr. Biol. 31, 1029–1036.
11. Cicchini, G.M., Benedetto, A., and Burr, D.C. (2021). Perceptual history propagates down to early levels of sensory analysis. Curr. Biol. 31, 1245–1250.e2.
12. Kuhn, G., and Land, M.F. (2006). There's more to magic than meets the eye. Curr. Biol. 16, R950–R951.
13. Rao, R.P.N., and Ballard, D.H. (1999). Predictive coding in the visual cortex: a functional interpretation of someextra-classical receptive-field effects. Nat. Neurosci. 2, 79–87.
14. Kiyonaga, A., Scimeca, J.M., Bliss, D.P., and Whitney, D. (2017). Serial dependence across perception, attention, and memory. Trends Cogn. Sci. 21, 493–497.
15. Collins, T. (2021). Serial dependence occurs at the level of both features and integrated object representations. J. Exp. Psychol. Gen. Advance online publication. https://doi.org/10.1037/xge0001159.
16. Taubert, J., Alais, D., and Burr, D. (2016). Different coding strategies for the perception of stable and changeable facial attributes. Sci. Rep. 6, 32239.
17. Fornaciai, M., and Park, J. (2019). Serial dependence generalizes across different stimulus formats, but not different sensory modalities. Vision Res. 160, 108–115.
18. Lisi, M., Morgan, M.J., and Solomon, J.A. (2022). Perceptual decisions and oculomotor responses rely on temporally distinct streams of evidence. Commun. Biol. 5, 189.
19. Maus, G.W., Potapchuk, E., Watamaniuk, S.N.J., and Heinen, S.J. (2015). Different time scales of motion integration for anticipatory smooth pursuit and perceptual adaptation. J. Vision 15, 16.
20. Wu, X., Rothwell, A.C., Spering, M., and Montagnini, A. (2021). Expectations about motion direction affect perception and anticipatory smooth pursuit differently. J. Neurophysiol. 125, 977–991.
21. Schütz, A.C., Braun, D.I., and Gegenfurtner, K.R. (2009). Object recognition during foveating eye movements. Vision Res. 49, 2241–2253.
22. Collins, T. (2019). The perceptual continuity field is retinotopic. Sci. Rep. 9, 18841.
23. Crespi, S., Biagi, L., d'Avossa, G., Burr, D.C., Tosetti, M., and Morrone, M.C. (2011). Spatiotopic coding of BOLD signal in human visual cortex depends on spatial attention. PLoS One 6, e21661.
24. D'Avossa, G., Tosetti, M., Crespi, S., Biagi, L., Burr, D.C., and Morrone, M.C. (2007). Spatiotopic selectivity of BOLD responses to visual motion in human area MT. Nat. Neurosci. 10, 249–255.
25. Gardner, J.L., Merriam, E.P., Movshon, J.A., and Heeger, D.J. (2008). Maps of visual space in human occipital cortex are retinotopic, not spatiotopic. J. Neurosci. 28, 3988–3999.
26. Goodale, M.A., and Milner, A.D. (2018). Two visual pathways—where have they taken us and where will they lead in future? Cortex 98, 283–292.
27. Rossetti, Y., Pisella, L., and McIntosh, R.D. (2017). Rise and fall of the two visual systems theory. Ann. Phys. Rehabil. Med. 60, 130–140.
28. Franz, V.H., Gegenfurtner, K.R., Bülthoff, H.H., and Fahle, M. (2000). Grasping visual illusions: no evidence for a dissociation between perception and action. Psychol. Sci. 11, 20–25.
29. Spering, M., and Carrasco, M. (2015). Acting without seeing: eye movements reveal visual processing without awareness. Trends Neurosci. 38, 247–258.
30. Lisi, M., and Cavanagh, P. (2015). Dissociation between the perceptual and saccadic localization of moving objects. Curr. Biol. 25, 2535–2540.
31. Simoncini, C., Perrinet, L.U., Montagnini, A., Mamassian, P., and Masson, G.S. (2012). More is not always better: adaptive gain control explains dissociation between perception and action. Nat. Neurosci. 15, 1596–1603.
32. Spering, M., and Gegenfurtner, K.R. (2007). Contrast and assimilation in motion perception and smooth pursuit eye movements. J. Neurophysiol. 98, 1355–1363.
33. Tavassoli, A., and Ringach, D.L. (2010). When your eyes see more than you do. Curr. Biol. 20, R93–R94.

STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Software and algorithms		
MATLAB 2021b	The MathWorks	https://mathworks.com/
Psychophysics Toolbox 3	http://psychtoolbox.org/	http://psychtoolbox.org/
JASP 0.16.1	https://jasp-stats.org	https://jasp-stats.org

RESOURCE AVAILABILITY

Lead contact
Further information and requests for resources should be directed to the lead contact, Alexander Goettker (Alexander.Goettker@psy.jlug.de)

Materials availability
There is no restriction for distribution of materials.

Data and availability
For data analysis, we used functions and routines available in MATLAB (version R2021b) in combination with JASP (version 0.16.1). Experimental data, as well as the analysis and experimental code are downloadable at an OSF repository: osf.io/wspuv

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Sixteen participants (Mean age: 25.2, range, 20-40, 14 female) took part in all experiment sessions. The sample size was determined based on previous work on serial dependence for oculomotor behavior.[8] All participants reported normal or corrected-to-normal vision and were naïve with respect to the study. Experimental procedures are in line with the declaration of Helsinki and were approved by the local ethics committee. Written informed consent was obtained from each participant.

METHOD DETAILS

Setup
Participants sat at a table in a dimly illuminated room with their head positioned on a chin rest. Their eyes were roughly aligned with the height of the center of a monitor (60 cm x 32 cm, 3840 x 2160 pixel, Phillips, Amsterdam, Netherlands) at a 70 cm viewing distance. Under these circumstances the monitor spanned approximately 49 x 26 deg of visual angle. The experiment was programmed and controlled with Matlab 2020a (MathWorks, Natick MA) using Psychtoolbox (Kleiner, Brainard & Pelli, 2007). Gaze was recorded from one eye with a desk-mounted eye tracker (EyeLink 1000 Plus, SR Research, Kanata, ON, Canada) at a sampling frequency of 1000 Hz. To ensure accurate recordings before each block a nine-point calibration was performed, and additional drift corrections were used at the start of each trial.

Experimental conditions
Across the main experiment, each trial consisted of two movements. First, the prior, where a drawing of a car moving across a drawing of a scene with perspective-induced illusory depth was presented, and the perceived depth as well as the size and/or speed of the car was varied (Figure 1). Second, the probe, where either a car or a Gaussian blob moving in front of a gray background was presented with a fixed velocity of 10 deg/s. For both probe stimuli, participants completed four consecutive blocks and the order was counterbalanced. In each block, we used nine different prior conditions. The first six conditions varied along the factors of perceived depth and speed of the car (car in front moving with 5, 10 or 15 deg/s; car in back moving with 5, 10 or 15 deg/s). The other three conditions were based on perceptually matching the size and speed of the car in the back to the car moving in the front with 10 deg/s: (1) car in back with matched perceived speed, but the same retinal size; (2) car in back with perceptually-matched size, but moving at 10 deg/s, (3) the full perceptual match, car in the back with perceptually matched size and matched speed. Each of the nine prior conditions could move either to the left or the right. Each combination was repeated 8 times, leading to a total of 144 trials per block (9 conditions x 2 directions x 8 repetitions). Therefore, each participant completed a total of 1152 trials (2 different probe stimuli x 4 blocks x 144 trials).

Perceptual task
To create the perceptually-matched prior conditions, each participant completed three psychophysical staircase procedures. In a 2AFC task, participants had to compare the size/speed of sequentially-presented cars, while the parameters were adjusted based

on two randomly interleaved, adaptive staircases. One staircase started from a low value, one started from a high value. In random order, the standard (which was always the 10 deg/s car in front) and the test trial from the staircase were shown. Depending on the response of the participant, the staircase was adjusted to make the perceived value more similar to the standard, e.g. When the presented stimulus was perceived/reported to move faster than the standard, it was adjusted to be slower for the next iteration. Each staircase consisted of 25 trials, leading to a total of 50 trials per psychophysics task.

In the first task, participants matched the speed of a car moving across the background to a car moving across the foreground, while the car in the background had a constant retinal size. For the 2AFC task, participants had to indicate which car (first or second) was faster. Here, the two staircases started at 6 or 14 deg/s with a shift of the velocity of 1 deg/s per trials. To improve the fitted estimate of the staircase, the shift value decayed exponentially, since it was divided by 1.05 after each trial. In a second task, participants had to judge the size of a car in the background to a car in the foreground (by indicating whether the first or second car was bigger). During this size-adjustment task, both cars were presented stationary in the center of the screen. The two staircases started at 10% or 100% of the retinal size of the car in the front and changed by 10% across trials, again with the same exponential decay. In the third task, participants also had to judge the perceived relative speed of the cars and the settings were similar to the first task. However, this time the car in the back was presented with the perceptually-matched size from the second task, leading to a full perceptual match. Within the 50 trials, for each of the tasks both staircases converged on one estimate (average std across the last 5 trials between the two staircases: 4.07% for the size match and 0.42 deg/s and 0.43 deg/s for the velocities estimated for the retinally-matched and perceptually-matched car). Therefore, the average staircase value of the last 5 trials across both staircases was used as perceptual estimate.

Main task

Each trial of the main task started with the prior. In the beginning a red fixation dot (diameter 0.2 deg) was presented at the center of the screen in front of the perspective scene drawing for a random time between 1 and 1.5 s. The scene was presented in a way that the relevant road in the drawing that the car moved along (foreground or background) was in the center of the screen. The scene was also slightly adjusted depending on the size of the car, so that the tires of the presented car always aligned with the lower line of the road. After the fixation duration, the red dot disappeared and the car appeared and moved either to the left or the right for 1s. Please note that the starting position of the car was chosen so that the center of the car crossed the center of the screen after 200ms to minimize the occurrence of initial corrective saccades (Rashbass, 1961). The size of the standard car was 6.8 x 2.0 deg. In the perceptually-matched prior conditions, the size was adjusted to a fraction of this standard size based on the psychophysical settings of the participants. After the movement, the scene disappeared and the probe screen appeared. Here, a new fixation dot in the screen center was presented in front of a gray background, again for a random time between 1 and 1.5s. After the fixation duration, the dot again disappeared and the standard car or a Gaussian blob (SD = 0.4 deg, max contrast = 0.1) appeared, depending on the respective condition. The target then also moved in step-ramp fashion and always with 10 deg/s, which allowed us to directly quantify the influence of the prior. The probe movement was always in the same direction as the prior movement.

QUANTIFICATION AND STATISTICAL ANALYSIS

Eye movement data were digitized on-line and analyzed off-line using Matlab software. As all targets moved horizontally, the horizontal-position was used for the analyses. First, eye position was filtered with a second-order Butterworth filter, with a cutoff frequency of 30 Hz. Then eye velocity was calculated as the first derivative of the filtered position traces. Saccades were identified based on the EyeLink criteria with a speed and acceleration threshold of 30 deg/s and 4000 deg/s^2, respectively. After the detection of saccades, a linear interpolation of the eye movement velocity around the time of the saccade (from 35 ms before saccade onset to 35 ms after saccade offset) was performed, and the eye movement velocity was filtered with an additional low-pass Butterworth filter with a cutoff frequency of 20 Hz. Please note that we also performed the complete analysis with saccades included, but the results did not qualitatively differ.

To compute the influence of the prior, all eye velocity traces during the probe were aligned on target movement onset. Trials were excluded if (1) blinks occurred during the target movement in the prior or probe and the median across all trials for each prior condition was computed, (2) eye velocity still was larger than 70 deg/s despite the interpolation of saccades. After applying these criteria we were able to use 17054 of 18432 trials for the analysis (93%). To quantify the influence of the prior, the average velocity in the probe trial for each prior condition was computed as the summed difference in the analysis window of 100 to 400 ms after motion onset normalized by the number of frames. To assess the influence of prior velocity, paired t-tests were performed between the priors moving at 5 (slow) & 15 (fast) deg/s either in the fore- or the background and for both probe stimuli (car and blob). To compare the magnitude of the effect across conditions, we computed the differences between the probe velocity profiles (fast-slow) and compared them with paired t-tests. We compared the two probe stimuli (for the foreground and background), as well as the foreground and the background (for both probe stimuli). To directly assess the influence of retinal and perceived speed, we again computed the average velocity in the analysis interval for the foreground comparison (10 deg/s), and the retinally-matched and the perceptually-matched car in the background and compared them with paired t-tests. Since non-significant t-tests do not allow us to accept the null-hypothesis of no difference between the groups, we conducted additional Bayes Factor analysis to quantify the evidence for the null-hypothesis. Bayes Factors were calculated in JASP using default priors.

Modelling

We used a very simple model with no free-parameters to disentangle the predictions made by perceived velocity, retinal velocity or eye-speed. For each participant, we computed the average retinal velocity and eye velocity in the analysis time window of 100 to 400 ms after motion onset across all trials for each prior condition. Based on the actual speed and the matches for perceived speed in our psychophysical tasks, we also had an estimate of perceived speed for each prior condition. We used the 10 deg/s car in the foreground as the standard and the 5 deg/s & 15 deg/s car in the foreground as the comparison. We computed the difference between the velocity profile of the probe stimulus of these conditions for each participant and divided this value by the difference in retinal velocity, eye speed and perceived speed in the respective priors. This gave us a set of transfer weights for each participant for each of the measures: one for an increase in prior retinal velocity, eye speed and perceived velocity; and one for a decrease for each of them. These weights indicate how much changes in retinal velocity, eye speed or perceived speed during the prior transfer to a change in eye velocity in the probe. Now we simply computed the difference in these three measures across the other prior conditions with respect to the 10 deg/s foreground condition, and used the calculated transfer weights to make a prediction of the expected difference in the probe (see Figure S1 for a detailed depiction of model predictions). The average transfer weights across conditions were 0.14 +/- 0.066 for retinal speed, 0.13 +/- 0.042 for eye speed and 0.06 +/- 0.022 for perceived speed.