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Spatial bias in anti-saccade endpoints following bilateral dorsal posterior parietal lesions

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Abstract

Anti-saccades are eye movements in which the saccade is executed in the opposite direction of a visual target and are often hypometric. Because the visual target and saccade goal are decoupled, it has been suggested that competition between the two locations occurs and needs to be resolved. It has been hypothesized that the hypometria of anti-saccades reflects this spatial competition by revealing a bias towards the visual target. To confirm that this hypometria is not simply due to reduced gain, we tested 10 healthy subjects on three different anti-saccade spatial configuration tasks: 90° away *across* hemifields, 90° away *within* the same hemifield and 180° away (*classic*, diagonally opposite). Specifically, we examined whether saccade endpoints showed evidence for the visual target location's interference with anti-saccade programming and execution processes. Among other neural substrates involved in anti-saccades production, the dorsal posterior parietal cortex (PPC) has been implicated in the spatial inhibition of contralateral visual target. To gain insight into the neural processes involved in spatial competition during anti-saccades, we also tested one patient with a bilateral dorsal PPC lesion. In all spatial configurations, we observed that anti-saccade endpoints demonstrated a spatial bias towards the visual target for all participants, likely due to an incomplete inhibition of the visual target location. This spatial bias was exacerbated in our patient, which suggests that the dorsal PPC contributes to the amalgamation of the two competing spatial representations.

KEYWORDS

inhibition, optic ataxia, priority map, saccade goal

Abbreviations: ADHD, attention deficit disorder with or without hyperactivity; ER, error rate; ITI, inter-trial interval; PPC, posterior parietal cortex; SD, standard deviation; SEM, standard error of the mean.

1 | INTRODUCTION

Anti-saccades are eye movements directed in the opposite direction of a visual target that require the inhibition

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of an automatic orienting response (Everling & Fischer, 1998; Munoz & Everling, 2004). The inhibitory processes involved in anti-saccades are often measured with parameters such as the percentage of erroneous saccades to the visual target or the latency of correctly executed anti-saccades. These parameters have been measured in different clinical populations, such as Parkinson's disease (Antoniades et al., 2015; Lueck et al., 1990), attention deficit disorder (ADHD) (Fernandez-Ruiz et al., 2020; Klein et al., 2003), patients with frontal cortex lesions (Fukushima et al., 1994; Guitton et al., 1985) and patients with parietal cortex lesions (Butler et al., 2009; Ouerfelli-Ethier et al., 2021), and demonstrated impairment of multiple inhibitory processes, including spatial inhibition, response inhibition or proactive inhibition (Aron, 2011; Fernandez-Ruiz et al., 2020; Hutton & Ettinger, 2006; Munoz & Everling, 2004; Ouerfelli-Ethier et al., 2021; Talanow et al., 2020; Zhang & Barash, 2000, 2004).

Besides error rates (ERs) and anti-saccade latencies, saccade endpoint inaccuracy during anti-saccades has also been shown to be exacerbated in most clinical populations such as Parkinson's disease (Matsumoto et al., 2011), bipolar disorder (Crawford et al., 1995), ADHD (Huang & Chan, 2020), unilateral optic ataxia (Ouerfelli-Ethier et al., 2021) and hemispatial neglect (Butler et al., 2009). In the healthy population, anti-saccades tend to be more hypometric than pro-saccades (Bahcall & Kowler, 1999; Hallett, 1978; Kowler et al., 1995; Krappmann, 1998). This has been hypothesized to reveal a bias towards the visual target (Huang & Chan, 2020). During anti-saccades, two competing motor programs are generated: an automatic motor program towards the visual target and one in the opposite direction (Kristjansson, 2007; Noorani & Carpenter, 2013). Theoretically, because the visual target and the saccade goal are decoupled, their corresponding neural spatial representations compete for attentional selection (Klapetek et al., 2016; Mikula et al., 2018). An incomplete resolution of the spatial competition between the representation of the visual target and its 'intentionally remapped' location would result in a bias in endpoints towards the visual target. These anti-saccade endpoint inaccuracies could thus provide insight into the attentional competition resolution in terms of inhibition of the visual target representation. However, these endpoint inaccuracies could alternatively correspond to a reduced saccadic gain caused by the planning of a saccade in the absence of a visual target as it is the case in memory-guided saccades in neurotypical populations (Ohtsuka et al., 1989; Pierrot-Deseilligny et al., 1991), and that are exacerbated in clinical population with cortical (Heitger et al., 2002; Mosimann et al., 2000; Pierrot-Deseilligny

et al., 1991) and subcortical dysfunction (Crawford et al., 1989; Müller et al., 1999).

In the specific case of memory-guided saccades, saccade gain has been attributed to spatial memory representations and oculomotor control (Heitger et al., 2002), where spatial miscalculations may reflect the combined contributions of both early parietal preparation (Gnadt & Andersen, 1988) and late integrated signals in the prefrontal cortex (Pierrot-Deseilligny et al., 1991). It is thus possible that spatial inaccuracies in anti-saccades similarly reveal the interference of an 'early' automatic motor plan to the visual target with a 'late' voluntary motor plan to the saccade goal. This interpretation would explain stimulus-driven behaviours in clinical populations with spatial inaccuracies (Chan et al., 2005; Goto et al., 2010) and, as such, would be more in line with the spatial bias hypothesis than the reduced gain hypothesis, as it suggests that the visual target is interfering with saccade goal selection. Classic anti-saccade paradigms (i.e., 180° spatial configurations) alone do not allow to distinguish between the two alternative hypotheses of reduced gain versus spatial bias towards the visual target. A specific spatial bias of anti-saccade endpoints towards the visual target should be evidenced in other types of anti-saccade spatial configurations like mirror 90° vector inversion, as tested in the present paper, to reflect an impaired spatial competition resolution.

The PPC has been implicated in spatial competition resolution (Bisley & Goldberg, 2003; Bisley & Mirpour, 2019; Falkner et al., 2010). Studies in humans more precisely point to the dorsal PPC in the dynamic encoding of locations in priority maps (Molenberghs et al., 2007) and in the spatial inhibition of the visual target location for anti-saccades (Ouerfelli-Ethier et al., 2021). Damage to the dorsal PPC results in optic ataxia, consisting of impaired visually guided movements and spatial attention for contralesional visual targets (Pisella et al., 2011, 2021). We have previously shown that unilateral dorsal PPC damage leads to increased ERs for ipsilesional anti-saccades when the visual target was presented in the contralesional field, particularly for anti-saccades requiring interhemispheric transfer (Ouerfelli-Ethier et al., 2021). This specific pattern of lateralized deficits points to the role of dorsal PPC in spatial inhibition of the contralesional visual target. We therefore hypothesized that inter-hemispheric rivalry between the left and right dorsal PPC priority maps contributes to the resolution of the attentional competition between visual target and saccade goal locations during anti-saccades. We also observed increased anti-saccade spatial inaccuracy in our unilateral patients' ipsilesional hemifields, which we posited could reflect a persisting attentional influence of the insufficiently inhibited visual target representation

(Ouerfelli-Ethier et al., 2021). However, this endpoint pattern was combined with global undershooting/overshooting of the saccade goal, most likely due to differences in lesions and probably in interhemispheric imbalance, which did not allow us to interpret our observations.

Here, we further explored this issue of endpoint distribution by testing a rare patient with bilateral optic ataxia along with age-matched controls. For all participants, if the hypometria classically observed in the 180° anti-saccade condition reflects spatial bias towards the target rather than a general reduction in gain, it should also be present along the visual target-saccade goal vector in 90° anti-saccade spatial configurations.

2 | METHODS

2.1 | Participants

We recruited one patient with parietal lesions presenting optic ataxia via the neurological and rehabilitation Hospitals, Lyon, France, and control participants were recruited from the community in both Lyon and Montreal.

Patient I.G. is a right-handed, 40-year-old female who shows specific problems with visually guided movements (bilateral optic ataxia) without neglect. An ischemic stroke related to acute vasospastic angiopathy resulted in the blockage of the posterior cerebral arteries causing lesions involving mainly Brodmann's area 7 and 39 almost symmetrically in both hemispheres (Figure 1), 15 years prior to testing. She has some damage to superior occipital areas (Brodmann's areas 18 and 19, leaving the human equivalent of V3a intact), but most of the damage is limited to the parietal cortex. I.G. shows no primary somatosensory or visual deficits except for quadrantanopia in the lower right visual field (Pisella

et al., 2000). She has visually guided reaching movements that are comparable with normal participants for targets presented foveally but exhibits impairments for on-line modification of goal-directed movements in response to a change of the goal occurring during or before movement execution (Gréa et al., 2002; Milner et al., 2001, 2003; Pisella et al., 2000; Rossetti et al., 2005); her reaching and grasping are inaccurate in her peripheral vision (for both left and right visual fields and hands), with a slightly greater inaccuracy for her right hand in her right peripheral field (Pisella et al., 2000).

We tested 10 age-matched control participants ($M = 39.8$ years, $SD = 3.4$ years; age range = 37–46 years, six females). Controls with neurological disorders or attentional deficits were excluded. All participants had normal or corrected to normal vision and gave informed consent to participate in the experiment. Procedures in Lyon were conformed according to the French law (4 March 2002) on human subjects' rights, and informed written consent was collected from all participants in accordance with CPP Northwestern 1046/2017 registration number 2017-A02562-51. Procedures also received ethics approval from the Ethics committee of Clinical Research at the University of Montreal. Upon completion of their participation, participants received financial compensation.

2.2 | Apparatus

Testing occurred at the University of Montreal (Montreal, Canada) and at the Centre of Neuroscience Research of Lyon (CNRL; Lyon, France) with similar apparatuses for eye-movement recording. Participants sat in a dark room 57 cm away from a high-speed computer screen (at CNRL: 15.7*11.8 in., Visual Stimulus Generator™ ViSaGe, Cambridge Research System, Rochester, UK; at the University of Montreal, 20.5*11.5 in., VIEWpixx 3D, VPixx Technologies, Montreal, Canada). Head movements were restricted with chin and forehead rests during the task. An eye-tracker, set in a binocular tower mount, recorded eye movements (at CNRL: ViSaGe, Cambridge Research System, Rochester, UK, frequency: 250 Hz; at the University of Montreal: EyeLink 1000 Plus, SR Research, Kanata, Canada, frequency: 1000 Hz).

2.3 | Procedure

As shown in Figure 2, participants performed saccades in four paradigms over a 1-h-long session: (1) pro-saccades, (2) mirror saccades (90° rotation) *across* (left and right) visual fields, (3) mirror saccades (90° rotation) *within* the

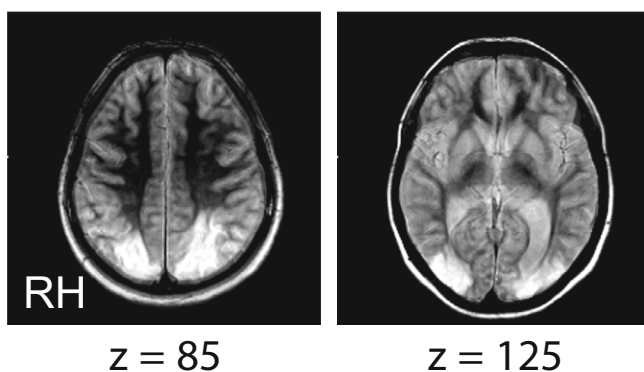


FIGURE 1 Lesions of patient I.G. T1 anatomical scan of patient I.G.'s bilateral posterior parietal and occipital lesions. RH, right hemisphere.

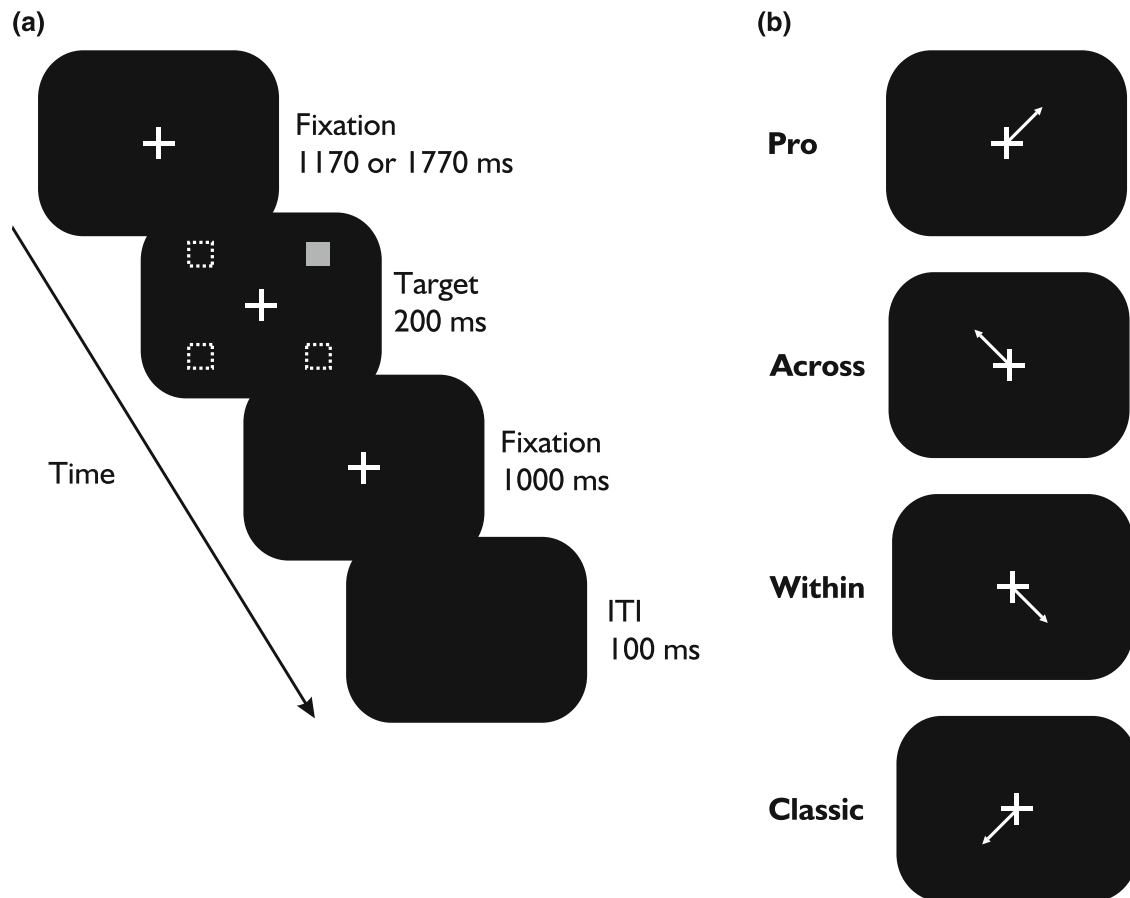


FIGURE 2 Experimental sequence and timings of the four conditions of the saccade task. In (a), the fixation cross remained on the screen for 1170 or 1770 ms. The target (filled grey square) appeared for 200 ms. White dotted squares represent possible target locations. These squares are shown for the purpose of clarity and were not presented on the screen to participants. The fixation cross remained on for an additional 1000 ms after target appearance. After the fixation cross disappeared, there was an inter-trial interval (ITI) of 100 ms. For all panels in (b), correct saccades relative to a right top corner target are illustrated by a white arrow.

same (left or right) visual field and (4) classic anti-saccades (180° rotation). These paradigms were identical to a previous paper published by our group (Ouerfelli-Ethier et al., 2021). Tasks were designed and implemented using MatLab (The MathWorks, Inc., Natick, Massachusetts, USA) with the Psychophysics toolbox (Brainard, 1997).

All paradigms consisted of the same stimuli presentation as follows: Each trial began with the presentation of white fixation cross (dimensions: 1 by 1°) centred on the screen against a black background. The fixation cross was aligned horizontally with the midpoint of the eyes and vertically at eye level. The fixation cross was present throughout the trial. After a variable duration (1170 or 1770 ms), a target was presented at one of four oblique locations at 7.78° from the fixation cross (5.5° horizontally and vertically). The target was a grey square with a diameter of 1° and was presented for 200 ms. The fixation cross remained illuminated for an additional 1000 ms and then was followed by a blank screen for 100 ms

signalling the next trial. Target presentation was pseudo-random across four possible target locations.

The four paradigms were performed in blocked order. Blocked paradigms were used to limit variables associated with switching associated with the interleaved pro-/anti-saccade paradigm (Munoz & Everling, 2004; Weiler & Heath, 2012). During pro-saccades, participants made a saccade towards the target as quickly as possible when it appeared. In the across condition, participants were asked to inhibit a saccade towards the target and to make, instead, a saccade 90° away from it across the other hemifield. For the within condition, participants made a saccade 90° away from the target vertically, or within the same hemifield. Finally, during the classic condition, participants gazed 180° away from the visual target. In Figure 2, the white arrow indicates the correct direction of the saccade relative to the target for each condition.

Participants performed all four paradigms in blocks within the same session or across two sessions, and the

paradigm order was counterbalanced across participants. Patient I.G. completed 40 trials for the pro-saccade paradigm and 144 trials each for the three other paradigms. Paradigm order for I.G. was established randomly; she performed the classic condition first, followed by the pro-saccade, the across and the within conditions. Control participants each performed between 80 and 240 trials per paradigm. The number of trials varied because of time and patient errors/constraints.

2.4 | Preliminary analyses

To accommodate the varying sampling rates of the two cameras, we independently extracted data using customized scripts specific to each sampling rate, ensuring that

timing remained intact. Subsequently, the data were analysed using identical methods. Saccade onsets and offsets were automatically calculated offline using a saccade detection algorithm with a velocity criterion of 15 visual degrees per second and verified visually. Saccade start and end X and Y positions were calculated as the average across 10 ms centred around 50 ms before and after the saccade onset and offset respectively; we visually verified that these positions were sampled when the eye position was stable.

We recorded a total of 5075 trials. In Figure 3, we provide the total number of trials included and excluded at each step of the data filtering described below. We removed all trials with end positions for the first saccade beyond 30 visual degrees from the centre fixation to account for blinks. Next, we normalized start positions

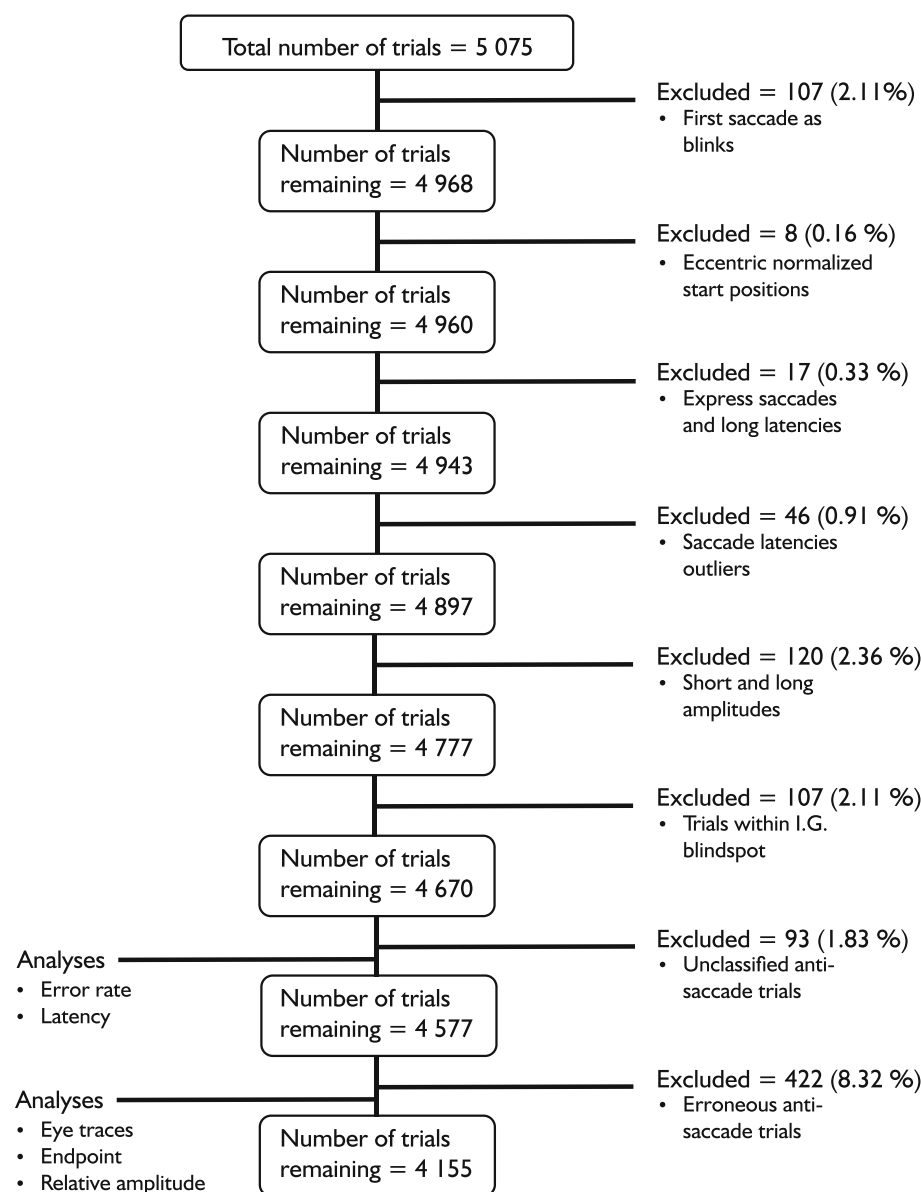


FIGURE 3 Flow chart of data filtering. Total and remaining number of trials are detailed in each box of the flow chart. Number of trials excluded as well as the summarized reason of their removal are indicated between each box on the right below the number of trials excluded. The percentage provided next to the number of trials excluded corresponded to the percentage of excluded trials over the total number of trials.

per participant according to their mean start X and Y positions across each block. From these normalized positions, we filtered out start positions beyond three visual degrees from the centre in both X and Y positions. Next, we removed all trials with saccade reaction times below 100 ms (i.e., anticipatory saccades) and beyond 1300 ms. We also filtered out, per participant, all trials with saccade reaction times outside of three standard deviations of their mean saccade reaction times. All trials where the first saccade was outside of 10 cardinal degrees of the saccade goal or had an amplitude smaller than 2 visual degrees were also removed.

For I.G., we removed all trials where either the saccade goal or the visual target was within her blind quadrant. This corresponded to the right bottom target for pro-saccades, the two bottom targets for the across condition, the two right targets for the within condition and the top left and bottom right targets for the classic condition.

We classified correct and erroneous saccades across anti-saccade conditions. Correct anti-saccades corresponded to saccades made towards the quadrant containing the saccade goal (excluding 10° of both horizontal and vertical cardinal directions). In contrast, we classified all saccades made towards the quadrant containing the visual target as erroneous saccades. In other terms, erroneous anti-saccades are saccades made towards the visual target rather than the correct saccade goal location. Anti-saccade trials with saccades that were not classified as either correct or erroneous were removed.

For the pro-saccade trials, erroneous pro-saccades (saccade directed in the opposite direction of the visual target) were of 0% for both I.G. and her controls. Mean latencies for pro-saccades were 298.64 ms for I.G. and 226.58 ms ($SEM = 5.31$ ms) for her controls.

Across the different anti-saccade conditions, mean ERs for I.G. corresponded to 6.38% for the across condition, 12.20% in the within condition and 0% in the classic condition. Controls' ERs reached 12.29% ($SEM = 5.00\%$) for the across condition, 15.75% ($SEM = 5.88\%$) for the within condition and 6.79% ($SEM = 1.84\%$) for the classic condition. Mean ERs for both I.G. and controls were within the same range as the ones reported previously in neurotypical controls by our group (Ouerfelli-Ethier et al., 2021) as well as other studies on neurotypical participants of the same age group (Coe & Munoz, 2017; Fukushima et al., 1994; Munoz et al., 1998; Pierrot-Deseilligny et al., 1991). In contrast, mean anti-saccade latencies for correct trials were high for I.G. (across: $M = 473.80$ ms; within: $M = 516.08$ ms; classic: $M = 857.98$ ms) compared with controls (across: $M = 341.45$ ms, $SEM = 9.51$ ms; within: $M = 346.91$ ms,

$SEM = 13.98$ ms; classic: $M = 327.71$ ms, $SEM = 13.53$ ms).

Subsequent analyses only concerned correct trials including both pro- and anti-saccades and were conducted on a total of 859 pro-saccade trials and 3296 anti-saccade trials. We examined mean saccade endpoints by averaging eye end positions in X and Y. We quantified the bias relative to the visual target in two ways: with the absolute distance between mean saccade endpoints and with relative amplitude. Specifically, we calculated for each condition the (1) absolute distance in visual degrees between the mean horizontal endpoints of the left and right targets separately for the targets in the upper and lower visual fields (then averaged this distance to obtain the horizontal distance for each participant), (2) absolute distance in visual degrees between the mean vertical endpoints of the upper and lower targets separately for the left and right visual fields (then averaged to obtain the vertical distance) and (3) the diagonal distance in visual degrees (average, distance between the upper/left and the lower/right targets, and the distance between the upper/right and lower/left targets). We then compared these three values across the four saccade conditions (pro-saccade, across, within and classic) for controls with repeated measures ANOVAs. We next compared I.G. and her controls with modified *t*-tests (Crawford & Garthwaite, 2005). These analyses are adapted for case studies and are adequate for a group control of six or more participants (Crawford et al., 2010; Crawford & Garthwaite, 2005).

To further investigate bias towards and away from the visual target, we calculated relative amplitudes. By 'visual target', we refer to the target, which is an incorrect saccade goal for anti-saccades. These were calculated as the amplitude of the saccade with the start position being the visual target location instead of the centre fixation position and the end position being the saccade endpoint. Relative amplitudes were then averaged per participant and per condition. We performed one-sample *t*-tests to test controls' and I.G.'s relative amplitudes against the ideal amplitude, that is, 11° for the across and within conditions, and 15.57° for the classic condition. To compare relative saccade amplitudes between I.G. and her controls across conditions, we used modified *t*-tests (Crawford & Garthwaite, 2005).

Finally, we evaluated pro-saccades accuracy to fully test the hypothesis of overall reduced gain against the one of spatial bias. To do so, we compared pro-saccade amplitudes between I.G. and her controls with modified *t*-tests (Crawford & Garthwaite, 2005). Amplitudes were calculated as the absolute distance between saccade start positions and saccade end positions.

3 | RESULTS

We show raw eye movement traces in one typical control and our patient across the saccade conditions below. For I.G. and her controls, we also characterized saccade endpoints relative to the saccade goal for each saccade condition and therefore also relative to the visual target location. Finally, we investigated anti-saccades relative amplitudes. Of note, all our analyses were conducted on correct anti-saccade trials.

3.1 | Raw eye movement traces

We randomly selected five correct raw eye movement traces for five saccades per visual target per condition and separately for one typical control and I.G. The eye traces were drawn from the 1500-ms timepoint until the end of the trial to include the beginning and end of the saccade. As seen in Figure 4, these eye traces are colour-coded according to the location of the visual target: in red for the top left target, in green for the top right target, in

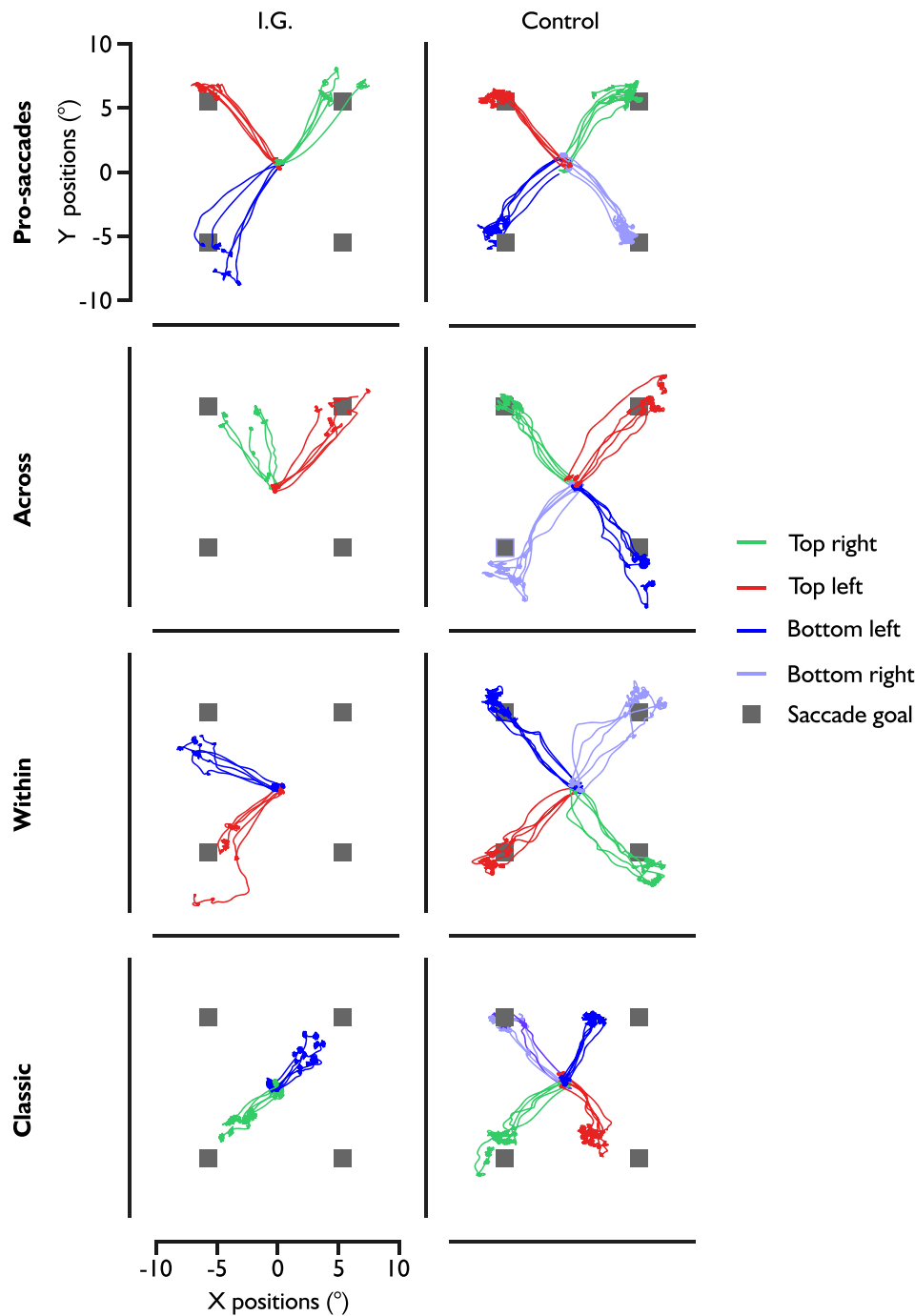


FIGURE 4 Raw saccade traces across saccade conditions for I.G. and one typical control. Example saccade traces from one patient I.G. (left panels) and on typical control (right panels) are presented for each paradigm. Each colour represents each visual target location: green for the top right target, red for the top left target, purple for the bottom right target and blue for the bottom left target. The positions of saccade goals are indicated with grey squares.

blue for the bottom left target and in purple for the bottom right target. Of note, because we removed I.G.'s trials where either the target or the saccade goal appeared within her blind quadrant (i.e., bottom right visual field), some of her eye traces are missing depending on the condition for some quadrants.

For our typical control, we observed rather precise eye traces towards each saccade goal in the pro-saccade condition. As there is no competition between the saccade goal and visual target in this condition, this is expected. In the other anti-saccade conditions, eye traces tended to land between the saccade goal and visual target and varied per condition. For example, in the across condition, the eye traces seemed to be more aligned with the saccade goal on the vertical than on the horizontal, which may reflect the competition between the visual target and saccade goal on the horizontal component (i.e., from left to right or from right to left). In the within condition, eye traces were in turn more aligned with the saccade goal on the horizontal than on the vertical component, which suggests once more the possible effect of the competition between the visual target and saccade goal (i.e., from up to down or from down to up). Finally, in the classic anti-saccade condition, eye traces were misaligned with the saccade goal on both the horizontal and vertical components. In sum, for the anti-saccade conditions, our observations support the hypothesis that the competition between the saccade goal and the visual target misaligned the eye traces on the horizontal or vertical or both components so they would fall between these two locations. This effect was absent in the pro-saccade condition where there is no competition, that is, the saccade goal and visual target are at the same location.

I.G.'s pro-saccade endpoints do not appear to show any biases, similar to those of the control participant. However, for the anti-saccade conditions, the misalignment of the eye traces was exacerbated compared to the control displayed in Figure 4, where some of her eye traces land almost halfway between the saccade goal and the visual target in the across and within condition. We also found shorter eye traces in the classic condition for I.G. compared with the control participant. These results point to a bias towards the visual target that is present overall but is more pronounced in our patient compared with her control.

3.2 | Saccade endpoints

In Figure 5, we have plotted mean saccade endpoints for controls in white and for I.G. in green. We have also plotted individual data points for I.G. (smaller green dots without a black outline). By connecting each mean

endpoint with a black line for our controls, we were able to draw a square that reflected the compression of the eye traces discussed in the previous section. This also allowed us to visually characterize more readily the bias towards the visual target for our patients and controls.

Controls' saccade endpoints reflected the task condition, observable by the shape of the dark lines linking their mean saccade endpoint for each saccade goal. In the pro-saccade condition, this shape is almost square, indicating no bias or competition because the visual target corresponds to the saccade goal. In the across condition, the shape linking their mean endpoints tends towards a longer vertical rectangle, because in this case, the anti-saccade vector inversion is 90° away on the horizontal. In the within condition, the vector inversion associated with a correct anti-saccade is 90° away on the vertical, thus the shape joining controls' saccade endpoints is compressed vertically in a longer horizontal rectangle. Finally, in the classic condition, we can observe a compression of the shape linking the saccade endpoints that is both vertical and horizontal as the vector inversion is 180°. The distinct effect of each saccade paradigm on saccade endpoints suggests a bias towards the visual target for our controls.

We confirmed these observed differences in shape by comparing the horizontal, vertical and diagonal distances across conditions. We expected that if there is a bias towards the visual target, the direction of the vector inversion should selectively affect absolute distance. In other terms, as the across condition relies on a horizontal inversion, the presence of a bias relative to the visual target would specifically affect absolute distance in the horizontal component compared with the pro-saccade condition, whereas a bias relative to the visual target in the within condition would affect the vertical absolute distance compared with the pro-saccade condition. Finally, a bias relative to the visual target in the classic condition would affect the diagonal distance compared with the pro-saccade condition as both the vector inversion relies on both the horizontal and vertical components.

For the horizontal distance, we found a significant main effect of saccade condition with repeated-measures ANOVAs, $F_{3, 27} = 7.58$, $P = 0.002$. Post hoc *t*-tests with Holm–Bonferroni corrections revealed a significantly smaller distance for the across condition ($M = 8.34^\circ$; $t_9 = 2.709$, $P = 0.046$) compared with the pro-saccade condition ($M = 9.68^\circ$) as well as the classic condition ($M = 7.91^\circ$; $t_9 = 3.598$, $P = 0.008$) compared with the pro-saccade condition. However, we found no significant difference between the within condition ($M = 9.53^\circ$; $t_9 = 0.305$, $P = 0.76$) and the pro-saccade condition.

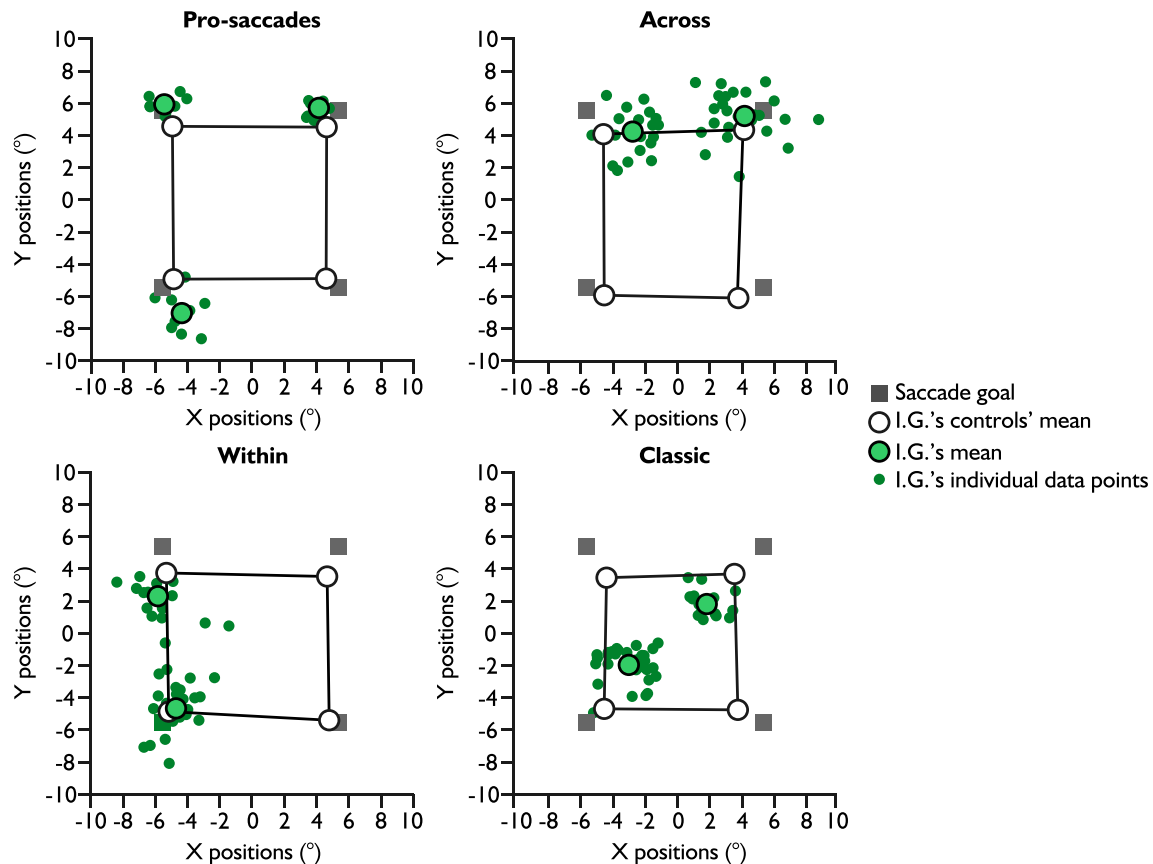


FIGURE 5 Mean saccade endpoints across saccade conditions. Mean saccade endpoints in visual degrees are illustrated with outlined circles for each saccade paradigm in white for controls and in green for I.G. Smaller green dots without outlines represent individual data points for I.G. The positions of saccade goals are indicated with grey squares.

For the vertical distance, we also found a main effect of saccade condition, $F_{3, 27} = 3.89$, $P = 0.02$. Holm-Bonferroni corrected post hoc t -tests revealed that whereas the vertical distance in the classic condition was smaller ($M = 8.34^\circ$) than in the pro-saccade condition ($M = 9.35^\circ$), it was not statistically different, $t_9 = 2.242$, $P = 0.167$. Whereas the vertical distance for the within condition did not reach a statistical difference ($M = 8.81^\circ$; $t_9 = 1.213$, $P = 0.71$), the mean vertical distance was smaller than in the pro-saccade condition. We also found no significant distance in the across condition ($M = 9.78^\circ$; $t_9 = -0.952$, $P = 0.71$), albeit it had a longer distance than in the pro-saccade condition.

For the diagonal distance, the saccade condition main effect also reached statistical significance, $F_{3, 27} = 4.82$, $P = 0.008$. With post hoc t -tests, we found a significantly smaller distance in the classic condition ($M = 11.54^\circ$) compared with the pro-saccade condition ($M = 13.47^\circ$; $t_9 = 3.593$, $P = 0.008$). In contrast, the diagonal distance in the other two saccade conditions did not differ from the pro-saccade condition ($M_{\text{across}} = 12.93$, $M_{\text{within}} = 13.02^\circ$; $P > 0.05$).

I.G. showed similar saccade endpoints to controls during pro-saccades. Further, we found the same bias towards the visual target across the three anti-saccade conditions than for controls. However, her saccade endpoints follow the shape of the lines drawn from the mean saccade endpoints for controls. This suggests that the endpoint bias was also present in I.G. but appeared exacerbated in her case. This was confirmed using the same distance analysis described above. For I.G., unlike for her controls, it should be noted that for the distance analysis, we only had one value rather than two, for example, horizontal distance was only for the upper two targets, due to her quadrantanopia. Specifically, we examined the reduction in distance relative to the pro-saccade condition for each condition (horizontal for across, vertical for within and diagonal for anti) for I.G. compared with controls with modified t -tests. Although she did not show a significantly smaller reduction in relative horizontal distance ($M_{\text{I.G.}} = 2.75^\circ$) compared with controls in the across condition ($M_{\text{controls}} = 1.33^\circ$, $SD_{\text{controls}} = 1.54^\circ$; $t_9 = 0.879$, $P = 0.201$), I.G. did show a significantly smaller reduction in relative vertical distance in the within

condition ($M_{I.G.} = 5.98^\circ$; $M_{controls} = 0.55^\circ$, $SD_{controls} = 1.27^\circ$; $t_9 = 4.086$, $P = 0.001$) as well as in diagonal distance in the classic condition ($M_{I.G.} = 9.23^\circ$; $M_{controls} = 1.93^\circ$, $SD_{controls} = 1.88^\circ$; $t_9 = 3.703$, $P = 0.002$).

In summary, the observed pattern of endpoint distributions for I.G. and her controls is inconsistent with the hypothesis of a reduction of saccade gain in anti-saccades. If it had been the case, we should have observed a similar pattern of undershooting for all three anti-saccade paradigms, all resembling the pattern observed in the classic anti-saccade condition. In other terms, their undershooting would have been independent of the different anti-saccade spatial configurations. Instead, we observed a systematic variation in endpoints with visual target location, consistent with a spatial bias hypothesis.

3.3 | Relative amplitude from the visual target position

To quantify the bias towards the visual target, we analysed relative amplitudes for correct anti-saccades. In the case of a bias towards the visual target, we would expect relative amplitude to be closer to zero (i.e., location of the visual target) than the amplitude corresponding to the saccade goal (i.e., 11° for the across and within conditions and 15.57° for the classic condition). In contrast, relative amplitudes corresponding to the amplitude of the saccade goal would indicate a smaller bias or the absence of one. As the visual target and saccade goal are identical for pro-saccades, we did not consider relative amplitudes for this condition. Mean relative amplitudes for our patient and her controls are illustrated in Figure 6.

First, with one-sample t -tests, we compared participants' relative amplitudes for each anti-saccade condition. This allowed us to determine whether there was a bias towards the visual target. In the case of an absence of bias, we would expect relative amplitudes to not differ from the visual target-saccade goal distance. For controls, we found significantly lower relative amplitudes for the across ($M = 9.89^\circ$, $SD = 0.75^\circ$; $t_9 = -4.648$, $P = 0.001$, $d = -1.47$), within ($M = 10^\circ$, $SD = 0.69^\circ$; $t_9 = -4.60$, $P = 0.001$, $d = -1.46$) and classic conditions ($M = 13.56^\circ$, $SD = 0.95^\circ$; $t_9 = -6.73$, $P < 0.001$, $d = -2.13$).

For I.G., mean relative amplitudes for each condition were respectively 9.17° for the across condition, 9.36° for the within condition and 10.97° for the classic condition. Like for her controls, we obtained significantly lower relative amplitudes across all conditions: across ($t_{43} = -6.91$, $P < 0.001$, $d = -1.04$), within ($t_{35} = -5.64$, $P < 0.001$, $d = -0.94$) and classic conditions ($t_{52} = -31.81$, $P < 0.001$, $d = -4.37$). Together, these results suggest an overall bias towards the visual target across all anti-saccade conditions for all our participants.

Next, with modified t -tests, we compared I.G.'s relative amplitude per condition to her controls. We found no significant difference between groups for the across ($t_9 = -0.95$, $P = 0.38$) and the within conditions ($t_9 = -0.88$, $P = 0.40$). However, we found significantly lower relative amplitudes for the classic condition for our patient compared with controls ($t_9 = -2.61$, $P = 0.03$). In sum, although I.G.'s mean relative amplitude was smaller than controls across all conditions, we only found a significant difference for the classic condition. This suggests a stronger bias towards the visual target for I.G. compared with controls in the classic condition.

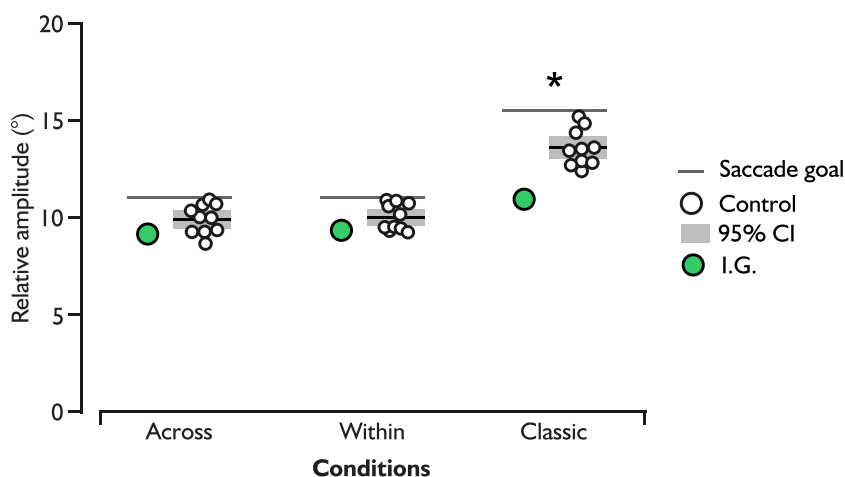


FIGURE 6 Relative saccades amplitudes from visual target location (0°) across conditions. Mean amplitude for I.G. is presented as a green dot, whereas means for each control are white dots. For controls, the 95% confidence interval is in grey and the black line in the middle of this interval defines the overall mean for the group. The positions of saccade goals relative to visual targets are indicated with grey lines.

3.4 | Pro-saccade amplitude

We compared mean pro-saccade amplitudes between I.G. and controls with modified *t*-tests. We found a significant difference between I.G. and controls ($t_9 = 3.254$, $P = 0.001$) where I.G.'s amplitudes ($M = 7.81^\circ$) were higher than controls' ($M = 6.75^\circ$, $SD = 0.31^\circ$). This suggests that I.G.'s pro-saccades were hypermetric compared with controls' as the distance between fixation point and the visual target was 7.78° . Thus, the absolute error from the visual target was of 0.03° for I.G. and 1.03° for her controls, which suggests that I.G.'s pro-saccades were slightly more accurate than controls'. This is inconsistent with an overall reduced gain.

4 | DISCUSSION

We observed that anti-saccade endpoints were biased towards the visual target for all participants and that this bias was exacerbated in our bilateral optic ataxia patient. This spatial bias was specific to the configuration of each anti-saccade paradigm with endpoints aligned on the visual target-saccade goal vector. This pattern of saccade endpoints was thus in line with the hypothesis of spatial competition resolution between saccade goal and visual target, and inconsistent with the alternative hypothesis of reduced saccade gain during anti-saccades associated with the absence of visual guidance. We quantified this spatial bias with an endpoint analysis of distance on the horizontal, vertical and diagonal distance as well as with an analysis of the amplitude of the saccade with the start position being the visual target location instead of the centre fixation position. We found overall greater distance in the horizontal component in the across condition, in the vertical component in the within condition and in the diagonal component for the classic condition. This is in line with the vector inversion specific to each anti-saccade condition. Further, relative amplitude was hypometric for all anti-saccade spatial configurations for all participants. It was even smaller for the patient I.G. despite her pro-saccades not being hypometric; this was significant compared with controls for classic anti-saccades. In sum, the observed error pattern reveals incomplete spatial inhibition of visual target location, and the bilateral dorsal PPC lesion exacerbates the spatial competition between the two locations.

The hypometria classically found in controls for 180° anti-saccades (Bahcall & Kowler, 1999; Hallett, 1978; Kowler et al., 1995; Krappmann, 1998) can therefore be explained in terms of attentional competition. Theoretically, attentional competition between objects in the visual scene is implemented in priority maps, which

needs to be resolved for correct target selection (Bisley & Goldberg, 2010). Selection occurs following a 'winner-take-all' strategy (Bays et al., 2010; Fecteau & Munoz, 2006; Ipata et al., 2009; Serences & Yantis, 2006). Specifically, priority is reflected in the enhancement of neuronal activity for correct target representation and suppression of competing distractor representations (Awh et al., 2006; Bisley & Goldberg, 2010; Kastner et al., 1998; McPeck & Keller, 2002; McSorley et al., 2006; Reynolds et al., 1999; Serences et al., 2004). However, our findings do not support the 'winner-take-all' process because in that case, we would expect complete spatial inhibition of the location losing the competition, that is, the visual target location in the case of anti-saccades. As such, the saccade plan should only be programmed based on the winning location. Instead, our results show some evidence of averaging or amalgamation where the location of the visual target still affects saccade metrics across all our participants and in a specific manner for each spatial configuration. This suggests that activity is maintained at a visual target location, which biases the saccade plan, rather than its full inhibition. This competition is consistent with visual representations of both the visual target and the saccade goal in the brain during anti-saccades (Collins et al., 2008; Lévy-Bencheton et al., 2013; Mikula et al., 2018), as well as temporal overlapping of activities and spatial averaging processes for anti-saccade production. During anti-saccades, a bias towards the visual target may be introduced by the failure to fully resolve the competition for saccade goal selection between the neuronal representations of the extinguished visual target and the imagined saccade goal mirror location, due to incomplete inhibitory processes.

The behaviour of our bilateral optic ataxia patient supplements past findings from our group on the contribution of the dorsal PPC to the competition resolution during anti-saccades (Ouerfelli-Ethier et al., 2021). Here, we report spatial inaccuracies in anti-saccades where saccade endpoints tended to be biased towards the visual target to a larger extent for our patient compared to controls. This exacerbated bias might reflect that the visual target has been insufficiently inhibited, such that its representation remains longer/stronger during the competition against the saccade goal. Our present study thus confirms the idea of a competition between locations on a spatial map for anti-saccades implicating the dorsal PPC.

We found larger biases towards the visual target during classic anti-saccades compared with the 90° conditions in both controls and in the patient. We also found significantly greater bias in patient I.G. compared with controls during classic anti-saccades, which we did not find in the 90° conditions. This could be due to the larger

distance between the saccade goal and the visual target for the classic condition (i.e., 15.57°) compared with the across and within conditions (i.e., 11°). It has been shown that the distance between two locations can modulate spatial competition; in the PPC, priority maps are suggested to topographically represent locations in space (Bressler & Silver, 2010) with greater competition between nearby locations compared with more distant ones (Deco & Lee, 2002; Itti & Koch, 2001; Koch & Ullman, 1985). As a result, farther representations are suppressed to a lesser extent than nearby ones. It is possible that the suppression of the nearby visual target locations in I.G. is still sufficient in the across and within conditions. However, suppression in the classic condition, where the saccade goal and the visual target are farther apart, may not have been enough and so resulted in a significantly stronger bias towards the visual target.

Multiple patient populations show evidence of inhibition impairments during anti-saccades although with different behavioural patterns. Consistent with the involvement of the frontoparietal network in spatial competition, we previously showed delayed resolution in unilateral optic ataxia patients with damage to the dorsal PPC, with increased ER for short anti-saccade latencies only when the visual target was presented in their contralesional visual field (Ouerfelli-Ethier et al., 2021). These patients also showed tendencies for spatial miscalculations in their anti-saccade endpoints. Along the same lines, the present results in the bilateral patient demonstrated an exaggerated bias towards the visual target. These findings are consistent with the crucial implication of the dorsal PPC in attentional priority for saccade planning and execution (Molenberghs et al., 2007). In contrast, patients with unilateral ventral PPC lesions and neglect show non-lateralized spatial deficits including longer latencies and global undershooting during anti-saccades (Butler et al., 2009). The right-hemispheric ventral PPC may be involved in creating the anti-saccade goal location and transferring its spatial coordinates to oculomotor structures (Pisella et al., 2011). Both saccade goal selection and anti-saccade programming implicate the prefrontal cortex (Everling & Munoz, 2000; Funahashi et al., 1993; Guitton et al., 1985; Pierrot-Deseilligny et al., 2005; Schall, 2004; Walker et al., 1998). Patients with unilateral DLPFC lesions show undershooting and overshooting tendencies in the ipsilesional and contralesional visual fields respectively (Walker et al., 1998), which may indicate an imbalance in competing signals during anti-saccades. Priority maps are also present in the prefrontal cortex (Jerde et al., 2012; Sprague & Serences, 2013), and this substrate

may particularly contribute to competition during anti-saccades (Pierrot-Deseilligny et al., 1991, 2005; Walker et al., 1998). Taken together, these impairments could be explained by a dysfunctional frontoparietal network with incomplete spatial competition resolution between the visual target and the saccade goal. Specifically, inefficient inhibitory processes that favour visual target selection rather than saccade goal selection could result in increased ERs or spatial inaccuracies in anti-saccade endpoints or both.

To conclude, we described and then quantified a bias towards the visual target that was systematic across participants and more pronounced in patient I.G. This implies some amalgamation of the visual target and saccade goal representations rather than a 'winner-take-all' competition resolution. We suggest that bilateral dorsal PPC damage affected I.G.'s overall ability to suppress the visual target, particularly for representations of distant locations on priority maps as in our classic condition. Overall, our results point to a contribution of the dorsal PPC in spatial competition inherent to anti-saccade as part of the frontoparietal attentional network.

AUTHOR CONTRIBUTION STATEMENT

Julie Ouerfelli-Ethier: formal analyses (lead), investigation (lead), visualization (lead), writing—original draft preparation (lead), writing—review and editing (equal). **Romain Fournet:** software (lead), formal analyses (supporting). **Aarlenne Z. Khan:** conceptualization (equal), formal analyses (supporting), investigation (supporting), supervision (equal), writing—review and editing (equal). **Laure Pisella:** conceptualization (equal), supervision (equal), writing—review and editing (equal).

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CONFLICT OF INTEREST STATEMENT

The authors declare no competing financial interests.

DATA AVAILABILITY STATEMENT

Data are available on request from the authors.

PEER REVIEW

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