Author Response to Brenner & Smeets

Matteo Lisi
Department of Psychology, Royal Holloway, University of London, London, UK

Patrick Cavanagh
Department of Psychology, Glendon College, Toronto, Ontario, Canada
Department Psychological and Brain Sciences, Dartmouth College, Hanover, NH, USA

Brenner and Smeets take issue with our derivation of the target direction and speed used by the saccade system to program the saccade landing (Lisi & Cavanagh, 2024). In our original analysis, we estimated the target velocity vector for which the saccade would have been maximally accurate based on the spatial offset between the target onset location, the saccade landing, and the temporal interval between target onset and saccade landing (see green line in Figure 1A below). In this case, the saccade system would assume a constant velocity (speed and direction) of the target over this interval. Brenner and Smeets propose that the saccade system would instead track the target along its physical path up to a certain point, then it would predict the future path of the target based on the perceived direction (which is very similar to the smooth pursuit direction). We had in fact proposed this same alternative in our Supplementary Figure S4 (below as Figure 1) and considered its implications in our discussion. This alternative allowed saccades and pursuit to use the same estimate of target direction and speed. To do so, the saccade system had to switch from estimating target location based on its physical direction to an estimation based on its perceived direction at about 110 ms before the saccade was launched. This delay corresponds well to Brenner and Smeets proposal of 100 ms before saccade onset (on average about 140 ms after target onset). However, our supplementary analysis aimed only at obtaining an estimate of the temporal scale over which saccadic might predict future target locations based on the perceived direction; we disagree with Brenner and Smeets's claim that this would correspond to a plausible computational model of saccadic extrapolation. Taking this two-segment explanation at face value requires the saccade system to entertain two different velocities for the same target: the physical velocity, used to track changes in target location over the initial ≈140 ms of target presentation, then the perceived velocity, used for programming the landing location of the saccadic movement. In the first segment, the estimated target position is unaffected by the internal motion, whereas in the second segment, the perceived velocity used by the saccade system is influenced by the internal drifting texture, biasing its predicted future location.

We believe that Brenner and Smeets's proposal is untenable for at least two reasons. First, it is unclear how the saccade system would track the physical target location over the initial ≈140 ms of target presentation. To be accurate, this estimate would have to be assisted by predictions based on the physical velocity otherwise estimated locations would lag behind the physical location by at least ≈50 ms (based on latency of visual responses in the superior colliculus; e.g., see Wurtz & Goldberg, 1972). If the physical velocity is used in the initial segment, the target tracking is not purely position based, and it is then unclear why this physical velocity would not also be used for extrapolating over the final 100 ms. Second, Brenner and Smeets use an illusory motion stimulus (their Movie 1) to support their claim that position can change independently of perceived motion (in the initial segment). Their example is flawed, however, by the presence of the static horizontal line that counteracts the effect of motion on position. Without the line, their stimulus is a version of the classic De Valois and De Valois (1991) and Ramachandran and Anstis (1990) motion-induced position shifts that clearly shows the effect of motion on position. Computational models of the double-drift stimulus have also pointed to a strong coupling between perception of visual motion and position (Kwon, Tadin, & Knill, 2015). Finally, we show here that Brenner and Smeets' proposal is inconsistent with our empirical finding. In their letter, Brenner and Smeets claim that their interpretation is "more consistent with the data." However, their interpretation predicts a decrease in direction bias with increasing saccade latency, a trend that, as they admit, was not seen in our analysis. Specifically, if saccades are extrapolated only over the last 100 ms before the saccade onset, as Brenner and Smeets propose, the saccadic bias measured as we do in our study must decrease with saccadic latency. With longer saccade latency, the target would be tracked according to the physical, as opposed to perceived, velocity over a larger fraction of the overall saccade latency. This should lead to a more accurate saccade landing in terms of the angle between the start point and the saccade landing. The physical offset

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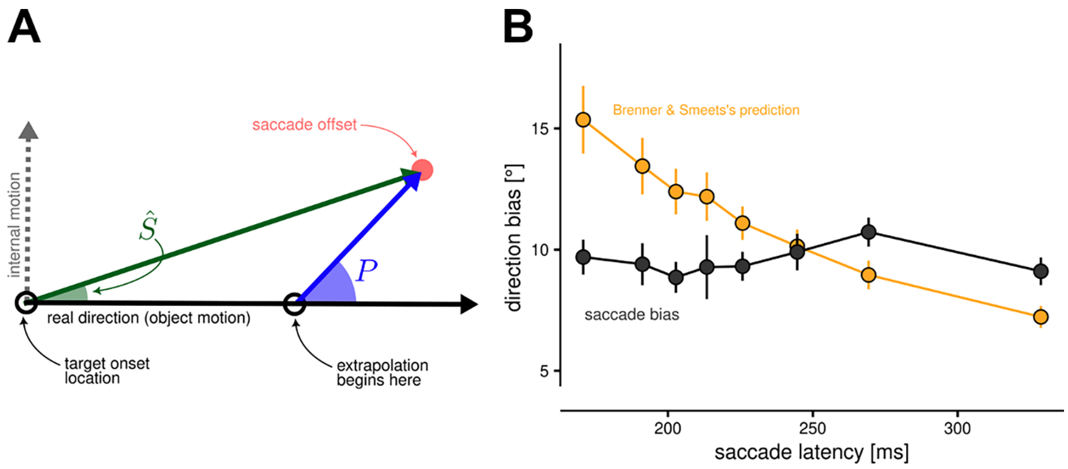

Figure 1. The mechanism assumed by Brenner and Smeets (**A**), as it was illustrated in Supplementary Figure S4 of our original supplemental material. Here $\hat{S}$ is the saccade direction bias, as measured in our study, and P is the perceptual direction bias that controls the extrapolation to the expected landing from the later start point. This perceptual direction has the same velocity and speed that was measured in the perceptual judgments and the smooth pursuit tasks. (**B**) The saccadic direction bias (corresponding to the angle $\hat{S}$) that we calculate based on Brenner and Smeet's proposal (orange symbols) shows a systematic decreases with saccade latency. However, the actual data (black symbols) do not show any such decrease. The predictions are computed by calculating trial-by-trial predictions according to Brenner and Smeets's model, then binning and averaging across participants in the same way as was done for the actual data (error bars are bootstrapped standard errors). The code to produce this figure has been added to the Open Science Framework repository containing the data of our study (https://osf.io/57hdm/).

will be constant because it always follows the perceived direction for a fixed duration (100 ms), but the angle from the start point will decrease for increasing saccade latencies, and this is how we plotted our results. As a result, the trial-by-trial predictions of saccade bias computed following the model of Smeets and Brenner display a decreasing trend in direction bias that was not seen in our analysis (Figure 1B).

Overall, we believe that the idea that saccades may integrate past inputs and predict target locations based on shorter temporal intervals is intriguing. It holds promise for explaining some of the discrepancies reported in the literature between eye movements and perception (Lisi & Cavanagh, 2015; Lisi, Morgan, & Solomon, 2022; Spering & Carrasco, 2015). However, the precise mechanisms underlying this phenomenon remain underspecified. Brenner and Smeets's proposal does not provide the necessary clarification, because it is implausible, for the reasons discussed above and fails to align with the experimental data. So for the moment, we stand by our single velocity model of the original article (the green line of Figure 1A).

Keywords: motion perception, saccades, smooth pursuit, space and scene perception

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Corresponding author: Matteo Lisi.
Email: matteo.lisi@rhul.ac.uk.
Address: Department of Psychology, Royal Holloway, University of London, London, UK.

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