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Reaching Fails Where Saccades Succeed: Nonrigid Motion Reveals a Dissociation Between Saccadic and Limb Pathways in Predicting Future Target Position

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Abstract

Intercepting a moving target requires prediction: knowing the current position is not enough due to sensorimotor delays. A moving “vortex” stimulus, which lacks a conventional velocity signal for smooth pursuit yet still elicits accurate saccade targeting, was used here to assess whether it also supports accurate reaching movements. In our experiments, participants reached to the vortex or to a rigid moving disk. Three manipulations probed prediction and online control: constant-speed interception, speed perturbations at reach onset, and target disappearance at reach onset.

Reaction times when reaching to the vortex did not depend on target speed in the way they do for rigid targets. Moreover, when reaching to the vortex participants made larger undershoots that increased with target speed, and they compensated less for speed changes. Thus, the vortex provides motion-related information that is sufficient for accurate saccadic localization, but that is not effectively exploited for predictive manual interception. This dissociation suggests that motion information may not be used in the same manner across motor effectors.

Introduction

Intercepting a moving object is a demanding form of sensory-guided motor control, as both sensory processing and motor execution incur temporal delays. Consequently, successful behavior depends on predicting the object's future position rather than reacting solely to its current one¹⁻³. Velocity signals are essential for anticipating future target locations in order to deal with such sensorimotor delays⁴. During the interception of a moving target with the eyes, saccades serve to rapidly reposition the fovea onto the target. Subsequent target motion is typically followed using smooth pursuit, which minimizes the need for additional catch-up saccades to re-establish foveal fixation. Intercepting a moving target with a limb requires substantially more time than doing so with the eyes, so the movement is continuously refined on the basis of incoming sensory information⁵⁻¹³.

Although one might expect all aspects of both eye and hand movements to rely on a shared motion representation, recent studies indicate the existence of multiple motion representations, not all of which are recruited uniformly across different effectors. These studies used a nonrigid “vortex” stimulus (Fig. 1A and supplementary video S1) which provides motion information that cannot be used to drive smooth pursuit but that does accurately guide saccades to moving targets^{14,15}. By examining visually guided reaching to the same stimulus, we test whether movements of the limb can be guided by this motion information for predicting a suitable endpoint, as in saccades, or whether the limb fails in a manner that mirrors the failure of smooth pursuit, thereby imposing new constraints on candidate neural architectures for sensory-guided motor action.

To quantify the performance in intercepting this nonrigid motion stimulus, we compared it with performance in intercepting rigid targets. In classic interception tasks with rigid targets, reaching typically incorporates target velocity for prediction and rapidly updates the movement when target motion changes^{3-6,16-23}.

To probe how motion information is used when reaching with one's hand, participants intercepted with their right index finger either a rigid moving disk or the translating vortex (Fig. 1B). In our first experiment (Fig. 2A), targets moved at constant velocities ($5^\circ/\text{s}$ or $10^\circ/\text{s}$), allowing us to quantify how interception accuracy depends on target speed under full visual feedback. In our second experiment (Fig. 2B), we introduced velocity perturbations at reach onset to examine the gain with which motion information is incorporated during execution. In our third experiment (Fig. 2C), targets (moving at $10^\circ/\text{s}$) disappeared at reach onset while participants were instructed to reach for the last seen position of the stimulus. This experiment removed any visual feedback of the target during execution to test how much participants used the motion during the planning phase.

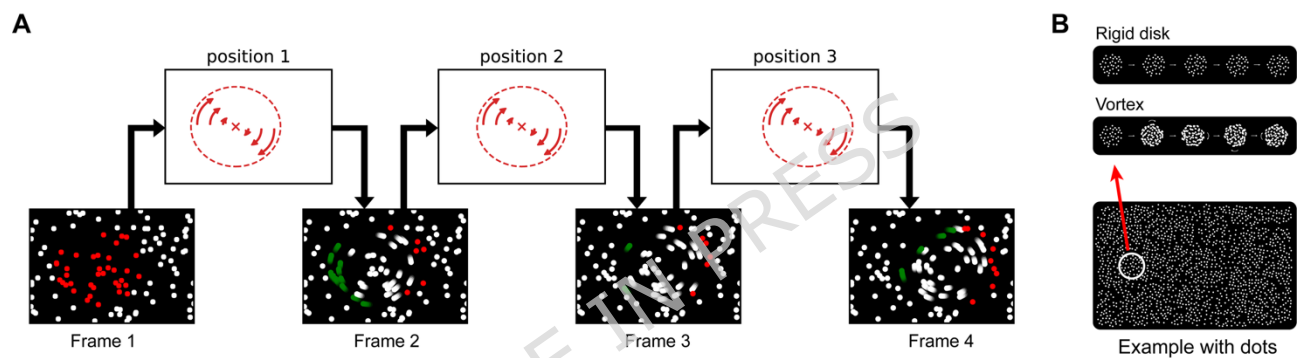


Figure 1. Visual stimuli used in the experiments: rigid disk and nonrigid vortex. A) The vortex stimulus¹⁴ consisted of a field of dots of which all within a certain distance from a certain point (the vortex) rotated around that point creating local rotational flow. The vortex itself translated across successive frames. As the vortex progressed rightward, background dots entering the leading edge were incorporated into the rotation in the next frame (illustrated in red), whereas dots at the trailing edge (green) were returned to the static background in the next frame. B) Illustration of the experimental display as presented to participants, including the background dot field and the two stimuli used: the rigid disk and the nonrigid vortex. The rigid disk stimulus consisted of a black disk with white dots, as in the background, that shifted rightward occluding the background.

Overall, our results indicate that the reaching system does not effectively extract velocity information from the vortex stimulus and instead relies primarily on positional information evolving over time. This produces less precise predictions of the vortex's future position and results in inaccurate reaching movements, similarly to what happens during smooth pursuit eye

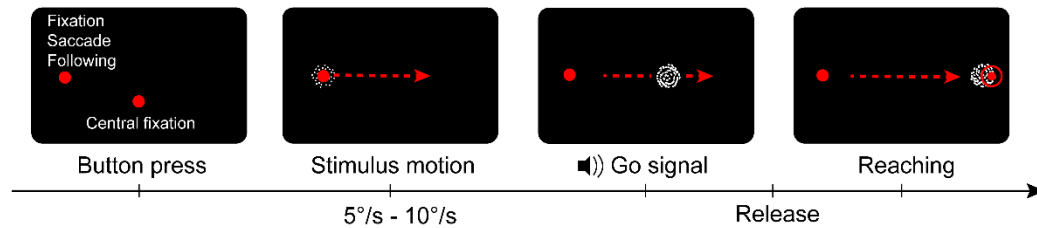
movements, that are unable to track vortex motion¹⁵. Consistent with this framework, our results support the presence of partially dissociable motion pathways: a pathway that is used by saccades that can deal with nonrigid motion for accurate targeting, and a pathway that is presumably shared (at least in part) by smooth pursuit and reaching in which nonrigid motion information cannot be used.

Results

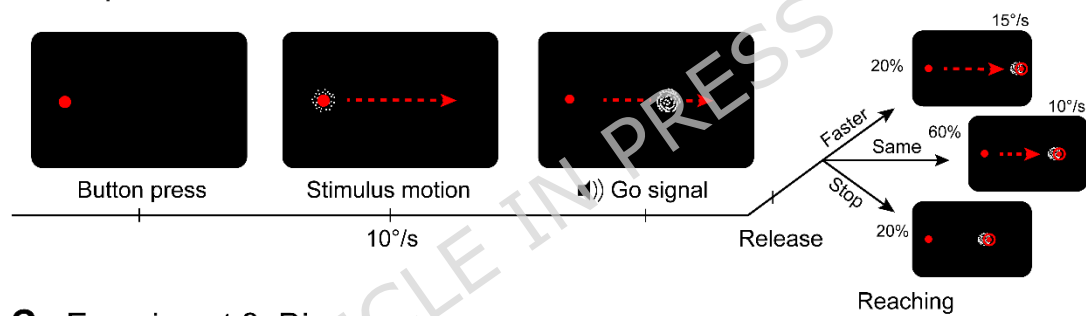
Different groups of participants took part in three interception experiments. In Experiment 1 (Constant Motion, Fig. 2A) each condition required participants to perform a reaching movement with their right index finger toward the right-edge (leading edge) of either the vortex or the rigid disk stimuli moving at either of two velocities: fast ($10^\circ/\text{s}$) and slow ($5^\circ/\text{s}$). There were four conditions combining the reaching task with different gaze behaviors: constant ocular fixation at the starting point of the target's movement (Fixation, Fig. 2A), target following (Following, Fig. 2A), constant ocular fixation close to the target's position at the timepoint of the go signal (Central fixation, Fig. 2A), and ocular fixation with a subsequent saccade just before the reaching movement (Saccade, Fig. 2A). Trials began with a fixation dot, at 18° to the left (starting point of the target's movement) or central, depending on the condition. Participants received different instructions depending on the condition. In the Fixation and Central fixation conditions, they were instructed to maintain fixation throughout the entire trial either on the left or centrally. In the Saccade condition, they fixated on the left until the go signal and then made a saccade to the stimulus. In the Following condition, they tracked the right edge of the moving stimulus from trial onset. Experiment 2 (Perturbed, Fig. 2B) only used the Fixation condition and a fixed initial speed of $10^\circ/\text{s}$. After reaching onset, the stimulus continued at $10^\circ/\text{s}$ on 60% of trials (*same* trials). It sped up to $15^\circ/\text{s}$ on 20% of trials (*faster* trials). It stopped on 20% (*stop* trials), during which the vortex maintained local rotation at the last location and the rigid disk softly brightened, preventing the target from perceptually blending into the background and preserving a clear position signal until touch. Experiment 3 (Disappear, Fig. 2C), again used only the Fixation condition and a $10^\circ/\text{s}$ starting speed. Following reaching onset, the stimulus and background dots disappeared, and participants were instructed to reach for the remembered right-edge location of the target, i.e. the last seen location before the target vanished.

Across all three experiments we tested reaching to the right-edge of two moving stimuli (Fig. 3A): a vortex (for nonrigid motion, see Methods for details) and a rigid disk (rigid motion). Stimuli always moved horizontally from left to right. Each trial was initiated by a button press, which triggered stimulus motion. After a variable delay, an auditory cue signaled participants to release the button and reach toward the stimulus edge.

A - Experiment 1: Constant Motion



B - Experiment 2: Perturbed



C - Experiment 3: Disappear

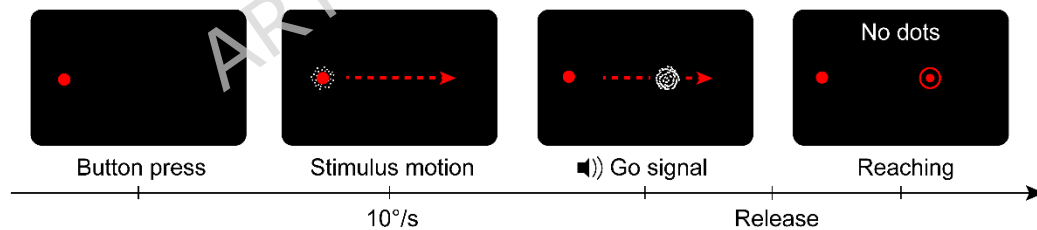


Figure 2. Experimental paradigms. A) Constant motion experiment: Four conditions: (I) Lateral fixation (Fixation), where fixation was maintained on a dot positioned 18° to the left of center. (II) Lateral fixation with saccade (Saccade), where participants fixated the lateral dot until the go signal, then performed a saccade to the moving stimulus before reaching it. (III) Following, where participants continuously tracked the right-edge of the moving stimulus. (IV) Central fixation, in which participants maintained fixation on a central dot throughout the trial. In all conditions stimuli moved horizontally from left to right at two velocities (slow: $5^\circ/\text{s}$; fast: $10^\circ/\text{s}$). Following an

auditory go cue, participants reached toward the right-edge of the stimuli (reaching endpoint represented by the red circle with a red dot inside). B) Perturbed experiment: Lateral fixation only (18° to the left from the center), starting velocity of $10^\circ/\text{s}$. After the reaching onset the stimulus either continued to move at the same velocity (*same* trials, 60%), sped up to $15^\circ/\text{s}$ (*faster* trials, 20%), or stopped (*stop* trials, 20%). C) Disappear experiment: Lateral fixation only (18° to the left from the center), starting velocity of $10^\circ/\text{s}$. After the reaching onset the stimulus and the noise disappeared, and participants reached to the remembered right-edge location.

Reaction times are not influenced by the velocity of nonrigid motion

In all the conditions of the “Constant motion” experiment, reaction times (RT) showed significant main effects of velocity and stimulus type (see Supplementary Table 1) and a significant interaction between stimulus velocity and stimulus type (four two-way rANOVA, all $F > 4.95$, all partial $\eta^2 > 0.2$, all $p < 0.04$; Fig. 3B). Specifically, as expected, participants presented faster RTs when reaching to fast rigid motion than to slow rigid motion (all Bonferroni corrected $p < 10^{-6}$, Fig. 3B-E). In contrast, the velocity of the vortex had no significant effect on RTs (all Bonferroni corrected $p > 0.3$, Fig. 3B-E), indicating that the RT computation for reaching toward nonrigid moving targets did not involve the velocity of the nonrigid stimulus. Finding a less clear influence of speed on reaction time is consistent with not relying on velocity, because reaction times are known to decrease with increasing target velocity^{24–26}. This finding was observed irrespectively of where participants were looking or of whether they had moved their eyes before the reach (Fig. 3B-E).

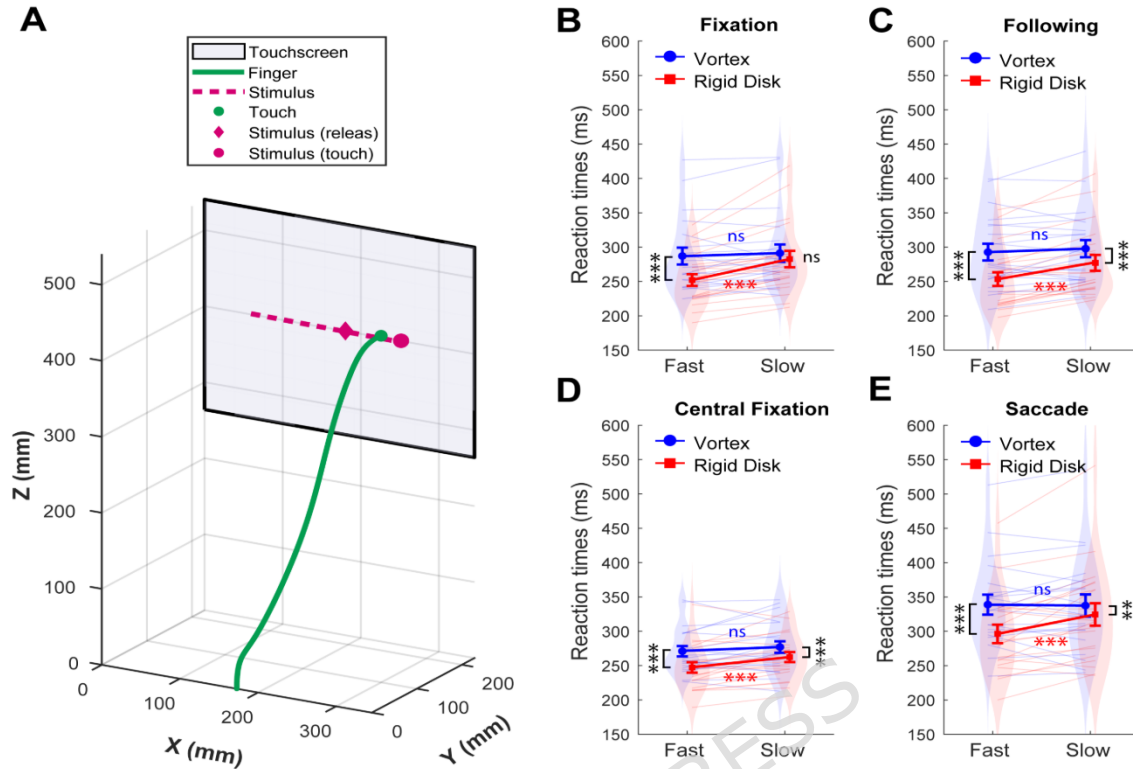


Figure 3. Reaction times do not systematically decrease with nonrigid motion. A) Reconstruction of hand and stimulus trajectories in a representative "vortex fast" trial of the constant motion experiment. The black opaque-filled rectangle represents the touchscreen surface. The magenta dotted line is the stimulus trajectory, the magenta markers are the stimulus position at time release (rhombus) and at touch (circle). The green line is the index finger trajectory, the green circular marker is the finger position at the time touch. B-E) Violin plots illustrating reaction time results of all the conditions of the Constant motion experiment. For all the result plots: Blue = vortex, Red = rigid disk. Error bars represent $\pm$ one SEM. Background lines indicate individual participants' data. The asterisks mark a statistically significant Bonferroni corrected post-hoc difference (***) = $p < 0.001$), ns = non-significant.

Velocity-dependent undershoots during reaching execution

To evaluate whether nonrigid velocity was appropriately incorporated during reach execution, we examined endpoint accuracy in the "Constant-motion" condition. For reaching accuracy, there were significant main effects of velocity and stimulus type (see Supplementary Table 1) as well as a significant interaction between stimulus velocity and type (four two-way rANOVA, all $F > 54.64$, all partial $\eta^2 > 0.74$, all $p < 10^{-6}$; Fig. 4A-D). For both velocities, reaching to the nonrigid target

was less accurate than reaching to the rigid disk (all Bonferroni corrected $p < 10^{-7}$), with this effect being more pronounced at higher stimulus velocities. Notably, these effects on reaching accuracy were consistent across all the conditions, suggesting that the presence or absence of ocular movements did not influence the general result: reaching to the vortex resulted in pronounced, velocity dependent undershoots regardless of the ocular movements (Fig. 4A-D).

In contrast with this velocity-dependent difference in endpoint errors between the vortex and the rigid disk for manual reaching, we found no statistically significant differences (two two-way rANOVA, all $F < 10^{-4}$, all partial $\eta^2 < 10^{-4}$, all $p > 0.98$; Fig. 4E-F) between the endpoints errors of saccades toward the vortex and toward the rigid disk before reaching (Saccade condition, Fig. 4F), nor between endpoints errors of saccades on the vortex and smooth pursuit of the rigid disk when participants tracked the target with their eyes before reaching (Following condition, Fig. 4E). For both kinds of stimuli the eyes landed very close to the target, irrespective of the target's speed. Thus, the vortex's position after the saccade was correctly anticipated, despite its velocity not being judged well enough to smoothly pursue it or to guide the hand to it.

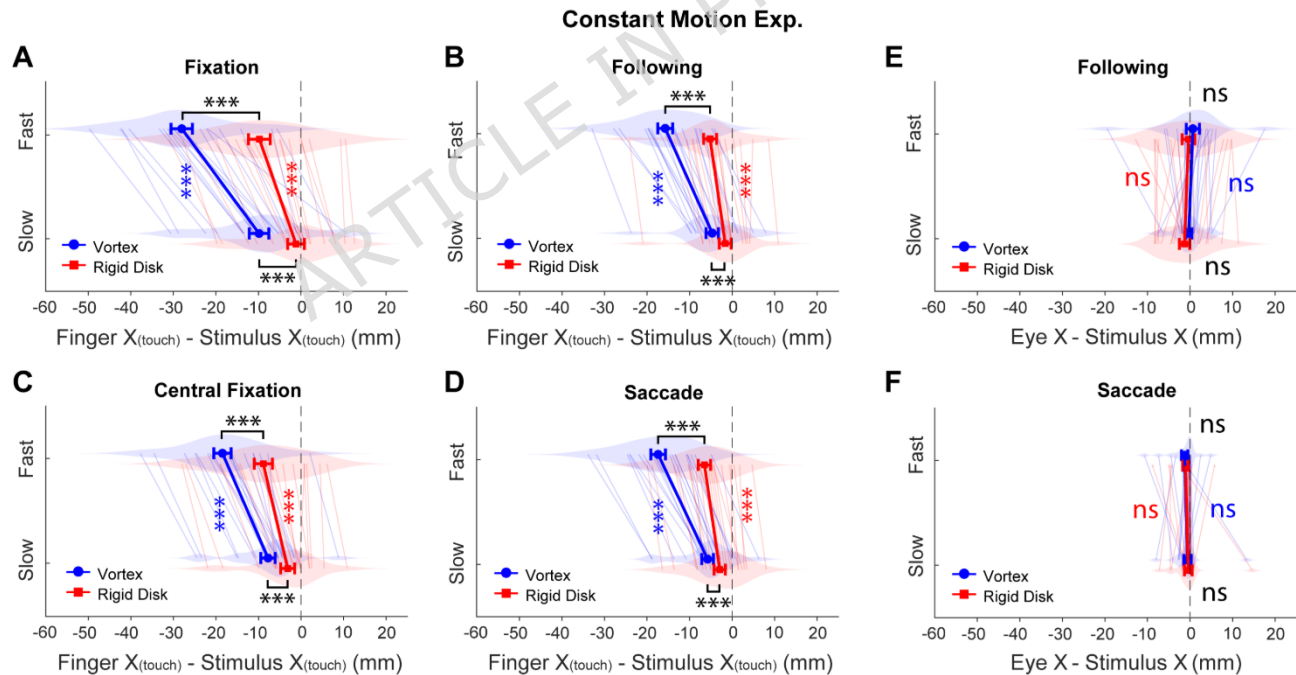


Figure 4. Reaching fails where saccades succeed. A-D) Violin plots illustrating horizontal accuracy of reaching endpoints in the Constant motion experiment in the Fixation, Following, Central fixation and Saccade Condition, expressed as horizontal (X) coordinate of the index finger subtracted of the horizontal coordinate of the stimulus, both at time of finger touching on the

screen. E) and F) Horizontal accuracy of saccade endpoints in the Constant motion experiment in the Following and Saccade conditions. For the Rigid Disk in the Following condition, we determined the average distance between gaze and target during 1000 ms of the target's motion rather than saccade endpoints, because the target is followed with smooth pursuit. For all the result plots: Blue = vortex, Red = rigid disk, All other conventions as in Fig. 3.

Online perturbations of target motion confirm that nonrigid motion induces velocity-dependent undershooting during reaching execution

In the “Perturbed” experiment, we observed a significant interaction between stimulus type and perturbation on reaching accuracy (two-way rANOVA, $F(2,38) = 147.97$, $\eta^2 = 0.89$, $p < 10^{-10}$; Fig. 5A). When the stimulus motion had a constant velocity (*same* condition), undershoot differences between the rigid disk and the vortex replicated the undershoot observed in the “Constant motion” experiment (Experiment 1). In the *faster* condition, the error (undershooting the target) was larger than for the *same* condition, both for the nonrigid and the rigid target (Fig 5A), but part of the change in velocity since reaching movement onset was considered: in the Fast condition, the final touch location was farther from the target position at reaching onset than in the Same condition. (Fig 5B; significant interaction between stimulus type and perturbation in two-way rANOVA, $F(2,38) = 118.91$, $\eta^2 = 0.86$, $p < 10^{-10}$). In the *stop* condition, endpoint accuracy differed only minimally between rigid-disk and vortex targets ($p = 0.049$), with the overall average error for the nonrigid target being very close to zero (upper yellow dot in Figure 5A). All this is consistent with the position being updated while failing to predict the target's further motion on the basis of its new (faster) velocity.

Assuming that the position is constantly updated while the motion is totally ignored until the last moment at which the movement endpoint can still be adjusted on the basis of new visual information, we would expect about the same fraction of the target's displacement, as of its additional displacement when its velocity increases, to be considered. To see whether this is so, we calculated two gains. The first compared the distance to the final reaching endpoint from the targets position at reaching onset, with the target's displacement during the reaching movement. The second compared the change in reaching endpoint with the additional target displacement when the target moved faster. In all cases (Fig 5 C-D) we found a similar gain (Fig. 5C), which was clearly lower for the vortex than for the rigid disk (all $p < 10^{-8}$, Fig. 5D, $p < 10^{-5}$), showing

that participants partially adjusted their reaches to the velocity of the target, as well as to any increased velocity after release, but that they consistently did so to a lesser degree for the vortex than for rigid targets. The similarity between the gains for the *same* and *faster* conditions suggests that only the motion after release is relevant, and that the fraction of the displacement that is considered is independent of the target's speed. The higher gain for the rigid disk is consistent with the target's position being updated until a later moment for the rigid disk, suggesting that the latency in determining its position is shorter than that of the vortex (i.e. that it takes longer to localize the vortex).

Endpoint errors reveal reduced planning accuracy for reaching to nonrigid targets

Our “Disappear” experiment was designed to evaluate reaching based on information available before movement execution, by removing all visual information about the target at movement onset. In this experiment, all visual stimuli vanished at movement onset and participants had to reach toward the remembered right-edge location of the target, with no visual feedback during execution. Participants showed a greater horizontal undershoot when reaching to the remembered vortex location than when reaching to the remembered rigid-disk location (Fig. 5E, one-way ANOVA, $F(1, 19) = 35.36$, partial $\eta^2 = 0.65$, $p < 10^{-4}$). Thus, when post-release visual information was unavailable, reaching to the vortex was less accurate than reaching to the rigid disk. Experiment 3 shows that if the vortex disappears during execution, participants reach for a position that it has already passed.

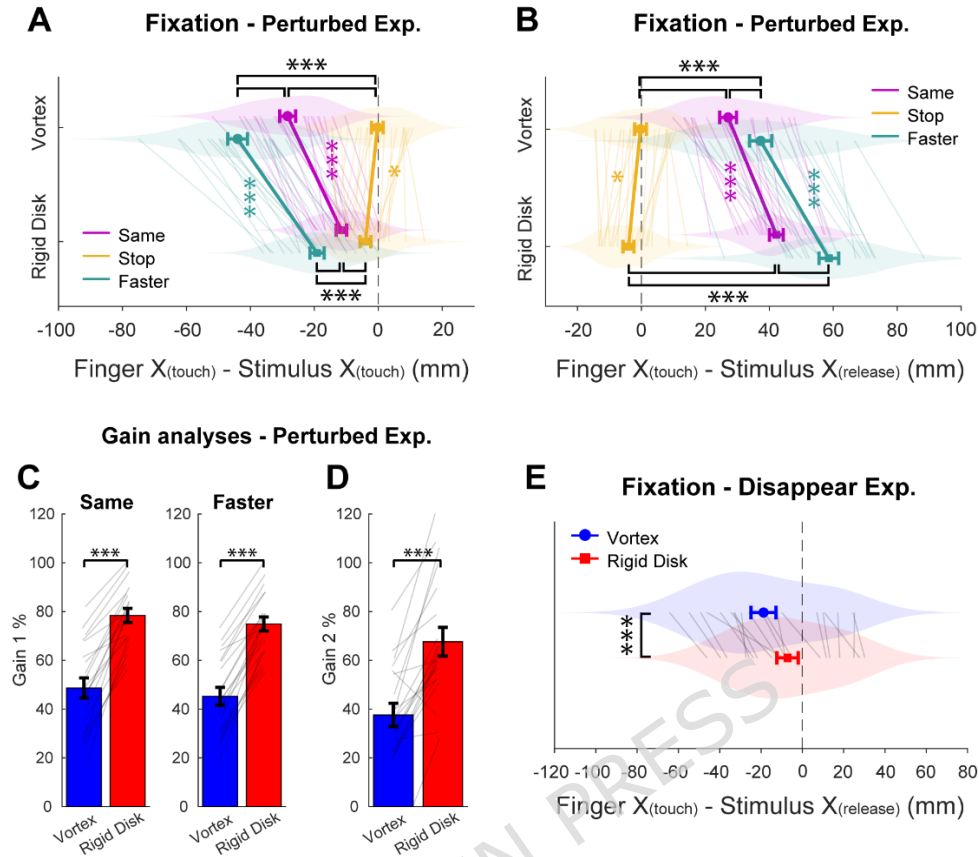


Figure 5. Further confirmation that the reaching system relies on vortex position, not vortex velocity. A) Violin plot showing horizontal accuracy of reaching endpoints in the perturbed experiment. B) Violin plot showing the horizontal distance from the final touch position to the target location at reaching onset. C) Gain 1 quantifies the proportion of the stimulus's total displacement that the finger covered during the interception movement, calculated separately for the same and faster conditions. D) Gain 2 quantifies how participants adapt their interception movements to changes in stimulus velocity, normalized by the actual difference in stimulus displacement across conditions. More information about both gains can be found in the Methods section. E) Violin plot of the horizontal accuracy of reaching endpoints in the Disappear experiment, assessed by subtracting the horizontal position of the index finger at time touch from the horizontal position of the stimulus at time release. For all the result plots: Blue = vortex, Red = rigid disk, Magenta = Same condition, Green = Faster condition, Yellow = Stop condition. All other conventions as in Figs. 3 and 4.

Discussion

The central challenge of moving-target interception is accurate prediction under sensorimotor delay. To probe how different effector systems obtain the motion information needed for extrapolation, we leveraged a nonrigid “vortex” stimulus that supports accurate saccade targeting but fails to provide a usable velocity signal for smooth pursuit. We tested whether reaching shows the same limitation. Our results indicate that vortex velocity also fails to provide a usable velocity signal to support velocity-based prediction in the reaching system: interception behavior is best explained by delayed position-based updating. In the sections below, we first examine how reaching performance constrains the motion information available for different sensorimotor tasks. We then discuss the implications of these constraints for the neural pathways underlying reaching, smooth pursuit, and saccadic eye movements.

The reaching system has limited access to nonrigid velocity

Across our experiments, multiple measures converged on the same conclusion: the reaching system has limited access to the vortex’s nonrigid velocity. A planning-stage signature of velocity use in interception is that reaction times (RTs) decrease for faster targets^{24–26}. In our “Constant motion” task, RTs for rigid motion scaled with target velocity, consistent with this literature (Fig. 3B-E). For the vortex, in contrast, RTs were indistinguishable between slow and fast motion (Fig. 3B-E), indicating that the nonrigid velocity information did not contribute to reaching initiation irrespectively of any oculomotor activity performed before reaching.

The interpretation that the reaching system has limited access to nonrigid velocity is reinforced by the endpoint patterns. In the “Constant motion” experiment, reaching toward the vortex showed a pronounced undershoot relative to the rigid disk, and this undershoot increased strongly with stimulus velocity (Fig. 4A-D). This effect was consistent across all experimental conditions, indicating that it was not influenced by any ocular interaction with the stimuli. Reaching toward the rigid disk was also not perfectly precise, but this is expected given the absence of trial-by-trial feedback and the inherent uncertainty involved in tapping moving targets²⁷. Moreover, velocity information for conventional moving targets is itself imperfectly used, as interception can be influenced by the speed of preceding targets²⁸. Together, these results indicate that the reaching system has limited access to a usable nonrigid velocity signal and therefore relies more heavily on position information. Because visuomotor processing is delayed, position-based control

necessarily becomes less accurate as target speed increases, producing the observed velocity-dependent undershoots.

The “Perturbed” experiment confirmed that the reach is continuously updated during execution, while also revealing the specific limitation underlying vortex interception. Changing target velocity at time of release produced systematic shifts in final touch position, demonstrating that participants did not simply execute a fixed preplanned movement. Critically, the *stop* condition provides a strong positive control for position processing: when the target stopped (Fig. 5A-B), participants corrected their trajectories and reached the vortex with accuracy comparable to the rigid target, demonstrating that the reaching system can access the visible position of the stationary, yet still rotating, vortex for online correction. When the target accelerated (Fig. 5A-B), performance for rigid and vortex targets diverged in a manner that was consistent with the original difference. For the rigid disk, the reaching system compensated for most of the additional target displacement induced by the acceleration (Fig. 5A-B), consistent with online control that can incorporate target motion. For the vortex, in contrast, compensation was markedly reduced, and the undershoot was more pronounced, consistent with either ignoring the higher speed in the *Faster* condition, or updating the position more slowly. The gains of movement incorporation were similar for the two speeds and for the change in speed for the vortex (Fig. 5C-D). This similarity is consistent with a delayed position-updating account, but is not independent evidence that velocity was ignored. If movement times are comparable, as they were across conditions (*same* vortex: 497 ms; *same* rigid: 482 ms; *stop* vortex: 520 ms; *stop* rigid: 529 ms; *faster* vortex: 485 ms; *faster* rigid: 466 ms), and position is updated only until a similar delay before movement end, then the gain for the additional displacement in the *faster* condition is expected to resemble the gain for the total displacement in the *same* and *faster* conditions. The gain analysis therefore mainly shows that this interpretation is quantitatively viable: vortex motion was incorporated to a similarly limited extent for constant and accelerating target motion. Thus, without sufficient access to velocity information, both conditions appear to impose the same position-driven control demand, namely delayed reactive correction to the evolving target position.

In summary, we suggest that our results are best explained by the reaching system having insufficient access to the vortex’s nonrigid velocity signal, as compared with such a velocity signal for rigid motion. As a result, reaching is guided by position information that is continuously

updated over time, rather than inferred from judged motion²⁹. This continuous updating is sufficient for online corrections once motion ceases, but is inadequate for accurate prediction when the target continues to move. In contrast, saccades reliably land on the correct vortex position, which necessarily requires using the target's velocity to predict its future location¹⁵. Together, these results suggest that the information given by nonrigid motion is exploited more effectively for saccadic localization than for manual interception. Moreover, participants may have perceived the vortex as moving and may have inferred its velocity from changes in position over time, but the available velocity information appears to have been insufficient to support accurate reaching, just as it was insufficient to support smooth pursuit.

Potential brain areas involved in these two separate sensorimotor systems

Previous research using the same nonrigid vortex stimulus demonstrated that the smooth pursuit system was unable to track nonrigid motion, but that saccadic tracking was highly accurate¹⁵. This finding suggests that nonrigid motion-related signals are not transmitted to brain regions specialized for smooth pursuit, such as the middle temporal (MT) and medial superior temporal (MST) areas^{30,31}. Our study presents novel evidence that the reaching system, like the smooth pursuit one, fails to access nonrigid motion.

The lateral intraparietal area (LIP) is a possible candidate for supplying nonrigid velocity estimates for interceptive saccades, given its involvement in saccadic planning^{32–34}, and the fact that it carries motion-related information that could predict accurate saccade targeting^{35,36}. However, it is important to note that the visual nonrigid motion input to LIP is unlikely to originate from regions such as MT or MST. It is more plausible that visual information related to nonrigid motion reaches LIP via areas such as V3, V3A^{37,38}, or V6³⁹, which is strongly activated by coherently moving dot fields at both the single-subject and group level^{40–42}. In macaques, areas V3A and V6 contribute to the analysis of form and motion within the visual field and contain a high proportion of neurons selective for motion direction^{40,43}.

In humans, area KO/V3B, located near V3A, is known to respond strongly to kinetic boundaries^{44–47}, (contours defined solely by differences in motion direction) a property shared by our nonrigid motion vortex stimulus. Since there is direct evidence of projections from KO/V3B to LIP^{37,48}, it is reasonable to speculate that this area represents a good candidate for processing and transmitting nonrigid motion velocity to LIP. Another good candidate for providing motion signals LIP could

be V6, which is strongly motion-sensitive, responding to coherent and global motion^{41,42,49} and unfamiliar movement sequences⁵⁰ and in macaques was found to project to LIP^{39,3839,4647}

Further insights into the brain regions potentially involved in processing nonrigid motion can be drawn from studies examining the double-drift illusion. This illusion causes observers to perceive a trajectory that gradually deviates along a slope from the actual physical path, which is strictly vertical with no inclination^{51–53}. For this stimulus, manual responses have been shown to be biased toward the illusory perceived position rather than the physical one^{54,55}, whereas saccades were initially reported to land on the physical location⁵². A later re-analysis, however, showed that when position and motion are modeled independently, saccade endpoints align with the extrapolated path implied by the biased motion signal⁵⁶. Moreover, an fMRI study on the double-drift illusion revealed that several regions, including hMT+ and V3A/B, exhibited significant decoding of the illusion. However, only activity in hMT+ successfully described the illusory trajectory⁵³. No activation of V6 was reported in this study.

In light of our findings, we propose a functional dissociation between the processing routes for nonrigid velocity and positional information. In the double-drift illusion, both saccades and reaching are impaired, and the illusory motion signal is decoded in both MT (hMT+) and V3A/B. In contrast, with our vortex stimulus, saccades land with high precision on the physical target¹⁵, suggesting that nonrigid velocity is preserved for saccade planning. Based on this contrast, we argue that nonrigid velocity signals reach V3A/B but fail to propagate to MT, where only the vortex's continuously updated positional information appears to be available. Area V6 also does not appear to access nonrigid velocity, if it did this information could have been transmitted to reach-related parietal areas such as V6A and PEc^{39,40,57–59}. Given that V3A/B is anatomically connected to both MT and LIP^{37,48}, and that MT is connected to parietal areas involved in reaching^{60,61} and V6³⁹, we suggest the following organization: non-rigid motion signals are transmitted to V3A/B and subsequently to LIP (supporting accurate saccade planning) while their absence in MT and V6 leads to the characteristic errors observed in smooth pursuit and reaching.

Conclusion

Intercepting a moving target is fundamentally a problem of prediction under delay: when sensory processing and motor execution lag behind the world, successful control depends on motion information (especially velocity) to extrapolate future target position. By using the nonrigid vortex

as a stimulus-based perturbation of motion-to-action processing, we could test whether the limb motor system has access to the same velocity information that supports saccade targeting, or whether it behaves more like smooth pursuit, which cannot use this stimulus for velocity-based tracking.

Across three complementary manipulations, reaching to the vortex showed a consistent absence of behavioral signatures that normally indicate velocity-based prediction. Unlike reaching to a rigid moving disk, reaction times did not scale with vortex speed, and interception errors grew steeply with speed. During execution, reaches were not simply ballistic: perturbations at reach onset shifted touch positions, indicating ongoing online updating. Yet this updating did not reflect access to a usable velocity signal. Instead, performance was best explained by delayed, position-driven correction: when motion ceased (*stop* trials), accuracy recovered to rigid-like levels, while for continued motion, whether constant (*same*) or unexpectedly faster (*faster*), similarly low gains were found for the vortex, consistent with a controller that cannot incorporate target velocity and must react to evolving position with delay.

Together with prior evidence that saccades remain accurate for the same vortex stimulus, the present findings suggest a principled dissociation in motion-to-action transformations: reaching and smooth pursuit share a motion pathway that has limited access to a usable nonrigid velocity signal, whereas saccadic targeting preserves a velocity-based representation sufficient for predictive localization.

Materials and Methods

Participants

Forty healthy individuals volunteered to participate in this study. Participants were divided into two groups: one group of twenty took part in the first experiment (10 females and 10 males; average age: 28.4 ± 6.66 years; age range: 21–50 years), and the other in the second and third experiments (10 females and 10 males; average age: 24.1 ± 6.88 years; age range: 19–50 years). In all experiments participants were naive about the purpose of the study. The participants were classified as right-handed based on the Edinburgh Handedness Inventory ⁶² and had normal or corrected-to-normal visual acuity in both eyes. Participants provided written informed consent, and the procedures were approved by the Bioethical Committee at the University of Bologna (Prot.

n 76043) and were in accordance with the ethical standards of the 2013 Declaration of Helsinki. Participants did not receive trial-by-trial performance feedback in any of the experiments.

Apparatus

Stimuli were displayed on a 19-inch touchscreen (ELO IntelliTouch 1939 L) set vertically on a desk, 40cm in front of the participant. For stimuli presentation, we used Matlab (Mathworks, Natick, MA, USA, RRID:SCR_001622) with the Psychtoolbox extension⁶³. Participants were seated on a chair in a darkened room, with their head stabilized by a head/chin rest to minimize head movements. In all trials, the reaching movement started with the participant's right hand on a button placed on the desk (home button) at ~22cm from the touchscreen, centered to the participant's head position. Eye-tracking data were recorded with an Eyelink 1000 (SR Research, Ontario, Canada). Calibration was performed with a white nine-point grid on a black background. The kinematics of reaching movements were used to evaluate performance. They were recorded using a motion tracking system (VICON motion capture system, 6 M cameras, 1024 × 1024 pixel resolution) by sampling the position of one marker attached on the nail of the index finger (reaching finger) at a frequency of 100 Hz. All data streams were synchronized via hardware triggers controlled by MATLAB: the Psychtoolbox EyeLink Toolbox allowed event markers to be time-locked to stimulus presentation, while a custom low-latency MATLAB-to-Arduino serial protocol enabled the Arduino to generate digital pulses for VICON. This setup ensured precise temporal alignment across visual stimuli, eye-tracking data, and kinematic measurements.

Stimuli

In all the experiments, each frame of the stimulus was presented on a black background filled with 10,000 randomly distributed white pixel-sized dots. Two types of stimuli were studied: a vortex pattern (nonrigid stimulus) and a rigid disk. The vortex had a diameter of 3.75° and rotated at a speed of $45^\circ/\text{s}$. Between each frame of the stimulus, the center of the vortex shifted progressively. Individual dots did not follow the trajectory of the vortex center. Instead, in each frame, they rotated locally around the current vortex center. As a result, the motion of the vortex was not carried by the dots but was perceived through the changing rotational pattern over time. This created a dynamic structure that continuously recruited and released dots as it moved. The rigid disk was composed of dots that translated as a coherent, non-rotating rigid body of the same size

as the vortex. As it moved across the display, this rigid structure occluded the background dots, in contrast to the nonrigid vortex stimulus, in which dots were continually replaced rather than carried along.

Experiment 1 – Constant Motion

This experiment presented four main conditions: central fixation, lateral fixation, lateral fixation with saccade, and following. Each condition was tested using both the vortex and rigid disk stimuli at two different velocities: 10°/s (fast) and 5°/s (slow). Each experimental condition started by presenting a black screen displaying only the fixation point (red dot, 3mm of diameter). The onset of the trial was triggered by a button press, which initiated the appearance of the moving stimulus (either the vortex or the rigid disk) traveling horizontally from the left to the right side of the screen. After a variable delay of 750-1300 ms (fast trials), and 750-2000 ms (slow trials) from stimulus onset, an auditory cue signaled the participant to release the button and reach toward the screen, aiming for the right-edge of the moving stimulus. The trial concluded upon screen touch, after which the intertrial black screen with the fixation point reappeared, awaiting the next button press to initiate the subsequent trial. In the central fixation condition, the fixation point was positioned centrally, slightly below the center of the screen to avoid overlapping with the trajectory of the moving stimuli. In the lateral fixation, lateral fixation with saccade and following conditions, the fixation point was positioned laterally on the left at 18° from the center, corresponding to the location where the stimuli began moving rightward at the start of each trial. In the central fixation and lateral fixation conditions, participants were instructed to maintain their gaze on the fixation point for the entire duration of the trial. In the lateral fixation with saccade condition, participants were instructed to maintain their gaze on the fixation point until the auditory cue was played. After hearing the cue, they were required to perform a saccade toward the right-edge of the moving stimulus and subsequently reach toward it. In the following condition, they were instructed to track the right-edge of the moving stimulus throughout the trial. Each experimental session lasted approximately one hour and was organized into blocks of 100 randomized trials of a single condition (central fixation, lateral fixation, lateral fixation with saccade, and following). Within each block, 25 trials were assigned to each subcondition (vortex fast, vortex slow, rigid disk fast, rigid disk slow). Participants completed two blocks for each of the four conditions, resulting in a total of 50 trials per subcondition.

Experiment 2 – Perturbed

The experiment involved a single main condition with three conditions: same, faster, and stop. Each condition was tested with both the vortex and rigid disk stimuli, using a constant pre-perturbation starting velocity of $10^\circ/\text{s}$. Each experimental condition began with a black screen displaying only a fixation point (red dot, 3mm of diameter), positioned laterally on the left at 18° from the center. Participants were instructed to maintain fixation on this point throughout the entire trial. The onset of the trial was triggered by a button press, which initiated the appearance of the moving stimulus (either the vortex or the rigid disk) traveling horizontally from the left to the right side of the screen. After a variable delay of 750-1300 ms from stimulus onset, an auditory cue signaled the participant to release the button and reach toward the screen, aiming for the right-edge of the moving stimulus. At time release, in 60% of the trials the stimulus continued moving at a constant velocity of $10^\circ/\text{s}$ (same condition). In the remaining 40% of trials, the stimulus velocity was perturbed: in 20% it increased its speed to $15^\circ/\text{s}$ (faster condition), and in 20% it stopped (stop condition). In the stop condition, the vortex stimulus kept rotating, while the rigid disk stimulus appeared slightly brighter, this was necessary to prevent them from blending into the background. The trial concluded upon screen touch, after which the intertrial black screen with the fixation point reappeared, awaiting the next button press to initiate the subsequent trial. Each experimental session lasted approximately forty minutes and was tested together with Experiment 2. Sessions were divided into blocks of 100 randomized trials. Within each block, 60 trials belonged to the same condition (30 vortex and 30 rigid disk), 20 to faster (10 vortex and 10 rigid disk), and 20 to stop (10 vortex and 10 rigid disk). Thus, each condition was tested with both vortex and rigid disk stimuli. Participants completed three blocks, a total of 90 trials for the same condition and 30 trials each for the faster and stop conditions.

Experiment 3 - Disappear

This experiment consisted in a single main condition tested with both the vortex and rigid disk stimuli, using a constant pre-perturbation starting velocity of $10^\circ/\text{s}$. Each experimental subcondition began with a black screen displaying only a fixation point (red dot, 3mm of diameter), positioned laterally on the left at 18° from the center. Participants were instructed to maintain fixation on this point throughout the entire trial. The onset of the trial was triggered by a button press, which initiated the appearance of the moving stimulus (either the vortex or the rigid disk)

traveling horizontally from the left to the right side of the screen. After a variable delay of 750-1300 ms from stimulus onset, an auditory cue signaled the participant to release the button and reach toward the screen, aiming for the right-edge of the moving stimulus. At time release, all stimuli disappeared from the screen, leaving only the fixation point on a black background. Participants were instructed to reach the last visible position of the stimuli, in other words, where they remembered the right-edge of the stimulus to be. The trial concluded upon screen touch, after which the intertrial black screen with the fixation point reappeared, awaiting the next button press to initiate the subsequent trial. Each experimental session lasted approximately forty minutes and was tested together with Experiment 2. Sessions were divided into blocks of 100 randomized trials. Within each block, 50 presented the vortex stimulus and other 50 the rigid disk. Participants completed one block.

Data analysis

We measured reaching reaction time (RT) as the interval between the go signal and movement onset, defined by release of the home button, movement offset corresponded to touchscreen contact. Touchscreen contact was identified through kinematic analysis by determining the time point after reaching start at which the reaching velocity decreased below 30 mm/s and remained below this threshold. In experiment 1, we conducted a two-way repeated-measures ANOVA on mean RT with stimulus velocity (fast, slow) and stimulus type (vortex, rigid disk) as within-subject factors. Horizontal reaching accuracy was defined as (horizontal coordinate of the index finger, Finger X – horizontal coordinate of stimulus, Stim X) at time of touch and analyzed with a two-way repeated-measures ANOVA using the same factors. We also quantified eye undershoots in the following and saccade conditions. For following rigid disk trials, which contained no saccades due to smooth pursuit, undershoot was the mean eye–stimulus horizontal difference over a 1000 ms window from trial start. For vortex trials, we excluded the first (typically noisy) saccade and averaged the remaining eye – stimulus differences at the saccade endpoints. In the saccade condition, undershoot was computed as the horizontal eye – stimulus difference at the end of the saccade (Eye X – Stim X) for the saccade executed at time release, for both stimulus types.

In experiment 2 we calculated the reaching accuracy, with the formula (Index horizontal coordinate at time touch – Stimulus horizontal coordinate at time touch), and performed a two-way rANOVA with perturbation condition (same vs. stop vs. faster) and stimulus type (vortex vs.

rigid disk) as factors. We also evaluated the reaching position in another way, with the formula (Index horizontal coordinate at time touch, Finger X – Stimulus horizontal coordinate at time release, StimX), and performed another two-way rANOVA with perturbation (same vs. stop vs. faster) and stimulus type (vortex vs. rigid disk) as factors.

On the same and faster conditions of experiment 2, we calculated two gain indexes to quantify the extent to which changes in stimulus velocity were incorporated into participants' reaching movements. Gain 1 quantifies the fraction of the stimulus displacement during the movement that the finger considers. This is calculated separately for the two conditions (same and faster):

$$Gain1\% = \frac{Finger_X^{Touch} - Stimulus_X^{Release}}{Stimulus_X^{Touch} - Stimulus_X^{Release}} \times 100$$

Gain 2 quantifies the fraction of the additional displacement during the movement when the stimulus moves faster than the finger considers:

$$Gain2\% = \frac{[(Finger_X^{TouchFaster} - Stimulus_X^{ReleaseFaster}) - (Finger_X^{TouchSame} - Stimulus_X^{ReleaseSame})]}{[(Stimulus_X^{TouchFaster} - Stimulus_X^{ReleaseFaster}) - (Stimulus_X^{TouchSame} - Stimulus_X^{ReleaseSame})]} \times 100$$

In experiment 3, we calculated the reaching accuracy, with the formula (Index horizontal coordinate at time touch – Stimulus horizontal coordinate at time release). We performed a one-way rANOVA with stimulus type (vortex vs. rigid disk) as a factor.

In all analyses, the threshold for significance was 0.05 and we Bonferroni corrected for multiple comparisons. All analyses of reaching accuracy in this paper derived endpoint estimates from hand kinematics, thereby avoiding potential timing delays inherent to the touchscreen registration.

Additional statistical results not reported in the main text, together with their corresponding p values and effect sizes, are provided in the Supplementary Materials.

Data availability statement

The anonymized datasets generated and/or analyzed in the present study are publicly available in the Open Science Framework repository (https://osf.io/etudh/overview?view_only=22e88951ff4b478c94b205852466234e). Numerical source data underlying all figures are provided in the Supplementary Data, along with an example video illustrating the vortex stimulus.

Code availability statement

This study used standard, custom-built MATLAB programmed scripts that are available from the lead contact upon request.

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Author contributions

Ri.B., K.K., M.L. and Ro.B. designed research; Ri.B. and K.K. programmed the experimental tasks; Ri.B. performed research and wrote the codes for data analyses; Ri.B., K.K., M.L., E.B. and Ro.B. analyzed data; Ri.B. wrote the first draft of the paper; PF and ML acquired funding. All authors have seen, revised and approved the final version of the manuscript.

Ethics declarations

Declaration of interests: The authors declare no competing interest.

Ethics approval: All procedures were approved by the Bioethical Committee at the University of Bologna (Prot. n 76043) and were in accordance with the ethical standards of the 2013 Declaration of Helsinki.

Consent to participate: Informed consent was obtained from all participants.

Competing interest statement

The authors declare no competing interests.

Declaration of generative AI and AI-assisted technologies in the manuscript preparation process

During the preparation of this work some authors used ChatGPT 5.2 (OpenAI) in order to check and refine the grammar, wording, and clarity of the manuscript. After using this tool/service, the authors reviewed and edited the content as needed and take full responsibility for the content of the published article.

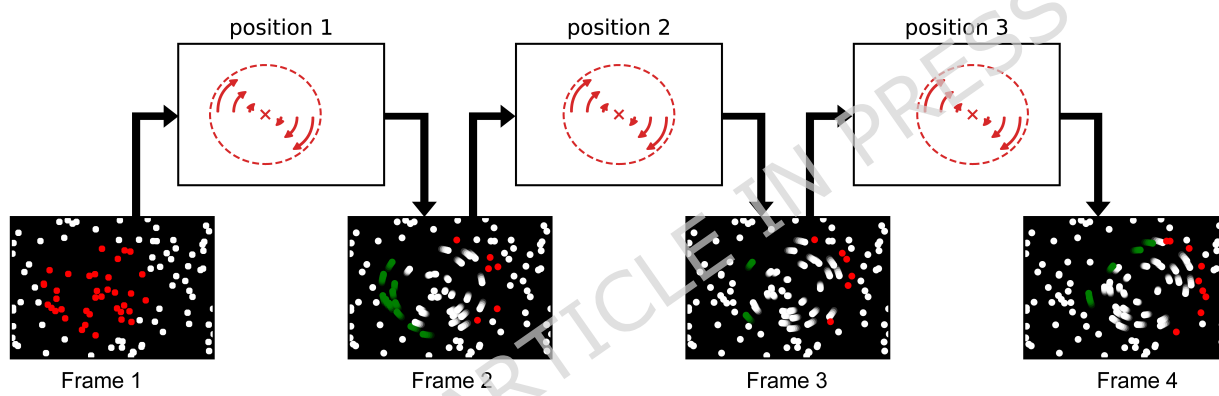
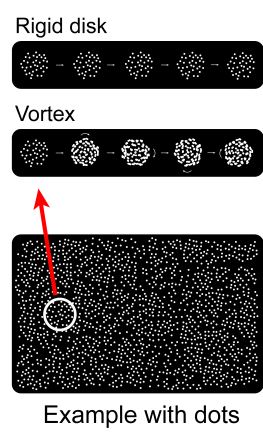
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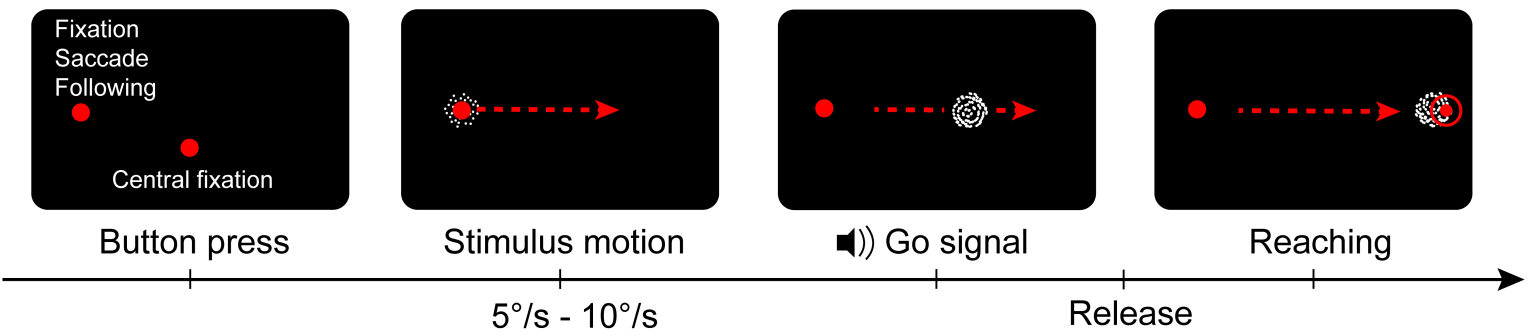
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A**B**

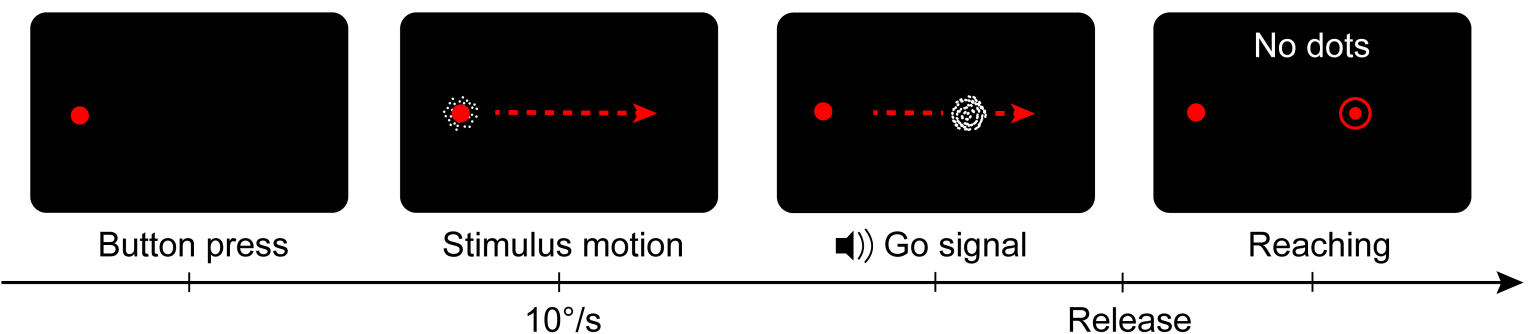
A - Experiment 1: Constant Motion

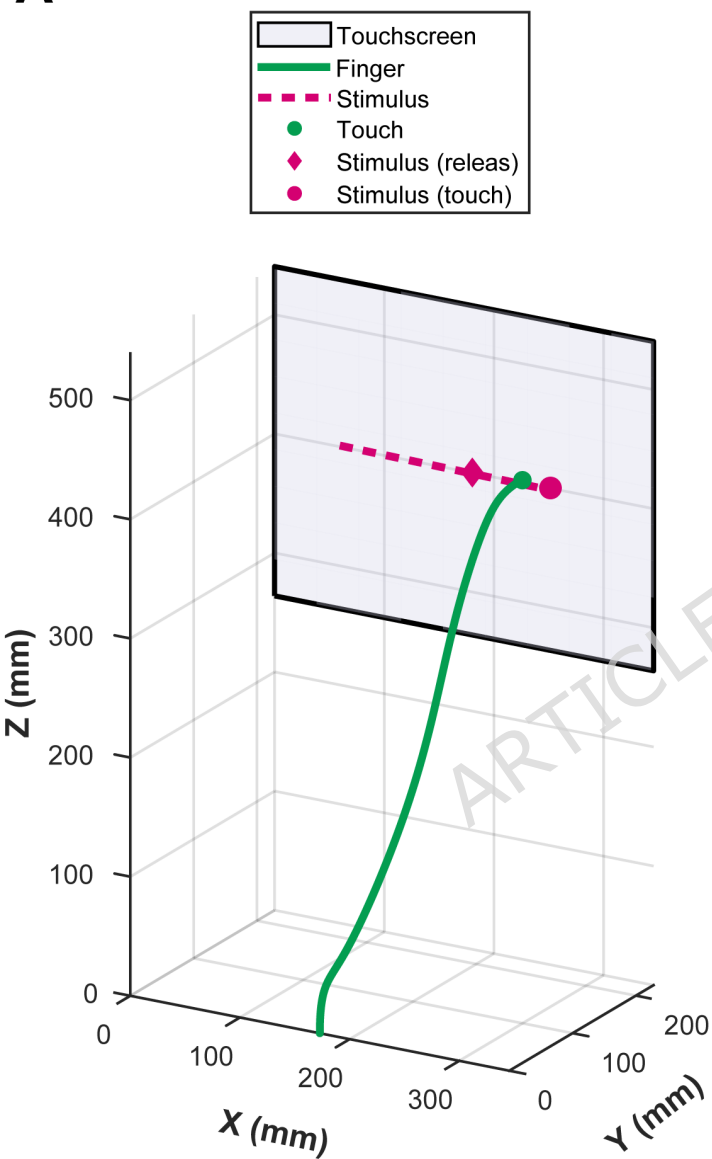
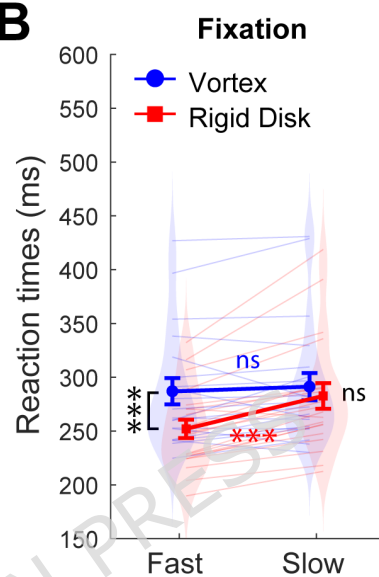
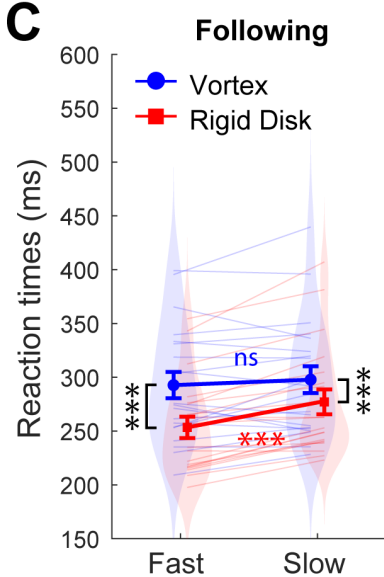
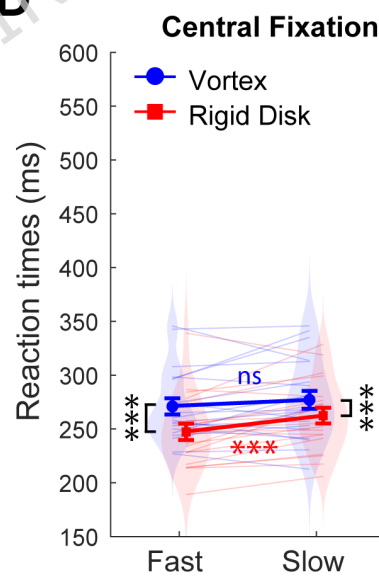
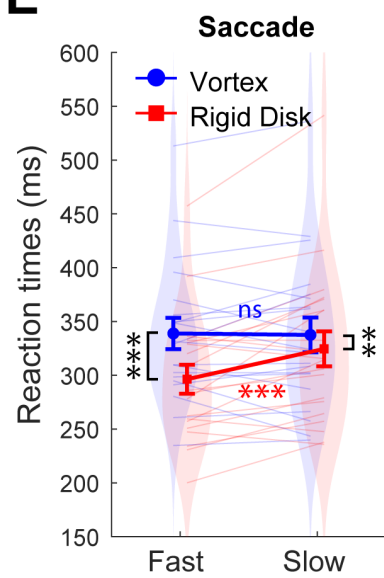


B - Experiment 2: Perturbed



C - Experiment 3: Disappear



A**B****C****D****E**

Constant Motion Exp.

