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Contribution of retinal motion toward the impulse control of target-directed aiming

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RUNNING HEAD: Moving background perturbation

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1 Abstract

Contemporary models of sensorimotor control contend that visually-regulated movement 2 adjustments may unfold early during a target-directed limb movement courtesy of an impulse 3 control process that makes use of anticipatory forward models. To-date, evidence surrounding 4 impulse control involves adjustments to a purported misperception in limb velocity following the 5 6 unexpected onset of a moving background. That is, the limb is perceived to move faster and 7 undershoots more whenever there is an incongruent moving background, and vice-versa. 8 However, it can be argued that this particular behaviour may alternatively manifest from an 9 independent oculo-manual-following response. The present study aimed to deconstruct these proposals, and with it, the processes that underlie impulse control. Participants had to rapidly 10 reach upward to land their index finger accurately on a target. On 33% of trials, the background, 11 over which the movement was made, moved in either the upward, downward, rightward, or 12 leftward directions. Displacements within the primary and perpendicular directions of the 13 14 movement showed spatial trajectories that were consistent with the directions of the moving backgrounds. This behaviour was most prevalent in measurements taken at the movements' peak 15 negative acceleration and endpoints. Moreover, the analysis of standardized displacements in the 16 17 moving background conditions indicated no significant differences in the extent of the movements toward each of the moving backgrounds. These findings indicate that movement 18 19 adjustments can manifest from an oculo-manual-following response rather than a misperception 20 in limb velocity. We suggest that the anticipatory forward model that comprises impulse control 21 may incorporate features of the environment that surround the vicinity of the limb.

1 Introduction

2 One role of the visuomotor system is to facilitate control of timely and accurate upper limb movements. Given that the need to move our hands quickly and accurately to specific 3 locations is a ubiquitous feature of the everyday human experience, there has been much 4 5 research devoted to the understanding of the processes that moderate the inherent trade-off 6 between speed and accuracy. Collectively, this work has established that we address this 7 challenge through organising our target-directed movements into two distinct phases; an *initial* 8 *impulse* phase that carries the limb most of the distance to the target, and a *current control* phase 9 that uses visual feedback during the movement in order to amend any error and successfully land on the target (Woodworth, 1899; see also, Beggs & Howarth, 1972; Elliott, Helsen, & Chua, 10 2001; Keele & Posner, 1968; Meyer, Abrams, Kornblum, Wright, & Smith, 1988). 11 While the characteristics of target-directed movements are generally consistent with this 12 concept, recent evidence has highlighted how visually-regulated limb adjustments may take 13 14 place even earlier than previously thought. Thus, the original concept has been adapted by more contemporary theoretical models including the Multiple Process Model (MPM; Elliott, Hansen et 15 al., 2010; Elliott, Lyons et al., 2017), which broadly states that there are multiple forms of 16 17 visuomotor control that are capable of making online limb adjustments (see also, Cluff, Crevecoeur, & Scott, 2015; Desmurget & Grafton, 2000; Smeets, Wijdenes, & Brenner, 2016). 18 19 Specifically, the limb velocity and/or direction of the moving limb may be adjusted 20 within the early portion of the trajectory (<100 ms) during a process known as *impulse control* (Hansen, Tremblay, & Elliott, 2008; Grierson & Elliott, 2008; Tremblay, Hansen, Kennedy, & 21 22 Cheng, 2013). In this regard, an unexpected perturbation to the limb would be adjusted almost 23 immediately by reinstating a trajectory path that could later enable the limb to land on the target.

Because this control process unfolds rapidly and relies upon response-produced feedback, it may
 be explained by a pre-response forward model that anticipates the upcoming sensory
 consequences of the movement in order to compare it with the actual sensory consequences
 (Gallivan, Chapman, Wolpert, & Flanagan, 2018; Wolpert & Ghrahmani, 2000; Wolpert, Miall,
 & Kawato, 1998).

6 On the other hand, the difference between the spatial locations of the moving limb and target may be adjusted within the late portion of the trajectory during a process known as *limb*-7 8 target control (Elliott et al., 2014; Grierson & Elliott, 2008; Heath, Hodges, Chua, & Elliott, 9 1998). Thus, in the event that the target position is suddenly shifted, then the performer would realign the spatial locations of the limb and target in order to minimize any distance between 10 them just prior to reaching the end of the trajectory. Because this control process is 11 comparatively slow and alternatively relies upon external visual feedback, it is not necessarily 12 determined by a pre-response forward model, but a more traditional closed-loop model (e.g., 13 Keele & Posner, 1968; Woodworth, 1899). 14

Although the MPM has proven valuable in explaining movement behaviour across a 15 number of highly relevant performance contexts (Deuble, Connick, Beckman, Abernethy, & 16 17 Tweedy, 2016; Trejos, Patel, Maltaner, & Schlachta, 2014; Elliott, Grierson, Hayes, & Lyons, 2011), and pathological conditions (Niechwiej-Szwedo, Goltz, Colpa, Chandrakumar, & Wong, 18 2017; Pardhan, Scarfe, Bourne, & Timmis, 2017; Foster et al., 2020; Vimercati, Galli, Rigoldi, 19 20 Ancillao, & Albertini, 2013; for a review, see Elliott et al., 2020), there is still some debate 21 specifically about the processes underpinning impulse control. To-date, much of the evidence 22 surrounding impulse control comes from the analysis of movement adjustments that performers 23 make following illusory perturbations to the perceived velocity of the moving limb (Grierson &

Elliott, 2009; Grierson, Lyons, & Elliott, 2011; Proteau & Masson, 1997; Roberts & Grierson, 1 2 2019). These studies have been designed to introduce an unexpected translation in the background over which the movement is executed. Specifically, a moving background that 3 moves in a direction that is incongruent with the direction of the moving limb is thought to create 4 5 the misperception that the limb is moving faster than expected. The consequence of this 6 misperception is that performers decelerate and undershoot the target more than they would 7 under normal conditions with an unperturbed background. Alternatively, a congruent moving 8 background may create the misperception that the limb is moving slower than expected, which 9 yields an inverse pattern of less deceleration and target undershooting (i.e., closer to targetcentre).¹ 10

While the velocity misperception explanation of these findings is highly appealing, these 11 studies have typically isolated the moving background manipulation only to influence perception 12 of the primary movement direction. Yet, there is a growing body of research which indicates that 13 14 a perturbation to the surrounding environment can cause movement adjustments that are independent of any limb velocity information. For example, the onset of a moving background 15 that is perpendicular to the aiming direction-no longer influencing the perceived velocity-can 16 17 cause the limb to move in the corresponding direction (Gomi, Abekawa, & Nishida, 2006; Zhang, Brenner, Duysens, Vershueren, & Smeets, 2018; 2019). This movement occurs even in 18 19 cases where performers try to actively oppose the direction of the moving background, which 20 suggests this form of adjustment is highly automatized (Saijo, Murakami, Nishida, & Gomi, 21 2005). These particular adjustments have been attributed to an oculo-manual-following response, 22 which is driven by the direction of retinal motion and akin to the ocular-following response that 23 accompanies reflexive optokinetic control (Gomi, 2008; Whitney, Westwood, & Goodale, 2003).

These sets of findings challenge the viability and sufficiency of the velocity misperception 1 explanation (Grierson & Elliott, 2009; Proteau & Masson, 1997). That is, it must be acknowledged 2 3 that adjustments to movements that follow the onset of a moving background perturbation may result from an oculo-manual-following response wherein the direction of the limb adjustments is 4 5 simply coincident with that of the moving background. Accordingly, the present study aimed to 6 more closely examine the responses that occur following the onset of a moving background 7 perturbation with a view to resolving the relative influence of these two proposed visuomotor 8 processes.

9 Participants executed rapid aiming movements in the upward direction with their dominant limb.² The aiming movements were executed in front of a textured background, which 10 was static for the majority of trials. However, on a portion of the trials, the background would 11 12 unexpectedly move in one of four directions: upward, downward, rightward, and leftward. Notably, the upward and downward moving backgrounds were parallel with the direction of the 13 14 moving limb, while the rightward and leftward moving backgrounds were perpendicular to the direction of the moving limb. Consistent with the MPM framework (Elliott et al., 2017), we 15 examined the influence of these moving backgrounds across the entire trajectory, including peak 16 17 acceleration, peak velocity, peak negative acceleration, and movement end. These kinematic landmarks are highly informative with the regards the nature of the adjustments to the moving 18 19 background because impulse control primarily comprises of the early landmarks, while limb-20 target control is indicated only at the end of the movement.

If the early-onset adjustments are specific to a misperceived limb velocity, then we may observe a typical counter-acting adjustment for the parallel moving backgrounds (as indicated by a shorter and longer displacement in the primary direction for the downward and upward moving

backgrounds, respectively), but no or minimal adjustment for the perpendicular moving 1 backgrounds. Alternatively, the potential of a retinal motion artefact may render the direction of 2 movements toward all of the moving backgrounds (parallel and perpendicular; e.g., rightward 3 4 aiming direction for the rightward moving background, leftward aiming direction for the 5 leftward moving background). As a further possibility, movement adjustments may unfold as a 6 result of a simultaneous interaction between the two forementioned visuomotor processes (for a similar logic using reaction time measures, see Sternberg, 1969; Grierson & Elliott, 2008; 2009). 7 Thus, while the influence of retinal motion may cause the limb to move in the same direction as 8 9 each of the moving backgrounds, the additional misperception in limb velocity that is caused only by the parallel moving backgrounds may elicit an even greater magnitude of adjustment. 10 Consistent with previous studies on the moving background perturbation, we predict that either 11 of these patterns of movement behaviour would begin to manifest at peak negative acceleration 12 (e.g., Grierson & Elliott, 2009; Grierson et al., 2011; Roberts & Grierson, 2019; for movement 13 adjustments ~100-200 ms, see Gomi et al., 2006; Whitney et al., 2003). 14

15

16 Methods

17 Participants

There were 17 participants (15 males, 2 females; age range = 20-24 years) recruited for the study. All participants self-reported that they were right-handed and clear of any neurological conditions, and provided informed consent according to the guidelines set out by the local research ethics committee and the Declaration of Helsinki (2013).

22

23 Apparatus and Task

1 Stimuli were presented on an LCD computer monitor (47.5 cm x 27.0 cm; temporal 2 resolution = 75 Hz; spatial resolution = 1920 x 1080 pixels), which was covered by a thin acrylic 3 sheet. The monitor was desktop-mounted and rotated 90° such that the long-edge was oriented in 4 the vertical axis. The monitor was adjusted to a height that aligned the center of the screen with 5 the eye-level for each participant.

6 Stimuli were generated via Matlab (2018b) (The Mathworks Inc., Natick, MA, USA) 7 running Psychtoolbox (version 3.0.11) (Pelli, 1997). The stimuli consisted of a grey target square 8 (5 mm x 5 mm), which was located upward at 160 mm from a centrally located crosshair (2×10) 9 mm intersecting lines). The crosshair represented the starting point, or 'home position', for each aiming movement. The stimuli also included a texture of black and white squares (48 squares; 7 10 mm x 7 mm each), which comprised the 'background'. On perturbed trials, this texture moved in 11 the prescribed direction at a rate of 0.21 m/s ($\sim 70^{\circ}$ /s). The background texture was continually 12 shifted so that when the squares reached the edge of the screen, it appeared as though they wrapped 13 14 around to continue moving in the same direction from the opposite edge.

Participants wore an NO/NC button micro-switch (Saia Burgess Electronics, Murten, Switzerland) on their index finger, which was connected to the computer via a serial port. Participants also wore a retro-reflective marker on the index finger of the right limb. This marker enabled high-resolution motion capture via an optoelectric camera system (Vicon Vantage, 16megapixel resolution). Marker locations were sampled at 200 Hz, and collected for a period of 4 seconds per trial.

21

22 Procedure

Prior to commencing the experimental trials, the screen display was calibrated with respect to the external motion capture system by having participants precisely locate their index finger with the attached marker near the centre of a crosshair, which represented the target location. The end target location for each individual participant was taken as the mean position from two separate recordings at the start and end of each data collection session.³

6 Participants completed a series of 60 trials in which they moved their right index finger from the home position to the target as quickly and accurately as possible. Each trial began when 7 8 the participant made contact with the central home position by depressing the micro-switch. The 9 aiming movement was then pre-cued via a grey unfilled square (20 x 20 mm; 1-mm thick lines) which appeared around the target for 1s. Following a variable foreperiod between 800-2300 ms, 10 the target would change colour from grey to yellow; which signalled the participant to make their 11 12 aiming movement. For 40 of the trials, the background texture remained stationary. However, on a random set of 20 trials (33%), the background would move in the upward, downward, rightward 13 14 or leftward directions as soon as the micro-switch was released at the start of the movement (5 trials per background direction). Participants were instructed to continue aiming toward the target 15 as quickly and accurately as possible regardless of whether the background moved. The 16 17 background movement was stopped as soon as the micro-switch was depressed again at the end of the movement. While participants received complete online and terminal visual feedback of each 18 19 movement, they were not provided with any further augmented feedback. Participants could 20 commence the next trial by returning the micro-switch to the home position in their own time.

21

22 Data Management and Analysis

The data pertaining to the spatiotemporal location of the index finger were subjected to a 1 second-order, dual-pass Butterworth filter with a low-pass cut-off frequency of 10 Hz. Cartesian 2 coordinates from the primary direction of the movement (z-axis) were differentiated to obtain 3 4 velocity, which was differentiated again to obtain acceleration. Movement onset was identified as the first frame that maintained a velocity greater than 20 mm/s for at least 40 ms (8 samples). 5 6 Movement offset was identified as the first frame following movement onset that reached a velocity less than 20 mm/s and greater than -20 mm/s. Movement time was calculated as the time 7 8 difference between movement onset and movement offset. The displacement from the primary and 9 perpendicular directions of the aiming movements was calculated at each of the kinematic landmarks of peak acceleration, peak velocity, peak negative acceleration and movement end. 10

For the analysis, we firstly wanted to ensure that any potential differences in the displacement were not a result of a mere trade-off between speed and accuracy, and thus analysed the participant mean movement times using a one-way repeated-measures analysis of variance (ANOVA). For the main analyses, we conducted a multivariate analysis of variance (MANOVA) (Wilks' Lambda) with moving background as a repeated-measures factor, and participant mean displacement within the primary and perpendicular directions at each of the kinematic landmarks as separate dependent variables.

Meanwhile, it is possible that any difference within each of the primary and perpendicular directions of aiming could also be discriminated by an independent or combined influence of multiple visuomotor processes. Specifically, there could be an additive contribution of both a misperceived limb velocity and external retinal motion. In this regard, a simultaneous interaction between each of these visuomotor processes would see an even greater movement adjustment for the upward/downward perturbation compared to the leftward/rightward perturbation. Thus, we

undertook an additional analysis that focused on only those conditions where the moving
background perturbations were consistent with either the primary or perpendicular directions of
the movement (i.e., primary aiming direction for the upward and downward perturbations, and
perpendicular aiming direction for the leftward and rightward perturbations).

5 However, rarely is there a standard comparison of a common dependent variable between 6 the primary and perpendicular aiming directions (Khan et al., 2006). Indeed, any difference 7 between the raw data values of each of these aiming directions may also be attributed to their 8 inherent variability following mere differences in scale or magnitude (as indicated by the often 9 elliptical spatial variability profile, where variability is more heavily accumulated in the primary compared to perpendicular aiming direction; Hansen, Elliott, & Khan, 2008; Gordon, Ghilardi, & 10 Ghez, 1994; Messier & Kalaska, 1999; see also Schmidt, Zelaznik, Hawkins, Frank, & Quinn, 11 1979). This difference is often taken as evidence of the primary and perpendicular aiming 12 directions being planned and controlled in separate, but simultaneous, fashion (Bard, Paillard, 13 14 Fleury, Hay, & Larue, 1990).

In order to avoid any such contamination, while more clearly isolating the influence of the 15 moving background perturbation, we initially standardized the mean displacements for the primary 16 17 and perpendicular aiming directions by separately converting them into absolute Z-scores (|Z| =within-participant condition mean – within-participant grand mean of aiming direction / within-18 19 participant standard deviation of aiming direction) (for a similar logic, see Lohse, Jones, Healy, & 20 Sherwood, 2014). Thus, if there was a simultaneous interaction between visuomotor processes that sees a combination of influences from a misperceived limb velocity and external retinal motion, 21 22 then we should observe higher Z-scores for the upward/downward perturbation within the primary 23 aiming direction compared to the rightward/leftward perturbation within the perpendicular aiming

direction. In a similar vein to the previous analysis, a MANOVA was conducted with moving
 background as a repeated-measures factor, and *Z*-scores at each of the kinematic landmarks being
 the separate dependent variables.

In the case of each MANOVA, statistical significance was followed up by univariate ANOVAs on each of the kinematic dependent variables with reference to the Greenhouse-Geisser adjusted value (original or Sphericity-assumed degrees-of-freedom are reported). Further significant effects were decomposed using the Tukey HSD post hoc procedure. Significance was declared at p < .05, and effect sizes were indicated by using partial eta-squared (η^2).

9

10 **Results**

One participant was removed from the analyses due to excess target error (omitted 11 participant range of mean absolute constant error = 15.41-21.51 mm; remaining participant range 12 of mean absolute constant error = .05-8.75 mm). Aiming movements were executed at an average 13 time of 521 ms (SE = 15), and did not significantly differ across the moving background directions, 14 $F(4, 60) = .89, p = .45, partial \eta^2 = .06$. Consequently, any differences between the spatial limb 15 trajectories as a result of the moving backgrounds could not be attributed to any differences in the 16 17 available visual feedback processing time. The average movement trajectories for each of the moving background directions are presented in Figure 1. 18

- 19
- 20

[Insert Figure 1 here]

21

MANOVA revealed a significant main effect of moving background perturbation, *F*(32, 197) = 3.87, *p* = .00, *partial* η² = .36. Subsequent univariate ANOVAs on the primary direction of

aiming at each kinematic landmark revealed no significant effect of moving background 1 perturbation at peak acceleration, F(4, 60) = .61, p = .61, partial $\eta^2 = .04$, or peak velocity, F(4, 60) = .61, partial $\eta^2 = .04$, or peak velocity, F(4, 60) = .61, partial $\eta^2 = .04$, or peak velocity, F(4, 60) = .61, partial $\eta^2 = .04$, or peak velocity, F(4, 60) = .61, partial $\eta^2 = .04$, or peak velocity, F(4, 60) = .61, partial $\eta^2 = .04$, or peak velocity, F(4, 60) = .61, partial $\eta^2 = .04$, or peak velocity, F(4, 60) = .61, partial $\eta^2 = .04$, or peak velocity, F(4, 60) = .61, partial $\eta^2 = .04$, or peak velocity, F(4, 60) = .61, partial $\eta^2 = .04$, or peak velocity, partial $\eta^2 = .04$, p 2 60) < .73, p = 53, partial $\eta^2 = .05$. However, the analysis yielded a significant effect of moving 3 4 background perturbation at peak negative acceleration, F(4, 60) = 3.94, p = .03, partial $\eta^2 = .21$, which indicated a significantly greater displacement when the background was perturbed in the 5 6 upward compared to downward direction (ps < .05, HSD = 11.59) (Table 1). There were no other significant differences at peak negative acceleration (ps > .05). In a similar vein, there was a 7 significant effect of moving background perturbation at movement end, F(4, 60) = 10.81, p = .00, 8 *partial* $\eta^2 = .42$. The post hoc analysis revealed that there was a significantly greater displacement 9 when the background was perturbed in the upward compared to stationary, downward, and 10 leftward directions, while it was also significantly greater for the rightward compared to leftward 11 direction (ps < .05, HSD = 1.09). In addition, there was a significantly shorter displacement when 12 the background was perturbed in the downward compared to stationary, rightward, and leftward 13 directions (ps < .05). 14

15

16

[Insert Table 1 about here]

17

For the perpendicular direction of aiming, there was no significant effect of moving background perturbation at peak acceleration, F(4, 60) = .48, p = .68, *partial* $\eta^2 = .03$, or peak velocity, F(4, 60) = 1.49, p = .23, *partial* $\eta^2 = .09$. However, there was a significant effect of moving background perturbation at peak negative acceleration, F(4, 60) = 5.27, p = .005, *partial* $\eta^2 = .26$, which indicated a significantly greater rightward limb movement when the background was perturbed in the rightward compared to all the other background directions (*ps* < .05, HSD =

1	1.50) (Table 2). Meanwhile, there was also a significant effect of moving background perturbation
2	at movement end, $F(4, 60) = 15.66$, $p = .00$, partial $\eta^2 = .51$. The post hoc analysis revealed that
3	there was a significantly greater rightward and leftward limb movement when the background was
4	perturbed in the rightward and leftward directions respectively as compared to all other
5	background directions ($ps < .05$, HSD = .92).
6	
7	[Insert Table 2 about here]
8	
9	Velocity misperception vs. manual-following response
10	Standardized Z-scores revealed no significant main effect of moving background
11	perturbation, $F(12, 111) = 1.52$, $p = .13$, partial $\eta^2 = .13$ (Table 3). Consequently, it is likely that
12	the previously cited influence on each of the primary and perpendicular directions of aiming did
13	not necessarily involve separate sets of visuomotor processes.
14	
15	[Insert Table 3 about here]
16	
17	Discussion
18	One of the emerging concepts from the sensorimotor literature is the discovery that
19	movement adjustments may unfold much earlier (i.e., < 100ms) than originally thought. This
20	feature has been heavily incorporated into the MPM (Elliott et al., 2017), where it is possible for
21	visually-regulated limb adjustments to be directed by early impulse and late limb-target control
22	processes. Because much of this framework has been adapted from evidence of early-onset
23	adjustments following moving backgrounds (Grierson & Elliott, 2009; Grierson et al., 2011;

1	Proteau & Masson, 1997; Roberts & Grierson, 2019), we aimed to elaborate upon this line of
2	research by incorporating moving backgrounds that continue to generate retinal motion without
3	necessarily perturbing the perceived velocity. That is, we introduced perpendicular moving
4	backgrounds that were independent of any manipulation on the perceived limb velocity.
5	Provided misperceived limb velocities underlie the early movement adjustments of target-
6	directed aiming, then we predicted that a counter-acting adjustment would solely manifest for the
7	parallel moving backgrounds (upward, downward), while there would be minimal adjustments
8	for the perpendicular moving backgrounds (rightward, leftward).
9	However, the findings generally indicated that the movement adjustments unfolded in the
10	same direction as the moving backgrounds regardless of its direction. What's more, the similarity
11	in the Z-scores for displacements that were consistent with the direction of the moving
12	background suggests that the adjustments to each of these directions did not necessarily manifest
13	from any different visuomotor processes. Thus, these data indicate that the movement
14	adjustments within target-directed aiming following a moving background perturbation may not
15	manifest from a misperceived limb velocity, but perhaps an oculo-manual-following response.
16	The possibility for illusory perturbations to the perceived velocity has long been known
17	(e.g., Duncker, 1929). Thus, the present findings should not be seen to contest such a
18	phenomenon, although it is debatable whether discrete target-directed aiming presents an optimal
19	setting for such a misperception to unfold. Indeed, previous examples of misperceived object
20	velocities typically require the ocular pursuit of the object in question (Raymond, Shapiro, &
21	Rose, 1984). When a moving background coincides with the object being tracked, then there is a
22	reflexive optokinetic response that causes retinal slip (Masson, Proteau, & Mestre, 1995). Thus,
23	it appears this illusion requires a combination of both extra-retinal (efferent) and retinal

(afferent) sources of information. However, the extra-retinal signals that contribute to this
misperception may be lost during target-directed aiming because it involves early fixation on the
target, while the parafoveal or peripheral visual field capture movement of the limb (Helsen,
Elliott, Starkes, & Ricker, 1998). While it is possible that a misperceived velocity may be
alternatively generated by combining the motor efference from the limb and retinal information,
it is highly unlikely that there is sufficient neurotransmission time for this to occur (Saijo et al.,
2005).

8 Alternatively, the present findings may be explained by evidence of a manual-following 9 response that is akin to the ocular-following response from reflexive optokinetic control (Gomi et al., 2006; Gomi, 2008). This process typically underlies the inference of self-motion (i.e., 10 displaced surroundings relative to one self within an otherwise stable world; yon Helmholtz, 11 1867; for examples, see Tarita-Nistor, González, Markowitz, Lillakas, & Steinbach, 2006; 12 Tarita-Nistor, Hadavi, Steinbach, Markowitz, & González, 2014), and may be attributed to the 13 14 middle temporal/medial superior temporal (MT/MST) neural area (Whitney et al., 2007). At the same time, there is an increasing argument that this manual-following response may not be 15 attributed to inferred self-motion, per se. Indeed, it has been shown that the manual-following 16 17 response only occurs when the moving background occupies the immediate vicinity of the target location as opposed to a large-field or global display (Brenner & Smeets, 2015), while it fails to 18 19 manifest even when self-motion is directly induced by galvanic vestibular stimulation (Zhang et 20 al., 2019).

Of further relevance to the present study was the distinct kinematic landmark where the movement adjustments could begin to take place. Indeed, the kinematic landmarks of peak acceleration, peak velocity and peak negative acceleration are synonymous with impulse control,

where pre-response predictions surrounding the sensory consequences are formed for subsequent 1 2 comparison with the actual sensory consequences (Elliott et al., 2017). Meanwhile, the end of the 3 movement may be additionally attributed to limb-target control, which is concerned with the relative spatial location of the moving limb and target. Consistent with previous findings on 4 5 target-directed aiming with a moving background perturbation (Grierson & Elliott, 2009; 6 Grierson et al., 2011; Roberts & Grierson, 2019), the moving background in this study appeared 7 to influence the movement from peak negative acceleration until the very end of the movement. 8 While peak negative acceleration is later than peak acceleration and peak velocity, it can still be 9 regarded as being a product of the pre-response arrangement of the initial movement before any delayed processing of online visual feedback (Keele & Posner, 1968; Woodworth, 1899). Thus, 10 by definition, movement adjustments that unfold at this particular landmark may be attributed to 11 impulse control. 12

Surprisingly, there appeared even more differences between the moving background 13 14 conditions at the end of the movement, which may arguably indicate an increased influence within a portion of the movement that is typically associated with limb-target control. This 15 outcome conflicts with previous accounts that examine the influence of the moving background 16 17 perturbation following a brief presentation of the target prior to movement onset (Gomi et al., 2006). Likewise, the tendency to move in the same direction as the moving background has been 18 19 previously shown to decrease whenever the target is presented throughout the entire aiming 20 movement (Whitney et al., 2003). Along these lines, it should be recognised that the magnitude 21 of the pairwise differences at the end of the movement were still substantially smaller than those 22 previously identified at peak negative acceleration (see Figure 1). Thus, it appears that limb-23 target control continues to unfold near the end of the movement in order to effectively diminish

at least some of the prior disruption that is caused by the moving background perturbation. 1 Moreover, it is possible that the differences found at the end of the movement were not 2 3 necessarily a direct result of the same visuomotor processes as those associated with impulse control. For example, the effect of the moving background within early impulse control may 4 have downstream consequences for late limb-target control by contaminating the final portions 5 6 of the movement. This conjecture is consistent with recent suggestions that the impulse and limb-target control processes are not as mutually exclusive as first thought, but alternatively 7 8 interact with one another (Grierson & Elliott, 2009; Elliott et al., 2017; Roberts, Lyons, Garcia, Burgess, & Elliott, 2017). 9

The data presented here highlights that the influence of a moving background within 10 target-directed aiming is more closely aligned with the retinal motion explanation than the 11 misperception of limb velocity explanation. To this end, it is relevant to reconcile the current 12 findings within the context of the over-arching MPM framework. Because of the numerous 13 14 sources of evidence surrounding early impulse control, including visual (e.g., Grierson, Gonzalez, & Elliott, 2009; Tremblay et al., 2013) and actual velocity-based (e.g., Grierson & 15 Elliott, 2009) perturbations, the present findings do not wholly contest this theoretical 16 17 perspective. Instead, it may be possible to incorporate the influence of surrounding environmental cues into this model. 18

Specifically, upon review of the time-course of the previously reported manual-following
responses (~100-200 ms; Gomi et al., 2006; Whitney et al., 2003) alongside the current effects
yielded at peak negative acceleration (see also, Grierson & Elliott, 2009; Grierson et al., 2011;
Roberts & Grierson, 2019), we can reason that these particular movement adjustments are
associated with early impulse control. Thus, the forward model of the predicted sensory

consequences that mediate impulse control may also comprise the retinotopic coordinates of the
limb and surrounding environment – when the moving background unfolds and the visual field
momentarily shifts, then impulse control processes may try to adjust the direction of the limb
accordingly. Future research is required to more closely examine this possibility, and
subsequently explore the precise sources of information that comprise the forward model of
impulse control.

7 In conclusion, we have identified that the early-onset adjustments within target-directed aiming following a moving background may be primarily attributed to the direction of retinal 8 9 motion. These effects on movement behaviour primarily manifest within early impulse control, which may continue to indirectly influence late limb-target control. We suggest that the early 10 impulse control may additionally incorporate a representation of the surrounding environment, as 11 well as the previously stated response-produced feedback. Consequently, future attempts to access 12 the sensorimotor processes of impulse control should appropriately distinguish between 13 14 perturbations to the illusory surround and actual limb trajectory (e.g., Grierson et al., 2011).

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1 Footnotes

2 While there is some debate surrounding a potential asymmetry in the pattern of movement 1) adjustments for congruent and incongruent moving backgrounds (e.g., smaller magnitude 3 adjustments appear to unfold for a congruent compared to incongruent moving background; 4 5 Proteau & Masson, 1997; for a discussion, see Roberts & Grierson, 2019), it still stands that 6 both these contexts conceptually differ in their manipulation of the perceived limb velocity, and with it, changes to the movement trajectory. 7 8 The current data are adapted from a previous study that was conducted with only the parallel 2) 9 moving background directions (upward vs. downward), while participants aimed to targets at upward and downward locations (see Roberts & Grierson, 2019). Thus, the previous 10 analysis only considered the congruent and incongruent moving background directions. 11 However, the present study additionally incorporates the perpendicular moving backgrounds 12 in the form of rightward and leftward directions. Because of the profound energy-13 14 minimization processes that contaminate downward aiming movements (i.e., increased undershooting to avoid energy-consuming overshoots against gravity), we primarily isolated 15 our analyses to the upward aiming movements. The visuomotor processes that potentially 16 17 discriminate these different aiming directions are of no theoretical value to the present study. The within-participant spatial variability of calibrated target recordings revealed a range of 18 3) 19 .57-5.72 mm and .86-5.39 mm for the horizontal and vertical locations, respectively.

Figure captions

- **Figure 1.** Mean displacement in the primary (y-axis) and perpendicular (x-axis) directions of the
- 3 movement. Symbols within the legend indicate the separate moving background conditions.

1 Figures



Figure 1.

1 Tables

2 Table 1. Mean displacement (±SE) in the primary direction of the movement as a fu	nction of
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	Stationary	Up	Down	Right	Left
PA	10.70	10.39	10.97	9.83	10.70
	(.57)	(.68)	(.81)	(.66)	(.69)
PV	63.49	65.57	64.05	64.87	63.90
	(1.40)	(1.51)	(1.43)	(1.92)	(1.46)
PD	132.00	136.44	124.63	132.70	128.52
	(2.74)	(3.48)	(3.06)	(4.20)	(3.77)
END	156.99	158.50	154.62	158.07	156.56
	(.57)	(.85)	(.75)	(.49)	(.42)

3 moving background and kinematic landmark.

4

Table 2. Mean displacement (\pm SE) in the perpendicular direction of the movement as a function

	Stationary	Up	Down	Right	Left
РА	1.75	1.73	1.40	1.72	1.87
	(.65)	(.84)	(.54)	(.64)	(.72)
PV	7.67	6.98	6.60	7.76	7.77
	(1.62)	(1.97)	(1.69)	(1.73)	(1.80)
PD	7.93	7.76	7.74	10.79	7.07
	(1.17)	(1.65)	(1.32)	(1.48)	(1.70)
END	1.32	1.49	1.27	3.98	-0.32
	(.97)	(1.16)	(.92)	(1.36)	(1.00)

6 of moving background and kinematic landmark.

	Congruent						
	Up	Down	Right	Left	Incongruent		
DA	.80	.93	.85	.89	.74		
PA	(.11)	(.13)	(.12)	(.12)	(.06)		
DV	.74	.87	.76	.69	.77		
PV	(.15)	(.11)	(.12)	(.11)	(.06)		
מת	.79	1.17	1.02	.77	.66		
PD	(.14)	(.11)	(.15)	(.10)	(.05)		
END	.72	1.08	1.24	.99	.59		
	(.13)	(.12)	(.08)	(.11)	(.06)		

2 directions for the congruent moving backgrounds across each of the kinematic landmarks. For

Table 3. Mean absolute Z-scores (±SE) in the displacement of the primary/perpendicula
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3 reference, the marginal means for the incongruent moving backgrounds are also presented.