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Attention attracts action in healthy participants: an insight into optic ataxia?

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Abstract

Patients with optic ataxia following lesions to superior parts of the posterior parietal cortex make large errors when reaching to targets in the peripheral visual field. These errors are characterised by a contraction, or *attraction*, toward the point of fixation. These patients also have a reduced ability to allocate visual attention away from the point of fixation, but it is unclear whether the core symptom of misreaching is related to these attentional problems. In neurologically-intact adults, we tested the effect of an attention-demanding dual-task performed at fixation upon visually-guided reaching to peripheral targets. The dual task was associated with delayed movement initiation, and a shortened deceleration phase of movement suggesting a reduced ability to benefit from online control. It also induced a small but consistent shift of reaching endpoints towards the side of fixation. Our experimental restriction of visual attention thus impaired both the programming and control of reaching, and induced a spatial pattern of errors that was qualitatively reminiscent of optic ataxia, albeit much less severe. These findings are consistent with a close functional link between attention and action in the healthy brain, and suggest that attentional disturbances could be a core component of optic ataxia following parietal lesions.

Keywords: attention, action, optic ataxia, peripheral, premotor, reaching.

1. Introduction

Optic ataxia is a visuomotor disorder defined by inaccurate reaching to visual targets that is not attributable to primary visual, primary proprioceptive, motor, cerebellar or cognitive impairments (Rossetti, Pisella, & McIntosh, 2019). It follows lesions to superior parts of the posterior parietal cortex, often close to the junction with the occipital lobe (Karnath & Perenin, 2005). Patients may be able to reach accurately for targets that they fixate, but make large errors when reaching to the peripheral visual field: a characteristic ‘non-foveal’ pattern of misreaching. Clinical examination of optic ataxia thus requires the presentation of peripheral targets (e.g. Borchers, Müller, Synofzik, & Himmelbach, 2013; Perenin & Vighetto, 1988). Optic ataxia is often bound up with deficits of visual attention, especially when the parietal damage is bilateral. For instance, the patient in whom optic ataxia was first described had simultanagnosia and neglect (Bálint, 1909; see Harvey & Milner, 1995), and subsequent bilateral cases have invariably exhibited simultanagnosia acutely, which manifests as an inability to process objects away from the focus of visual attention (e.g. Michel & Henaff, 2004; Pisella et al., 2000).

A detailed characterisation of optic ataxia has been carried out in unilateral cases. Perenin & Vighetto (1988) reported that optic ataxia expresses two major patterns: patients may misreach with either hand for targets in the contralesional visual field (field effect), and/or they may misreach with the contralesional hand throughout the visual field (hand effect). The field-effect usually dominates the clinical picture. Blangero and colleagues (2010) further characterised these patterns of misreaching, in seven patients with unilateral optic ataxia, who showed a consistent bias towards fixation when reaching for targets in the contralesional field (see also: Ratcliff & Davies-Jones, 1972; Rossetti et al., 2005). Subsequent modelling of these data indicated that the field effect can be characterised by an attraction (or contraction) towards the point of fixation, which increases exponentially with target eccentricity (Vindras et al., 2016). One implication would be that, if the attraction were sufficiently strong, patients would reach irresistibly for the point of fixation, regardless of the target position. This extreme manifestation, known as ‘magnetic misreaching’, has indeed been observed following bilateral parieto-occipital lesions (Buxbaum & Coslett, 1997; Carey, Coleman, & Sala, 1997; Jackson et al., 2004).

A characteristic attraction to the point of fixation has inspired three related accounts of optic ataxia (Buxbaum & Coslett, 1997; Jackson, Newport, Mort, &

Husain, 2005; Vindras et al., 2016). These all assume that the default visuomotor coupling for reaching is for the hand to be yoked to point of gaze, and that reaches to non-fixated targets are normally achieved by a transformation of this default plan. Buxbaum and Coslett (1997) suggested that the coordinate transformations that allow a visual target to be coded with respect to the limb are impaired in optic ataxia, so that reaches remain locked to an eye-centred system. Vindras and colleagues (2016a) suggested that the transformation of the default reaching plan depends upon superior parietal-occipital networks with a rich representation of the peripheral visual field (Rossit, McAdam, Mclean, Goodale, & Culham, 2013), damage to which induces optic ataxia. Finally, Jackson and colleagues formulated the critical deficit in more functional terms, suggesting that the computation of a reaching vector to a non-foveal target requires the target and the point of fixation to be represented *simultaneously*, and that this ability is impaired in optic ataxia (Jackson et al., 2009, 2005). This seems to portray optic ataxia as a visuomotor form of simultanagnosia, raising the possibility of a functional relationship between visuomotor and attentional symptoms.

Indeed, although optic ataxia is a visuomotor disorder, these patients are rarely if ever free of attentional disturbances. Perenin and Vighetto (1988) observed some reduction of visual detection or discrimination in the contralesional field in all ten of their unilateral patients, and visual, tactile or auditory extinction in six cases. One patient with right-field optic ataxia (Cavina-Pratesi, Connolly, & Milner, 2013; Cavina-Pratesi, Ietswaart, Humphreys, Lestou, & Milner, 2010; Rice et al., 2008) has elsewhere been studied for right visual neglect (Humphreys & Heinke, 1998) and for right visual extinction (Kitadono & Humphreys, 2007; Snow, Miranda, & Humphreys, 2013). Moreover, stringent testing of perceptual detection and discrimination has invariably revealed impairments in ataxic fields (Blangero et al., 2010; McIntosh, Mulroue, Blangero, Pisella, & Rossetti, 2011; Perenin & Vighetto, 1988; Pisella et al., 2007, 2009; Striemer et al., 2007, 2009). Striemer and colleagues (2009) reported that detection time was raised in the ataxic field of a patient with optic ataxia, though it increased much less steeply with target eccentricity than did reaching error. The authors suggested that the attentional impairment was functionally separate from the visuomotor symptoms in this patient. In another patient, McIntosh and colleagues (2011) found that the latency to respond to changes in target position were closely correlated between visuomotor and perceptual tasks. They suggested a shared functional basis for at least some visuomotor and attentional symptoms in optic ataxia.

The proposed functional relationship seems possible, given evidence for close functional links between attention and action in the healthy brain, not only for saccades, but also for target-directed reaching (for an overview, see Smith & Schenk, 2012). It is well-established that perceptual discrimination is selectively enhanced at the target of an upcoming reaching or grasping movement, suggesting that the reach preparation is normally accompanied by selective attention to the target (Baldauf, Wolf, & Deubel, 2006; Castiello, 1996; Deubel, Schneider, & Paprotta, 1998; Schiegg, Deubel, & Schneider, 2003). Selective attention may even play a functional role in action, because requiring a participant to focus attention away from the reaching or grasping target interferes with the preparation and execution of the action (Hesse & Deubel, 2011; Hesse, Schenk, & Deubel, 2012; Liu, Chua, & Enns, 2008; Mahon, Bendžiūtė, Hesse, & Hunt, 2020; Sandoval Similä & McIntosh, 2015). This attention-action coupling makes it plausible that the attentional deficits observed in optic ataxia might be causally-related to the reaching deficits. If so, we can hypothesise that an experimental manipulation designed to limit the ability of healthy participants to allocate attention away from the point of fixation should induce reaching errors that mimic the character of those observed in optic ataxia.

In the present study, we test this hypothesis by using a dual-task approach employed by several prior studies of attention in action (Hesse & Deubel, 2011; Hesse, Schenk, & Deubel, 2012; Liu, Chua, & Enns, 2008; Mahon, Bendžiūtė, Hesse, & Hunt, 2020; Sandoval Similä & McIntosh, 2015). A common way to impose an attentional demand at a fixed location is by delivering a rapid serial visual presentation (RSVP) stream of shapes or characters, which the participant must monitor for target items (e.g. Broadbent & Broadbent, 1987; Lavie, Beck, & Konstantinou, 2014; Shapiro, Raymond, & Arnell, 1994). When there is a high monitoring demand at the fixated location, processing resources are withdrawn from more peripheral locations (Lavie et al., 2014; Schwartz et al., 2005). We apply this method to reduce the ability to allocate attention away from fixation, whilst requiring participants to execute reaches to peripheral targets. We are interested in whether this restriction of attention will induce reaching errors that mimic the spatial character of field-dependent misreaching in optic ataxia. That is, we will test the prediction that the dual-task demand will cause reaching responses to deviate towards the point of fixation in healthy participants.

The experimental design has evolved from preliminary work in our lab. Ingle and McIntosh (2016) required participants to reach with the right hand to dots appearing at

various positions on a touchscreen, whilst monitoring an RSVP stream of shapes at the screen centre and pressing a key with the left hand whenever a specific shape appeared. The attentional load of the monitoring task was manipulated, and reaching responses were found to deviate further towards the screen centre in higher load conditions. This dual-task effect was slight, and apparent only for the more eccentric targets, at 14° of visual angle. The present experiment will advance on this preliminary work in several ways. First, we will use a more extensive display, to test a more eccentric range of reaching targets (9-36°). Second, we will include an open-loop condition in which the participant is unable to see their hand, which may limit the scope for online correction, and potentially amplify dual-task effects. Additionally, we will use eye-tracking to ensure that fixation is maintained, and motion capture to record the whole movement, allowing for further exploration the reaching profile. The critical prediction is that reaching endpoints will be biased relatively towards fixation when the dual task is performed. This would support the plausibility of the idea that deficits of visual attention may contribute to the typical character of misreaching in optic ataxia.

Methods

2.1. Open data statement

We report how we determined our sample size, all data exclusions, all inclusion/exclusion criteria, whether inclusion/exclusion criteria were established prior to data analysis, all manipulations, and all measures in the study. No part of the procedures or analyses were pre-registered. Experiment Builder code, and full raw and processed data and analysis scripts are archived at <https://osf.io/kgevr/>.

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2.2. Participants

Thirty-four young adult participants were recruited (21 female, 13 male; aged 18-30 years). All had normal vision, or vision corrected to normal with contact lenses, and were right-handed by self-report. Seven participants were excluded (see Section 2.6), so that the final sample comprised 27 participants (16 female, 11 male; aged 18-30 years). The study was approved by the Psychology Research Ethics Committee at the University of Edinburgh.

2.3. Power considerations

The original target sample size was 30. This was informed by data from the preliminary experiment described in the Introduction (Ingle & McIntosh, 2016), which suggested a standardised effect size of dual-task interference on our critical variable (angular error) of $d_z=0.53$. A sample size of 30 would provide 80% power to detect this effect in a within-subjects design (alpha .05, two-tailed). Our achieved sample size of 27 would have 80% power to detect an effect size slightly larger than this ($d_z=0.56$).

2.4. General set-up (Figure 1)

Participants sat with their head in the chinrest of a tower-mounted Eyelink 1000 eyetracker (SR Research), tilted forwards by 30°, so that they were looking down towards a semi-silvered mirror, at a horizontal plane about 170 mm below eye-level (Figure 1a). Stimuli were presented on a 21 inch CRT monitor suspended face-down 250 mm above the mirror, with a stimulus display area 400 mm wide by 300 mm deep (front-to-back). From the participant's perspective, the display was projected optically to a working surface 250 mm below the

mirror, which extended for 150 mm to either side of the display area. The working surface, and the inside surfaces of the apparatus, were matt black, and the room was completely dark. The only illumination was from the monitor, and from LED strip-lighting on the inside flanks of the chamber below the mirror. The participant's hand was visible only when the lower chamber was lit, which was under the experimenter's control.

The chinrest was aligned with the horizontal midline of the working surface, and a start button was fixed to the working surface, 40 mm to the right of the midline, in a comfortable position for the participant's right (dominant) hand. The left hand was kept on the participant's lap, throughout. A fixation cross (10 mm) was presented 180 mm to the left of the midline, at a depth of 200 mm with respect to the start button. The straight line viewing distance from the participant's eye to the fixation cross was 570 mm; at this viewing distance, 10 mm subtends one degree of visual angle ($^{\circ}\text{VA}$). On each trial, the reaching target was a (10 mm) dot presented at one of eight possible locations (Figure 1b). There were two target locations at each of four visual eccentricities with respect to fixation (9, 18, 27, 36°VA). At each eccentricity, one (near) target position was at a straight line distance of 260 mm from the start button, and one (far) target position was at a distance of 280 mm. This minor manipulation of reaching distance was included to increase the variety of target locations, but the analysis of performance at each eccentricity was averaged across near and far distances.

The back of the apparatus was open to provide a view for the Optotrak Certus (Northern Digital Inc) motion-tracking camera array, which sampled at 100 Hz the position of an infra-red emitting marker attached to the nail of the right index finger. The Optotrak was pre-calibrated with an accuracy of 0.1 mm, and was registered to the apparatus such that the working surface defined an XY plane aligned with the display orientation, where X is horizontal and Y is depth (Figure 1b). The task was programmed in Experiment Builder (SR Research). Before the task began, the participant was familiarised with the task requirements, and then completed a 16 point calibration, placing the fingertip over each of 16 target dots with the hand visible, whilst the marker coordinates were recorded. This allowed us to transform marker coordinates into fingertip coordinates during analysis, adjusting for the offset of marker placement. Eyetracking was used to monitor fixation, and the eyelink was calibrated with a three-point horizontal calibration at the same depth coordinate as the fixation cross. The eyelink was calibrated at the beginning of each trial block.

2.5. Procedure

Before each trial, the lower chamber was lit so that the participant could see their hand, and a black screen was shown for 500 ms, followed by the onset of the fixation cross. The participant was required to fixate the cross and hold down the start button to begin the trial. This initiated a rapid serial visual presentation (RSVP) stream of 20 characters at the fixation location, with each character shown for 9 screen cycles (= 106 ms), so that the RSVP stream lasted for 2120 ms, the final character being replaced by the original fixation cross until the trial ended at 3000 ms. Coincident with the onset of the 11th character (i.e. after 1060 ms), a reaching target appeared at one of eight peripheral locations (Figure 1b), and remained on screen until the end of the trial. The participant was required to reach for the target quickly and accurately, and to leave the index finger where it landed. Provided that fixation was not broken at any point, the trial end was signalled by a green screen at 3000 ms. But if at any time the eye position deviated more than 0.9° VA from the fixation point, in the direction of the target, then the trial was aborted immediately by a red screen (< 5% of trials overall). The green or red screen was dismissed by a keypress from the experimenter, after which the participant could begin the next trial. Each target location was presented 5 times in each block, for a total of 40 trials per block; aborted trials were reshuffled randomly into the sequence until all 40 trials were successfully completed.

Trial blocks were performed in two task conditions (single-task and dual-task) and two visual feedback conditions (closed-loop, open-loop), with these factors crossed. In single-task blocks, the participant was required to fixate the RSVP stream, but did not have to monitor its contents. The RSVP stream contained 20 uppercase letters drawn randomly with replacement from the set of symmetrical uppercase letters (A, H, I, M, O, T, U, V, W, X, Y), with no letter repeated within four consecutive characters. In dual-task blocks, the participant was informed that the letter stream could include the number 8, once, twice, three times, or not at all. The participant was required to count the number of times it appeared, and to report this number (between zero and three) verbally at the green screen; the experimenter manually entered the participant's response. This dual-task condition required continuous focused attention, and the rate of visual presentation (~ 9 Hz) had been established through piloting to reliably produce sub-ceiling performance. The visual monitoring component of the dual-task was experienced as difficult by participants; there was also a small demand on working memory, to keep count of up to three targets, but this was very minor by comparison.

In closed-loop blocks, the lower chamber was lit, so that the hand was always visible. In open-loop blocks, the lights in the lower chamber were turned off when the start button

was pressed to begin the trial, and remained off until the green (or red) screen appeared. The participant thus had no feedback from their hand during reaching in open-loop blocks, but could view it in between trials in order to prevent proprioceptive drift. Feedback condition was crossed factorially with task condition to create four block types. The task condition followed the same ABBA order for all participants, beginning with the single-task. The single task was put first in order to facilitate familiarity with the basic task before the more complex dual-task was performed; our experience of piloting the task had indicated that this was necessary. The feedback condition was alternated in an ABAB order, with the order reversed between participants. Practice sets of 15 trials were completed before the first and second trial blocks, and repeated until the participant was comfortable with the task.

2.6. Data processing and exclusions

Four participants were excluded prior to data analysis, due to an inability to collect full data: one participant was unsuitable for eye-tracking due to heavy eyelashes; two were excluded due to an inability to follow the task instructions; and one was excluded due to recording errors. One further participant found the task extremely difficult, breaking fixation on 25% of trials (2.7 SD above the group mean rate of fixation errors). A decision was made during data analysis to exclude this participant, because they had been unable to perform the task reliably. For the remaining 29 participants, verbal responses in the dual-task blocks were checked, to ensure adequate attention to the visual monitoring demand. The number 8 could appear 0-3 times, so the chance level of correct responding would be 25%. We applied a conservative a priori threshold, excluding any participant performing below 50% correct. Two participants were excluded by this criterion, with accuracies of 30% and 32%. The remaining 27 participants had accuracies ranging from 59-95% (mean 84%, SD 7.2).

For the final sample of 27 participants, the motion tracking data were analysed in custom software written in LabVIEW (National Instruments). The raw marker time-series were filtered by a dual pass through a Butterworth filter with a low-pass cut-off of 20 Hz, and marker speed was calculated by second-order central differentiation of the filtered 3D coordinates. Movement onset was defined as the first sample in which the speed exceeded 50 mm s^{-1} , provided that this was maintained for at least 10 samples (100 ms). Movement offset was defined as the next sample in which the speed fell back below 50 mm s^{-1} . This threshold criterion was chosen to capture the end of the primary reaching movement, excluding

subsequent minor adjustments. By this criterion, 98% of the reaching movements ended within 5 mm of the level of the working surface, suggesting a touchdown of the fingertip. In the remaining 2% of trials, the main movement ended in a more elevated position, up to 53 mm above the surface; the majority (64%) of these elevated offsets were due to one participant. These trials were retained in the analysis, but our findings would not be substantively altered by their exclusion. Across the 27 participants, 101 trials (2.3% of total trials) were excluded as anticipations, in which the movement began less than 100 ms after target onset, and 71 trials (1.6% of total trials) were excluded because the movement was not completed within the two-second window during which the target was present; these criteria had been decided in advance. For all other trials, kinematic variables were extracted.

The focus of interest was the terminal position of the reach with respect to the target. The XY co-ordinates of the fingertip at movement offset were transformed to a polar coordinate system with its origin at the start button (see Figure 1c). Our critical dependent variable was Angular Error, calculated as the angle of the response minus the angle of the target, where errors towards fixation were negative and errors away from fixation were positive. Angular Error is measured in degrees with respect to start position, which we will designate as degrees of heading angle ($^{\circ}\text{HA}$), to avoid possible confusion with target eccentricity measured in $^{\circ}\text{VA}$ with respect to fixation.

We extracted the following dependent variables for exploratory analyses: Amplitude Error (mm), the distance of the terminal position of the reach from the start position minus the distance of the target from the start position (see Figure 1c), where undershoot errors are negative and overshoot errors are positive; Reaction Time (RT), the latency of movement onset after target onset; Peak Speed (PS) attained during the movement; Time to Peak Speed (TPS) from movement onset; Time After Peak Speed (TAPS) until movement offset. We also extracted Movement Time, the total duration of the movement, but this was dropped as redundant for the exploratory analyses, as it is the simple sum of TPS and TAPS.

2.7. Statistical analysis

For each dependent variable, for each participant, the mean value was calculated for each of the eight target positions for each of the four blocked conditions. These means were then averaged across near and far targets at each eccentricity (Figure 1b) for each of the four blocked conditions. A confirmatory repeated-measures ANOVA was run on the critical

dependent variable, Angular Error, with the within-subject factors of task (single, dual), feedback (closed-loop, open-loop) and target eccentricity (9, 18, 27, 36°VA), and a conventional alpha significance criterion of .05 (two-tailed). The same ANOVA design was used for the exploratory analyses of the five additional dependent variables, but an adjusted significance criterion of .01 ($=.05/5$; two-tailed) was set, to guard against false discoveries. Potentially interesting effects with p-values below .05 are reported in Results, but our theoretical interpretation of “significant” findings is restricted to effects below the adjusted criterion of .01. For all ANOVAs, Greenhouse-Geisser adjustments were applied to the degrees of freedom where sphericity was violated.

3. Results

3.1. Confirmatory analysis: Angular Error (Figure 2)

There were significant main effects of all factors on Angular Error, with no significant interactions (Figure 2). Reaches erred progressively more leftward (towards fixation) for targets at higher eccentricities [$F(1.4,36.48)=37.56$, $p<.001$, $\eta^2p=0.59$, $\eta^2G=0.16$], but this function was shifted rightward in the open-loop relative to closed-loop condition [$F(1,26)=4.87$, $p<.05$, $\eta^2p=0.16$, $\eta^2G=0.05$]. Thus, whilst closed-loop performance had slightly rightward errors at the nearest location, with leftward (fixation-directed) errors at higher eccentricities, the open-loop performance was roughly symmetrical around the middle of the target array, with rightward errors for the left two targets and leftward errors for the right two targets. This may represent a contraction bias toward the centre of the target array, due to greater uncertainty in the open loop condition. As predicted, there was a significant shift of responses toward fixation in the dual-task relative to the single-task condition [$F(1,26)=7.79$, $p<.01$, $\eta^2p=0.23$, $\eta^2G=0.01$]. The magnitude of this shift was greater in the open-loop (mean -0.92° SD 2.13) than in the closed loop condition (mean -0.35° SD 0.72), but was also more variable. Expressed as a standardised effect size, the dual-task effect was roughly equivalent in the open- and closed-loop conditions ($dz=-0.43$ vs -0.48).

To give a sense of this spatial effect in the context of the overall workspace, Figure 3a shows a scattergram of mean reaching endpoints in each condition. At this scale, the shift of reaching endpoints towards fixation in the dual-task condition is hardly discernible for the closed-loop condition, but is clearly visible in the open-loop condition. Figure 3b shows the mean reaching trajectories for the open loop condition, created by normalising each reaching movement to 100 frames spaced equally in time, before averaging for each task and target condition. Qualitatively, the dual-task shift seems to emerge as the reach progresses.

3.2. Exploratory analyses (Figure 4)

For Amplitude Error (Figure 4a), there was a general tendency to overshoot the reach distance, but this decreased significantly with target eccentricity [$F(1.68,43.59)=58.54$, $p<.001$, $\eta^2p=0.69$, $\eta^2G=0.13$]. The trend towards greater overshoot in the open-loop feedback condition was not significant [$F(1,26)=4.96$, $p=.04$, $\eta^2p=0.16$, $\eta^2G=0.03$]. Feedback condition did interact significantly with target eccentricity [$F(1.42,37.01)=4.2$, $p<.01$,

$\eta^2p=0.14$, $\eta^2G=0.004$], but this effect (which did not involve the dual task) was not theoretically interesting enough to explore further.

Reaction Time was elevated significantly in the dual-task condition [$F(1,26)=66.31$, $p<.001$, $\eta^2p=0.72$, $\eta^2G=0.31$] (Figure 4b). The average delay incurred by the dual-task was 115 ms (SD 73, $d_z = 1.57$).

Peak Speed (Figure 4c) was higher for more eccentric targets [$F(1.2,31.09)=81.47$, $p<.001$, $\eta^2p=0.76$, $\eta^2G=0.16$], but the slight elevation in the dual-task condition was not significant [$F(1,26)=4.54$, $p=.04$, $\eta^2p=0.15$, $\eta^2G=0.01$].

Figure 4d displays a negative relationship with target eccentricity for both Time to Peak Speed [$F(1.49,38.63)=6.11$, $p<.01$, $\eta^2p=0.19$, $\eta^2G=0.03$] and Time After Peak Speed [$F(1.41,36.79)=26.94$, $p<.001$, $\eta^2p=0.51$, $\eta^2G=0.1$]. Note that the dual-task condition led to a significant reduction in the duration of Time After Peak Speed [$F(1,26)=10.38$, $p<.005$, $\eta^2p=0.29$, $\eta^2G=0.02$]. The average reduction was 26 ms (SD 42, $d_z = 0.62$).

4. Discussion

This experiment tested the effect of an attention-demanding dual-task performed at fixation upon visually-guided reaching to peripheral targets. The dual-task was intended to deplete the attentional resource available for reaching. Our main interest was in whether this would induce a fixation-directed bias, qualitatively reminiscent of field-dependent misreaching in patients with optic ataxia. This is exactly what we found: there was a significant shift of spatial errors towards the side of fixation, in both closed- and open-loop conditions, replicating and extending preliminary observations on an earlier version of this task (Ingle & McIntosh, 2016). Further exploratory analyses showed that participants were slow to initiate reaches under dual-task conditions, and there was a reduction in the duration of reaches after the point of peak speed. The dual task thus affected the programming (initiation) and control (execution) of reaching, both of which are known to be impaired in optic ataxia (Blangero et al., 2008; Gréa et al., 2002; McIntosh et al., 2011; Milner, Dijkerman, McIntosh, Rossetti, & Pisella, 2003; Pisella et al., 2000).

Our findings extend a prior literature using similar dual-task approaches, which implicate visual attention in the planning and execution of visually-guided reaching and grasping (Hesse & Deubel, 2011; Hesse et al., 2012; Liu et al., 2008; Sandoval Similă & McIntosh, 2015). The interference effects that we observed would be consistent with a close coupling between the selection of a target as an object of visual attention, and its selection as an action target. For instance, in a biased competition model of attention, sensory inputs at different spatial locations compete for prioritisation within sensory and motor systems (Desimone, 1998; Desimone & Duncan, 1995; Duncan, 1998; Smith & Schenk, 2012). Within this scheme, the focusing of attention on the visual monitoring task at fixation would bias activity within pragmatic maps for movement, so that the fixation stimulus would become an attractor, pulling the representation of the reaching targets towards it. Unless this was actively inhibited, it would induce a reaching bias towards the point of fixation. The allocation of attention to the monitoring task might also limit the resources available for monitoring the movement online, which would be consistent with a reduction in the duration of the deceleration phase of the movement, after the point of peak speed, which is classically associated with feedback-based adjustments as the hand closes in on the target.

Our main result confirms a prediction derived from the common association of optic ataxia with impaired allocation of attention to ataxic fields (Blangero et al., 2010; McIntosh

et al., 2011; Perenin & Vighetto, 1988; Pisella et al., 2007, 2009; Striemer et al., 2007, 2009). As such, it provides circumstantial evidence for the idea that an impaired ability to attend to an ataxic field could be causally involved in the visuomotor field effect in optic ataxia. It is important to emphasise that this would not be incompatible with optic ataxia reflecting a disruption of visuomotor processes in the dorsal visual stream, given that there may be a very close coupling between visually-guided action and (some forms of) selective attention (see Smith & Schenk, 2012). Moreover, although not specifically predicted by them, the present results could also be consistent with models of optic ataxia as an impaired ability to transform a default reach fixation-directed reaching plan (Buxbaum & Coslett, 1997; Jackson et al., 2009; Vindras et al., 2016), provided that we allow that attentional loading can reduce the efficacy of these transformations in the healthy brain. That is, we do not intend to propose a novel model of optic ataxia, but simply to highlight a possible contribution of attentional impairments to the character of non-foveal misreaching.

There are limitations to the present findings as a possible model of optic ataxia. First, the spatial biases attributable to the dual-task, though statistically reliable, were metrically small, with raw effect sizes of -0.35° (SD 0.72) and -0.92° (SD 2.13) in the closed- and open-loop conditions respectively. The largest total fixation-directed bias elicited in our experiment was a mean angular error of -3.7° [95% CIs $-4.7, -2.7$] for the most eccentric target (36°) in the closed-loop condition. This maximum bias would correspond to around 1.75° VA, which is an order of magnitude smaller than the average spatial errors made for peripheral targets in a group of patients with unilateral optic ataxia (around 11.5° VA for reaching targets at 40° eccentricity; see Figure 4 of Vindras et al., 2016). On the other hand, it is not surprising if a manipulation of attention in healthy adults does not have a comparable impact on behaviour to that of organic damage to the parietal lobe. It is the qualitative resemblance, rather than the size of the errors that is of interest. By the same token, subtle biases in visual search or spatial judgement tasks, induced by transient neurodisruption (Ellison, Schindler, Pattison, & Milner, 2004), behavioural manipulations of arousal (Dufour, Touzalin, & Candas, 2007; Manly, Dobler, Dodds, & George, 2005), or visuomotor adaptation to prisms (McIntosh, Brown, & Young, 2019) have been widely taken to be informative about the catastrophic symptoms of spatial neglect.

A second limitation is that, whereas the fixation-directed bias of optic ataxia increases non-linearly with eccentricity (Vindras et al., 2016), the bias induced by the dual task did not vary with target eccentricity. There was some qualitative suggestion, for the closed-loop

condition, that the effect of the dual-task was stronger at higher eccentricities, and almost absent for the least eccentric targets (see Figure 2), but no interactions approached significance within the ANOVA model. We may perhaps rationalise the constant bias induced by the dual task in terms of the constant nature of the visual monitoring demand. If an impaired ability to allocate attention away from fixation in optic ataxia becomes more severe at higher eccentricities, then this would need to be mimicked by a dual-task that became increasingly difficult as the eccentricity of the target was increased. Nonetheless, the overall pattern of angular errors was increasingly fixation-directed with increasing target eccentricity, consistent with the observations of a prior investigation of peripheral reaching in healthy participants (Prablanc, Echallier, Komilis, & Jeannerod, 1979). It may be that this normal tendency is pathologically exaggerated in patients with optic ataxia.

Third, since we always had the fixation point to the left of the target array, we cannot exclude the possibility that the induced bias is not fixation-directed *per se*, but is merely leftward (or ipsilateral to the responding hand). We think it is reasonable to assume that the bias is indeed fixation-directed, though varying the location of fixation and/or the laterality of the responding hand would be worthwhile checks for future studies. More importantly, since we placed the dual-task demand at the point of fixation, we cannot disambiguate whether the induced bias is towards fixation (as a default hand-eye coupling) or towards the focus of attention. It may be of theoretical interest for future studies to disentangle the focus of attention from the point of fixation, in order to separate their contributions. One recent study has in fact shown that visual monitoring at a non-fixated location other than the reach target can interfere with reaching accuracy. Mahon and colleagues (2020) reported that participants made larger errors in reaching for an extrafoveal target (5° eccentricity) when feedback from the movement was expected at a mirror image location on the other side of the fixation point. However, the dependent measure in that study was absolute reaching error, so it is unclear whether this involved a consistent directional bias, as in the present data.

Finally, our exploratory analyses suggested that the dual-task induced a reduction in movement duration, specifically localised to the (deceleration) phase after the point of peak speed. It is possible that this reflects a more ballistic approach to reaching in the dual-task condition, due to a reduced ability to make use of visual feedback to adjust the movement in its terminal stages. If so, then we could propose that our restriction of visual attention has induced a second characteristic that is typical of reaching behaviour in optic ataxia: a reduced capacity for online corrections (Blangero et al., 2008; McIntosh et al., 2011; Pisella et al.,

2000). However, we should be wary of making this connection prematurely, since it is possible that a more ballistic approach to reaching was a secondary compensation for the retardation in Reaction Time in the dual task condition (Figure 4b). Given the longer latency of responding, participants may have truncated the movement durations in order to complete the response comfortably within the (approximately) two second response window.

In summary, our experimental manipulation of visual attention induced a consistent spatial bias towards the point of fixation, qualitatively reminiscent of field-dependent misreaching in optic ataxia, although much more subtle. The demonstration that reaching responses can be pulled towards the point of fixation by attentional depletion reinforces the possibility of a functional connection between field-dependent misreaching in optic ataxia, and attentional deficits for the same field in those patients. Attentional deficits are unlikely to be the main cause of field-dependent misreaching in optic ataxia, but they may play a role in shaping its character and/or arise as a consequence of damage to visuomotor processes.

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Figure 1. (a) Participants viewed the stimuli displayed on the monitor via a semi-silvered mirror, so that the display was projected optically to the working surface. The participant's hand was visible only when the lower chamber was lit. (b) Layout of the working surface, showing the position of the start button (START), the fixation point (FIX), and the eight possible target locations. These were at four eccentricities: 9, 18, 27 and 36 degrees of visual angle from fixation. At each eccentricity, there was a near target (N) 260 mm from the start button, and a far target (F) 280 mm from the start button. The vertical dotted line indicates the participant's midline, and the dotted box indicates the active display area (these lines were not marked on the apparatus). (c) The Angular Error of the reach in degrees of heading angle ($^{\circ}\text{HA}$) was defined as the angle between the straight line from the start position to the reach endpoint (SR) and the straight line from the start position to the target (ST), where leftward deviations (towards fixation) are negative and rightward deviations positive. Amplitude Error was defined as the distance of the reach endpoint from the start position (SR) minus the distance of the targets from the start position (ST), where undershoot errors are negative and overshoot errors are positive. In the hypothetical example shown, both the Angular Error and the Amplitude Error are negative.

Figure 2. Angular error by target eccentricity in the closed- and open-loop conditions, for the single-task (filled symbols) and dual-task (unfilled symbols) conditions. Angular error is measured in ° heading angle with respect to the start button, whereas target eccentricity is expressed in ° visual angle with respect to fixation (see Section 2.6).

Figure 3. (a) Mean terminal position of reaching for the single task (black) and dual task (grey) conditions, showing hand start position (S), fixation position (F) and target positions (x). **(b)** Mean reaching trajectory after temporal normalisation (to 100 frames) for the single task (black) and dual task (grey) conditions, for the open-loop condition only. These plots are for qualitative descriptive purposes, to give a sense of the scale of the dual-task effect relative to the workspace, and its emergence during the course of the reach trajectory.

Figure 4. (a) Amplitude error by target eccentricity in the closed- and open-loop conditions, for the single-task (filled symbols) and dual-task (unfilled symbols) conditions. Positive amplitude errors indicate reaches that land further from the start button than the distance of the target, and negative amplitude errors less far. (b) Reaction Time by target eccentricity in the closed- and open-loop conditions, for the single-task (filled symbols) and dual-task (unfilled symbols) conditions. (c) Peak Speed by target eccentricity in the closed- and open-loop conditions, for the single-task (filled symbols) and dual-task (unfilled symbols) conditions. (d) Time to Peak Speed (squares) and Time After Peak Speed (circles) by target eccentricity in the closed- and open-loop conditions, for the single-task (filled symbols) and dual-task (unfilled symbols) conditions. Error bars show 95% confidence intervals for within-subject effects (Morey, 2008).