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Laura Mikula[1, 2], Gunnar Blohm[3], Éric Koun[1], Aarlenne Z. Khan[2], and Laure Pisella[1]
[1] Centre de Recherche en Neurosciences de Lyon (CRNL), Trajectoires Team, Inserm U1028, CNRS UMR 5292, Université Claude Bernard Lyon
[2] École d'Optométrie, Université de Montréal
[3] Centre for Neuroscience Studies, Queen's University

When vision is removed, limb position has been shown to progressively drift during repetitive arm movements. The posterior parietal cortex (PPC) is known to be involved in the processing of multisensory information, the formation of internal hand estimate, and online motor control. Here, we compared hand position drift between healthy controls and 2 patients with PPC damage to gain insight into the mechanisms underlying movement drift and investigate the possible role of the PPC in this process. To do so, we asked participants to perform back-and-forth movements between 2 targets, in the dark and under different gaze fixation conditions. Each individual participant consistently drifted to the same end position for a given hand and gaze condition. We found that the final drift distance was related to small systematic errors made on the very first trial in the dark, with an approximate 3.5 fold increase in magnitude. Furthermore, PPC damage resulted in greater movement drift in patients when the unseen hand was in the contralesional oculocentric space and also when the target was located in the lower visual field. We conclude that the PPC is involved in the proprioceptive representation of hand position in oculocentric coordinates used for reach planning and motor control.

> **Public Significance Statement**
> This case study report shows that patients with lesions to the posterior parietal cortex experience difficulties performing repetitive movements in the dark. Their hand progressively drifts away from its initial location, and this effect is exacerbated when gaze fixation is imposed. This suggests that the posterior parietal cortex builds an estimate of the hand location relative to the position of the eyes in space.

Keywords: hand position estimate, movement drift, optic ataxia, posterior parietal cortex

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It has been observed that limb position considerably drifts during continuous blind performance. When performing repetitive movements between two targets without visual feedback of the hand, it has been shown that the hand drifts 3 to 8 cm away from its initial location without being detected by participants (Brown et al., 2003a, 2003b; Cameron et al., 2015; Patterson et al., 2017).

Some authors have suggested that the drift in hand position over the course of repetitive movements results from the accumulation of execution errors due to motor bias (Cameron et al., 2015) or from the sensorimotor transformation error arising when vision of the hand is absent (Brown et al., 2003a). Interestingly, although drift direction has been reported to be highly variable between

participants, it seems to be idiosyncratic (i.e., subject-specific); thus ruling out the hypothesis of random error accumulation. Indeed, Smeets et al. (2006) have shown that every participant consistently drifts toward the same end position over multiple blocks, suggesting that movement drift is driven by a subject-specific misalignment between vision and proprioception. When visual feedback is removed and as repetitive movements are made, there is an increasing discrepancy between the memory of the visual hand position estimate and the proprioceptive hand position estimate. As a result, the moving hand drifts away from its initial position (Patterson et al., 2017; Smeets et al., 2006).

One brain region that may be involved in the estimation of visual and proprioceptive information driving movement drift is the posterior parietal cortex (PPC). Indeed, the PPC is a sensorimotor interface involved in visually-guided hand movements as well as multisensory integration (Andersen et al., 1997; Buneo & Andersen, 2006; Burnod et al. 1999; Cohen, 2009). Electrophysiological recordings in nonhuman primates showed that the PPC combines visual and proprioceptive signals to encode arm position (Graziano et al., 2000; Mountcastle et al., 1975). Furthermore, different regions of the PPC have been associated with the alignment of visual and proprioceptive representations during reaching (Ghilardi et al., 2000; Gregoriou & Savaki, 2003). The possible implication of the PPC in hand position drift was confirmed by a case study on a patient with a lesion to the left superior parietal lobule, affecting mainly Brodmann's area 5. In the absence of vision, this patient reported conscious drift of the location of her right upper and lower limbs. When asked to track the position of her unseen contralesional arm using the opposite hand, the perception of her static arm started to gradually drift, and the tracking error reached 30 cm after about 40 seconds without visual feedback (Wolpert, Goodbody, et al., 1998). This is in contrast with neurologically intact participants who drift by just a few centimeters over the course of a couple minutes in the dark (Paillard & Brouchon, 1968; Wann & Ibrahim, 1992). Wolpert, Goodbody, et al. (1998) concluded that their patient was unable to store her own body state estimate across time, which impaired both perception and action. This and other observations suggest an important role of the parietal cortex in maintaining the internal representation of the body (Sirigu et al., 1996; Wolpert, Goodbody, et al., 1998; Wolpert, Miall, et al., 1998).

We hypothesize that damage to the PPC should impact movement drift following repeated reaches in the dark. To test this, we studied movement drift in patients with optic ataxia (OA). OA patients do not report any conscious drift sensation across time when vision is not available. However, their visuomotor deficit resulting from brain damage to the superior parieto-occipital cortex (superior parietal, lobule and intraparietal sulcus) that usually affects Brodmann's area 7 (Karnath & Perenin, 2005) is characterized by inaccurate visually-guided movements when patients use their contralesional hand — « and effect » — and when reaching within their contralesional visual field — « field effect » — (Buxbaum & Coslett, 1998; Garcin et al., 1967; McIntosh et al., 2011; Perenin & Vighetto, 1988; Rossetti et al., 2003; Vighetto, 1980). Neuropsychological studies of OA patients have shown that the PPC is involved in the oculocentric (or gaze-centered) coding of visual and proprioceptive information (Dijkerman et al., 2006; Khan, Pisella, Rossetti, et al., 2005; Khan, Pisella, Vighetto, et al., 2005). It has been reported that OA patients exhibit impairments during proprioceptive reaching (i.e., when pointing to one hand using the

opposite hand without visual feedback). More specifically, reach errors were greater when proprioceptive (hand) targets were located within the contralesional space, and the direction of these errors were modulated by eye position (Blangero et al., 2007). These observations are consistent with the field effect of OA initially described for visual targets, which depends on the target location in oculocentric coordinates (Khan, Pisella, Vighetto, et al., 2005).

To our knowledge, the influence of gaze fixation on movement drift has not been examined yet. If hand position drift depends on the representation of proprioceptive information in oculocentric coordinates, then OA patients would exhibit a drift characteristic of an erroneous representation of their hand relative to gaze position. A unilateral OA patient is expected to show larger movement drift when the hand reaches within the contralesional hemispace. In the case of a bilateral OA patient, no differences are expected between left and right hands or left and right visual fields. However, we predict increased drift when moving in the lower visual field since it is known to have a larger representation than the upper visual field within the PPC (Pitzalis et al., 2013; Previc, 1990; Rossit et al., 2013).
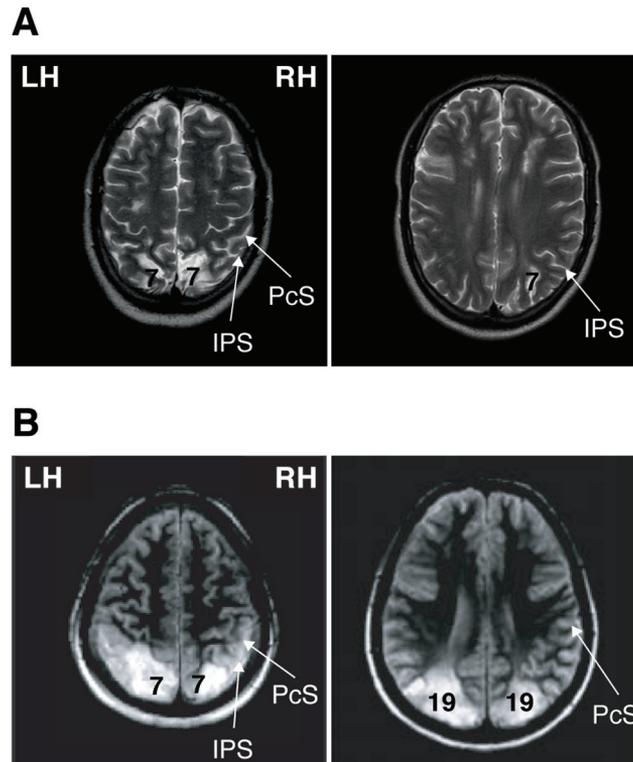
We thus asked a patient with left OA and a patient with bilateral OA, as well as 10 age-matched neurologically intact control participants, to make 50 repetitive movements between two visual targets and removed visual feedback about hand position after 5 movements. In order to have a reference condition consistent with previous studies about movement drift, control participants and patients did the experiment in free gaze (i.e., eye movements were not constrained). All participants were also required to perform the same task while maintaining gaze fixation to evaluate how drift is affected by hand position in the oculocentric reference frame. Depending on which of the two targets they fixated, participants made movements in the upper or lower visual field. Both left and right hands were tested in all conditions to reveal any hand effect in patients with OA. To provide answers regarding the possible systematic nature of hand position drift, we also investigated the relationship between initial and final drift orientation and drift distance.

Method

Participants

Two patients with OA took part in the present study. Patient CF was a right-handed male who was 40 years old at the time of testing. In 2003; he suffered from a posterior watershed infarct resulting in distributed and asymmetrical bilateral lesions of Brodmann areas BA 18, 19, 7, 5 and 2 with a minute extension to the centrum semiovale. Chronically, he exhibited isolated unilateral OA predominantly in his left visual field, thought to be the consequence of larger damage in the right hemisphere of both BA 7 and the intrahemispheric parieto-frontal fibers (Figure 1A, Blangero et al., 2008; Khan et al., 2007; 2009; Striemer et al., 2009). Patient IG was a right-handed 48-year-old woman who, in 1998, suffered from an ischemic stroke related to acute vasospastic angiopathy in the posterior cerebral arteries. The lesion involved mainly BA 18, 19, 7, a limited part of area 39 as well as the intraparietal sulcus of both hemispheres (Figure 1B). Examinations after the stroke demonstrated a chronic bilateral optic ataxia (Gréa et al., 2002; Khan et al., 2016; Khan, Pisella, Rossetti, et al., 2005; Pisella et al., 2000).

Figure 1
Magnetic Resonance Imaging Scan of Optic Ataxia Patients

Note. A. Patient CF. The white areas at the bottom of the scan show asymmetrical lesions to the posterior parietal cortex, especially around Brodmann's area 7. The damage is larger in the right than in the left hemisphere. B. Patient IG. The lesion is fairly symmetrically located in the posterior parietal cortex and the superior occipital gyrus (Brodmann's areas 7 and 19). LH = left hemisphere; RH = right hemisphere; PcS = postcentral sulcus; IPS = intraparietal sulcus.

As reported in previous studies, neither patient show any purely motor or sensory deficit or signs of neglect (Granek et al., 2012; 2013). The clinical evaluation of the static and dynamic proprioception of the upper limbs revealed no primary proprioceptive deficit for either arm. While keeping their eyes closed, both patients were able to perceive a passive flexion or extension applied on each joint (index, wrist, elbow, shoulder), to report its direction and to reproduce single joint angles with the opposite limb (Rivermead Assessment of Somatosensory Performance [RASP] subtests). Conventional testing including sensory stimulation tests, neurological evaluation of reflexes, muscle tone, and joint movement showed no signs of visual and tactile extinction or of fading grip force, nor any specific inaccuracy for slow movements. Patients CF and IG did not exhibit any neglect symptom as assessed by standard line bisection, star cancelation, and drawing tasks. Visual acuity, binocular vision, and visual field perimetry were preserved except for patient IG, who presented with a quadrantanopia in the lower right visual field (Bartolo et al., 2018; Khan, Pisella, Rossetti, et al., 2005; Pisella et al., 2000).
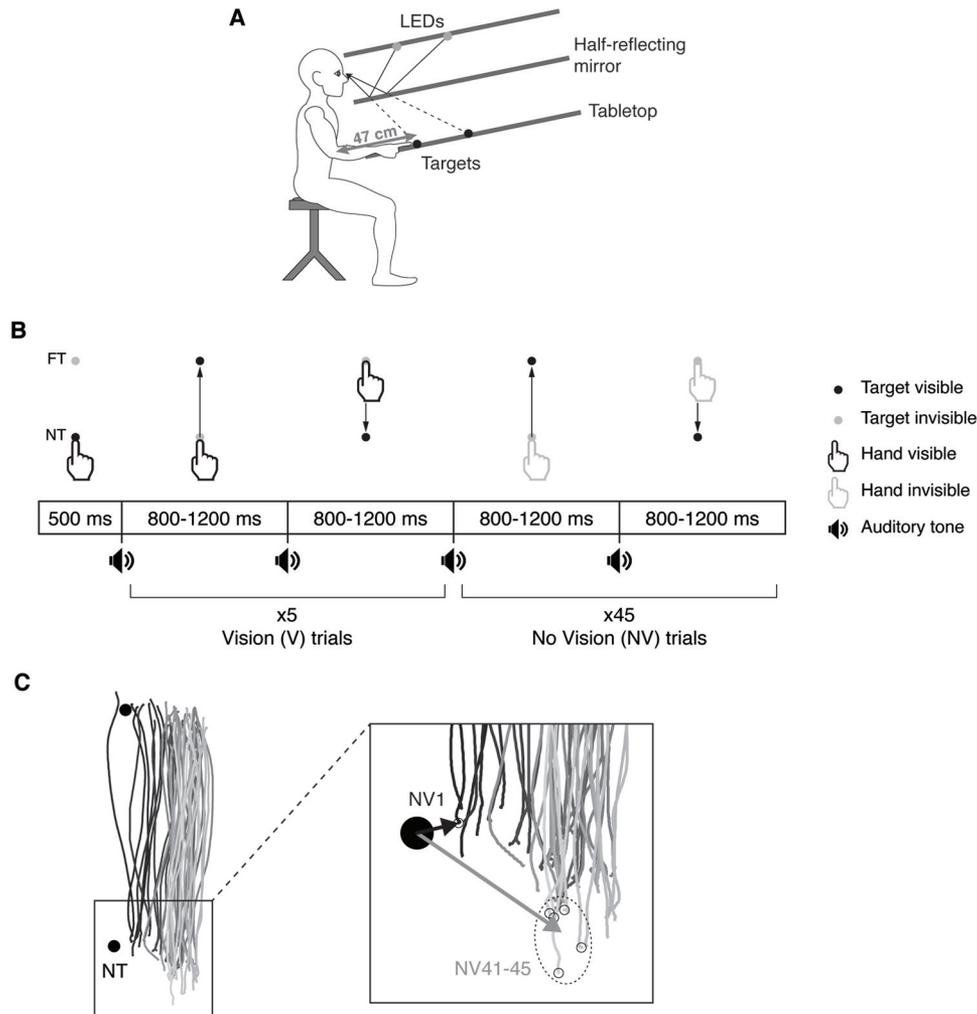
In addition, we tested ten neurologically intact control participants (5 females, mean age = 47.3 ±8.5 years). They were all right-handed, as assessed by the Edinburgh Handedness Inventory, and all had normal or corrected-to-normal vision. All participants (including patients) were administered a questionnaire to ensure that they did not suffer from neurological, sensory or motor deficits during the 6 months prior to the experiment, which may have interfered with their performance. Participants gave informed written consent to participate in this experiment which conformed to the Declaration of Helsinki for experiments on human subjects. All experimental procedures were approved by the Health Research Ethics Committee (CPP Nord-Ouest I, Lyon, 2017-A02562-51) in France and at Université de Montréal in Canada (17–034-CERES-D).

Apparatus

Participants sat in a dark room on a height-adjustable chair in front of a slanted table. Their head was held steady on a forehead rest, aligned with their body midline. Light emitting diodes (LEDs) and a half-reflecting mirror were positioned above the table so that the LEDs appeared to be on the tabletop surface (Figure 2A). The half-reflecting mirror allowed participants to see both their real hand and the LEDs when a light source was illuminated underneath the mirror. When in the dark, the LEDs but not the hand remained visible. Participants were required to reach with the index finger toward two visual targets aligned with the body midline. The distance between the near target (NT) and the far target (FT) was 13 cm. The NT was located 40 cm away from the table's edge and approximately 47 cm relative

Figure 2
Experimental Paradigm of the Study

Note. Participants made reaching movements on the tabletop. Targets were reflected onto the tabletop using a half-reflecting mirror that allowed vision of the hand when the workspace underneath was illuminated. (A) Experimental setup. (B) Sequence of events during the experimental block. The near target (NT) and the far target (FT) were aligned with participants' body midline and were separated by 13 cm. Targets and hand depicted in black were visible whereas those in gray were not. Participants were instructed to reach toward the illuminated target when hearing tone. One trial consists of a reach to the FT, followed by another one to the NT. Participants had hull vision of their hand throughout the 5 first trials (V trials), whereas it was occluded during the 45 remaining trials (NV trials). In the hand vision condition, participants performed all 50 trials with their hand visible. (C) Hand position drift orientation and distance. Hand drift was characterized by the vector joining the near target and the hand position on the first trial without visual feedback (trial 6, NV1) or the average hand position across the last 5 trials without vision (trials 46 to 50, NV41-45). The drift orientation and distance correspond, respectively, to the angle (in degrees) and the magnitude (in mm) of this vector.

to the participants' midline. The position of the index finger was measured using an Optotrak motion-analysis system (NDI, Waterloo, Canada); the 3D position (in mm) of an infrared emitting diode attached to the index fingertip was recorded, and data were sampled at 1000 Hz. Eye movements were recorded binocularly through an electrooculogram (EOG) using a DC electrooculograph system (50 Hz, model BM623, Biomedica Mangoni, Pisa, Italy). Two electrodes were placed outside the left and right eyes, and a third one was positioned on the first thoracic vertebra and served as the reference electrode.

Experimental Task

Participants were asked to reach back and forth between the NT and the FT, in time with auditory cues. The sequence of events during the task is depicted in Figure 2B. At the beginning of each block, participants aligned their index fingertip with the illuminated NT, which served as a start location. After 500 ms, an auditory tone was presented, and the NT was extinguished while the FT was illuminated. Participants were instructed to move quickly and accurately to the illuminated target upon hearing the tone. The NT and the FT were presented successively, and the time between

two consecutive targets was randomly selected in 100-ms intervals between 800 and 1200 ms. Each block was composed of 50 back-and-forth movements and lasted approximately 3 minutes. One trial comprised a movement to the FT and one toward the NT, thus corresponding to one back-and-forth movement. In each block, during the first 5 trials, participants could see the targets as well as their hand moving in between (V trials). Then, visual information about the hand position was removed for the remaining 45 trials (NV trials). Participants were informed in advance that vision of the hand would be occluded after the fifth trial.

Participants were asked to make reaches under four different experimental conditions. In the "free gaze" condition, eye movements were unconstrained, whereas gaze fixation was imposed on the NT and the FT in the "near fixation" and "far fixation" conditions, respectively. These two fixation conditions were introduced to test for deficits in the oculocentric representation of proprioceptive information in patients with OA during repetitive movements. As OA is associated with large misreaching errors biased toward fixation when peripheral targets are presented (Blangero et al., 2010; Carey et al., 1997; Jackson et al., 2005), we decided to use the reach targets as fixation targets to avoid introducing errors unrelated to drift in patients. The "hand vision" condition served as a control to make sure that OA patients did not exhibit drift when eye movements were free and when they were able to see their hand during the entire 50-trial block. Eye positions were monitored to ensure that participants maintained fixation on the required target during the fixation conditions.

Experimental Design

All participants' left and right hands were tested during two sessions in order to address hand effects in patients, as mentioned in the introduction. Each session comprised 10 blocks: 1 block in the "hand vision" condition and 3 blocks for each of the three other experimental conditions ("free gaze", "near fixation," and "far fixation"). Bilateral patient IG did a first session with her right (most affected) hand and a second session using her left hand. Unilateral patient CF completed the first session with his left (contralesional) hand and the second one with his right (ipsilesional) hand. For controls, the order of the hand used during the first session was counterbalanced across participants.

Data Analysis

Data were analyzed off-line using custom-written Matlab software (The MathWorks, Natick, MA, U.S.). For each trial, the 3D start and end positions of the index fingertip were sampled respectively 200 ms before and after the velocity threshold time (80 mm/s), when the hand position was stabilized. Hand drift over time was characterized by the Euclidean distance (i.e., drift distance in mm) and the angle (i.e., drift orientation in degrees) of the vector between the near target and the hand position at the end of each trial. The drift distance and drift orientation were more extensively analyzed at two different moments: on the first trial without visual feedback (trial 6, NV1) and the average across the last 5 trials without vision (trials 46 to 50, NV41-45) (Figure 2C). The intertrial drift distance variability corresponds to the standard deviation of the drift distance across all trials without vision. For every participant, the drift orientation, the drift distance and its intertrial variability were first computed for each

block and then averaged within experimental conditions (except for the hand vision condition which only had one block). To take into account the periodicity of angular data, analyses regarding drift orientations (averages, standard deviations and correlations) were done using circular statistics, as calculated by the CircStat toolbox for Matlab (Berens, 2009).

To assess whether the performance of OA patients was significantly different from that of healthy participants, we used the Singlims_ES.exe software (https://homepages.abdn.ac.uk/j.crawford/pages/dept/psychom.htm) to run Crawford's modified t-tests, which are relatively robust to departures from normality and specifically designed to compare a single case to a control group with a sample size as small as 5. In contrast to standard procedures, single-case methods treat the statistics of the control sample as sample statistics rather than population parameters derived from a normal distribution (Crawford et al., 2006; Crawford & Garthwaite, 2002; Crawford & Howell, 1998). Effect sizes (z_{cc}) and 95% confidence intervals (CI) were reported when Crawford's tests were found to be significant.

To investigate whether control participants systematically drifted to the same positions across multiple testing blocks, equivalence tests were performed. In contrast to traditional significance tests, equivalence testing provides support for the null hypothesis (Lakens, 2017; Lakens et al., 2018). The two one-sided test (TOST) procedure was used, in which equivalence is established at the α level if the 90% confidence interval for the difference in means falls with the equivalence interval $[-\Delta; \Delta]$. Two t-tests are performed, and equivalence is declared only if both tests are statistically rejected. In our study, Δ was set to 15 mm since the average width of the index finger was estimated to be between 16 and 20 mm. In order to determine if initial drift distance (orientation) was related to final drift distance (orientation), correlational analyses were used. Pearson's correlation coefficients were computed for drift distances to measure the strength of the linear relationship between paired data. In the case of drift orientations, circular-circular correlations were calculated to assess the strength of the relationship between angular variables using the CircStat Matlab toolbox.

Statistical threshold was set to .05. Following Crawford's tests and equivalence testing, the alpha threshold for statistical significance was corrected for multiple comparisons using Bonferroni type adjustment.

Results

General Observations

Reach trajectories of a typical control participant exhibiting a small drift is shown in Figure 3A. Movements during the first block for each of the 4 experimental conditions are depicted. Only reach trajectories from trial 6 to 50 are shown as they correspond to movements performed without visual feedback of the hand in the free gaze, near fixation and far fixation conditions. As expected, when visual feedback of the hand was available (hand vision; leftmost panel), reaches remained accurate throughout the block and did not deviate much from the targets. Reaching movements performed in free gaze, as well as in near and far fixation conditions, were slightly deviated from the targets when vision of

Figure 3

Reach Trajectories of a Typical Control Participant (A), Bilateral OA Patient IG (B) and Unilateral OA Patient CF (C)

Note. Individual reach movements during the first block of each experimental condition (free gaze, near fixation, far fixation and hand vision). In the near and far fixation conditions, the cross indicates where participants were asked to maintain fixation throughout the block. Only trials 6 to 50 are represented since they correspond to movements performed without visual feedback of the hand in the free gaze, near fixation and far fixation conditions. The color shade of the trajectories represents the progression of trials throughout the block, with early trials being darker than late trials.

the hand was removed but nevertheless remained quite accurate. For this typical participant, the amplitude and the direction of movements were maintained over time, despite the absence of visual feedback of the hand (Supplementary Figures S1 and S2).

Reach trajectories are also illustrated for both patients IG (Figure 3B) and CF (Figure 3C), in all experimental conditions. Just like the typical control, bilateral patient IG and unilateral patient CF were very accurate when doing the task in the hand vision condition (Figures 3B and 3C, leftmost panel). As a general observation, similar to

control participants, it can be seen that both OA patients progressively drifted when in the dark (free gaze, near and far fixation conditions). At first, movements were closer to the targets, and then the hand progressively moved away throughout the block. Reach trajectories suggest that OA patients might show more variable movement execution compared to controls (see also Figure 5). Interestingly, OA patients seem to move each hand within the opposite side of the work space, relative to midline. Their right hand tended to drift toward the left, whereas their left hand tended to move toward the right. This

means that patient CF's ipsilesional (healthy) hand was in his contralesional (ataxic) hemispace. Finally, bilateral patient IG seemed to be particularly impaired when reaching in the far fixation condition (Figure 3B, rightmost panel). Movement amplitude was extensively increased, and by the end of the block, IG's hand was about 200 mm below the near target in the vertical axis (see also Supplementary Figures S1 and S2).

Movement Drift Analysis

The drift distance (i.e., the Euclidean distance between the near target and hand reach endpoint) was calculated for each trial and then averaged across blocks for each control participant as well as for patients IG and CF, as shown in Figure 4. In the hand vision condition (Figure 4, leftmost panel), similar to control participants, patients IG and CF showed no drift and overall very small endpoint errors throughout the block when using either hand. This confirmed that there was no drift in OA patients in free gaze and when vision of the hand is provided, no matter which hand (ipsi- or contralesional) was tested.

In the free gaze condition (Figure 4, second panel), IG showed a drift pattern that was comparable to controls, for both her left (top panel, magenta trace) and right (bottom panel, red trace) hand. We tested whether she showed larger drift than in control participants at the end of the first trial without hand visual feedback (trial NV1). There was no significant difference in drift distance compared to controls on trial NV1 when using either left or right hand (Crawford's tests; both $p > .05$). For each hand, the drift then gradually increased and reached a plateau around trial 20. However, drift distance in IG did not significantly differ from controls by the end of the block (trials NV41-45) for either left or right hand (Crawford's tests; both $p > .05$). In the free gaze condition, CF seemed to be more impaired when moving his right hand. In fact, drift distance for his left hand (top panel, light blue trace) was not significantly different from that of control participants on either trial NV1 or trials NV41-45 (Crawford's tests; both $p > .05$). When using his right hand (bottom panel, dark blue trace), patient CF showed greater drift than controls on trial NV1 (Crawford's test; $t = 3.41$, $p = .004$, $z_{cc} = 3.57$, CI [1.83, 5.30]) and there was a trend for trials NV41-45 (Crawford's test; $t = 2.23$, $p = .026$, $z_{cc} = 2.34$, CI [1.10, 3.56]; not significant after Bonferroni correction).

In the near fixation condition (Figure 4, third panel), drift for IG's left and right hands and CF's left hand was similar relative to controls (Crawford's tests; all $p > .05$). In contrast, CF's right hand exhibited greater drift than in control participants on trial NV1 (Crawford's test; $t = 3.18$, $p = .006$, $z_{cc} = 3.34$, CI [1.69, 4.97]) and on trials NV41-45 as well (Crawford's test; $t = 4.34$, $p = .001$, $z_{cc} = 4.55$, CI [2.39, 6.70]).

In the far fixation condition (Figure 4, rightmost panel), patient IG showed a drastic increase in drift when using either hand. For both left and right hands, she already started to drift from the target when visual feedback of the hand was available. As a consequence, IG exhibited significantly greater drift than controls for both hands on trial NV1 and trials NV41-45 (Crawford's tests; all $t > 4.03$, all $p < .002$, all $z_{cc} > 4.23$). By the end of the block, IG had drifted by close to 200 mm and 150 mm with the right and left hand, respectively. As for patient CF, the left hand did not significantly drift more than in controls on either trial NV1 or trials NV41-45 (Crawford's tests; both $p > .05$). Regarding his right hand, CF showed a larger drift distance relative to control participants on trials NV41-45 (Crawford's test; $t = 2.91$, $p = .009$, $z_{cc} = 3.05$, CI [1.52, 4.56]) but not on trial NV1.

We further examined the free gaze, near fixation and far fixation conditions, in which drift was observed. We looked at the intertrial drift variability and noticed that, in the absence of visual feedback, OA patients showed more trial-to-trial variability in conditions where their final hand position drift was larger than in controls. As depicted in Figure 5, patient CF showed large intertrial drift variability in near and far fixation conditions when using his right hand specifically. Furthermore, patient IG was more variable in far fixation condition for both left and right hand. The only exception being CF's right hand in the free gaze condition, which did not significantly drift more than controls at the end of the block (see Figure 4) but seemed to exhibit larger intertrial drift variability.
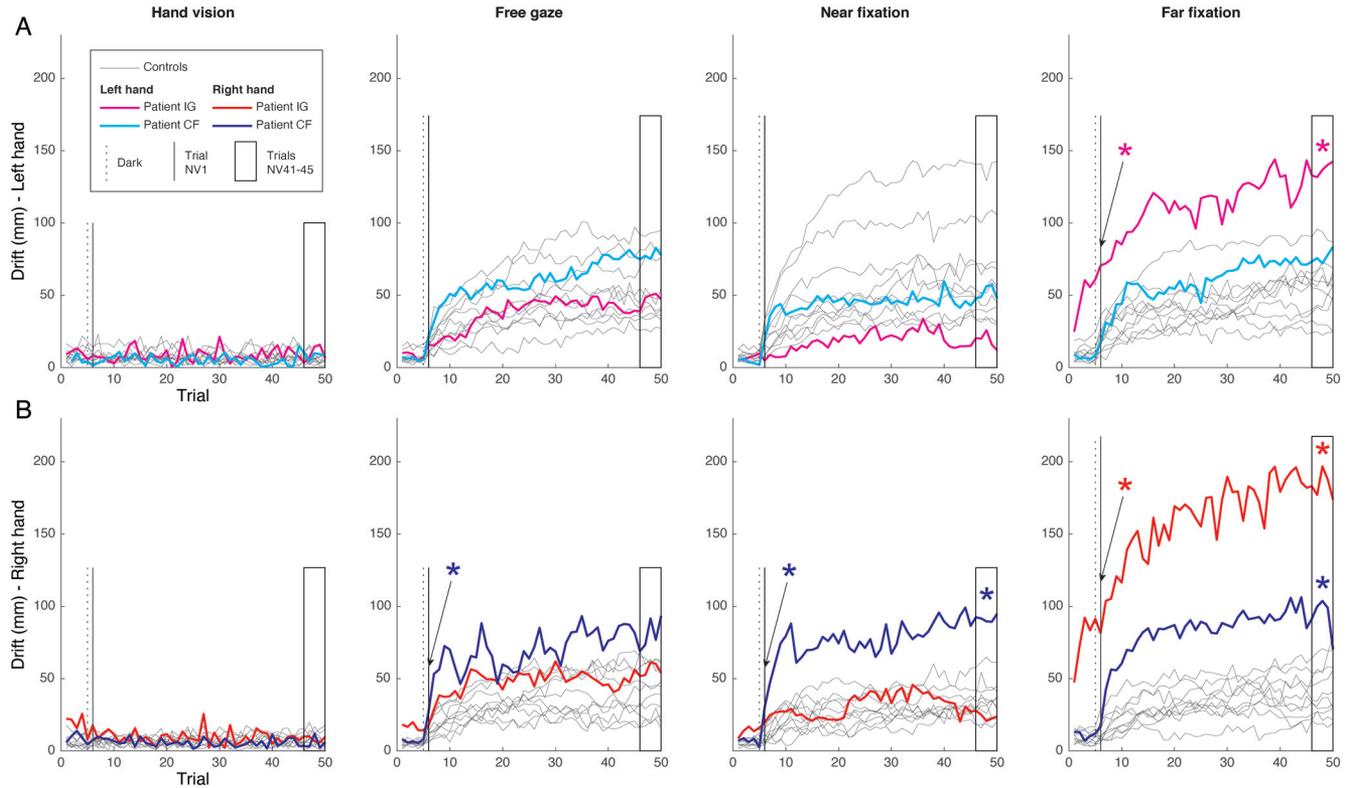
To summarize, all participants showed some hand position drift in the free gaze, the near fixation, and the far fixation conditions. However, this drift seems to be generally larger and more variable in OA patients than in control participants. In addition, we observed in patients that drift distance and intertrial drift variability varied depending on the gaze position and the hand being used. This confirms the assumption that the proprioceptive estimate of hand position is represented in oculocentric (gaze-centered) coordinates. In the next section, we will identify the nature of this drift by testing whether participants drift to a similar position across blocks.

Systematic Hand Position Drift

We tested whether the observed drift results from a systematic misestimation of proprioceptive hand position in the oculocentric reference frame. According to this hypothesis, within the same fixation condition, each participant should exhibit similar final hand positions across the three testing blocks. Furthermore, if the hand repeatedly moves toward a proprioceptive misestimate, the drift orientation and distance on the first trial in the dark are likely to be retained over subsequent trials but with increased magnitude. In that case, one would predict correlations of drift orientations and drift distances between trial NV1 and trials NV41-45.

We first tested whether the final hand positions were similar across the three blocks performed in each gaze fixation condition. In order to do so, TOST procedures were used to compare X and Y final positions (on trials NV41-45) in all possible combinations of two blocks (blocks 1 vs 2, 1 vs 3, and 2 vs 3) separately for the free gaze, near fixation and far fixation conditions. The equivalence region was set to 15 mm. The equivalence tests reported that all the 90% confidence intervals for the differences in average X and Y hand positions on trials NV41-45 were statistically within the equivalence region ([−15; +15]) across the three blocks performed in each gaze fixation condition ($p < .05$, see Table 1). There was one exception in the near fixation condition, where Y position showed a trend for equivalence between blocks 2 and 3 ($p = .064$). These findings suggest that overall the hand of control participants repeatedly drifted to very similar X and Y positions when reaching in the dark, thus toward a certain proprioceptive estimate that is consistent across blocks for a given gaze fixation condition.

Figure 4
Hand Position Drift as a Function of Trials

Note. Drift distance (in mm) for the left (A) and right (B) hands. Data was averaged across the 3 blocks performed in each gaze fixation condition. Each gray line corresponds to one control participant and the colored lines represent OA patients. The vertical dotted line represents the last trial with hand vision (trial V5), the vertical solid line represents the first trial without hand vision (NV1) and the rectangle represents the last 5 trials of the block (NV41-45).
* $p < .05$.

We then investigated whether final drift orientation (distance) was determined by the initial drift orientation (distance). More specifically, we looked at the correlations between the hand position error on trial NV1 and trials NV41-45, in control participants for the free gaze, near fixation and far fixation conditions (Figure 6, see also Supplementary Figure S3 for the same data represented in space). Data from OA patients are depicted but were not included in the computation of correlation coefficients. Figure 6A shows the circular-circular correlations between drift orientations on trial NV1 (inner ring) and trials NV41-45 (outer ring). In these plots, a strong correlation is characterized by straight lines between two pairs of observations directed toward the middle of the circle and very few to no lines crossing the inner circle. For each experimental condition, the individual initial drift orientations were found to be highly correlated with the final drift orientations. Similarly, there was a significant linear correlation between the drift distance on trial NV1 and on trials NV41-45 in all three experimental conditions (Figure 6B). Moreover, the significant linear regressions indicate the relationship between drift distance on trial NV1 and trials NV41-45. The inverse slopes of the regression lines suggest that final drift distance is about 4.4 times more than initial drift distance in the free gaze condition. The inverse slopes are 2.6 and 3.5 in the near and far fixation conditions, respectively. Interestingly, data for OA patients lie within or close to the
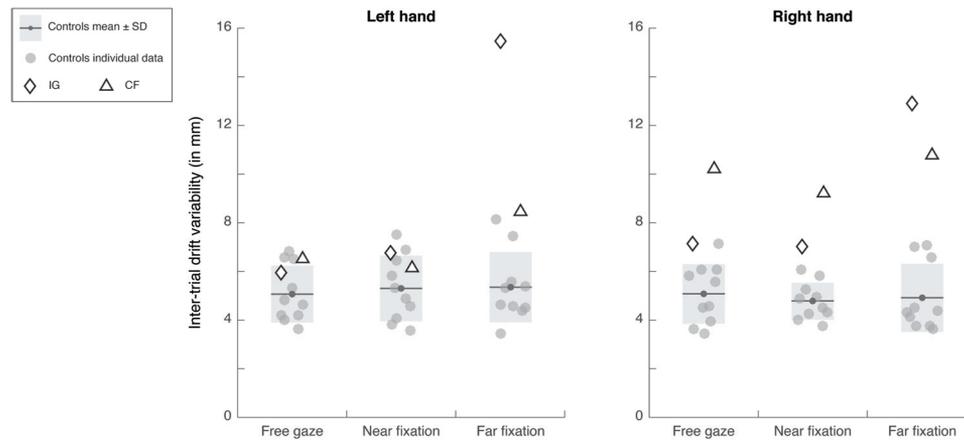
confidence intervals of each regression fit computed (Figure 6B). This suggests that patients IG and CF tend to behave like control participants in the three gaze fixation conditions, albeit showing larger drift distances in far fixation.

In summary, all participants exhibited an idiosyncratic drift orientation and distance; each one's hand consistently drifted to the same position in a given gaze fixation condition. Accordingly, the initial drift orientation was closely related to that of the final drift. Moreover, the reach error on the first trial without hand vision appeared to predict the final drift distance. These findings suggest that, when repetitively reaching in the dark, the hand progressively drifts toward a systematic proprioceptive position estimate, encoded in oculocentric coordinates.

Discussion

The results we found in control participants are consistent with previous literature showing that making repetitive movements in the absence of visual feedback induces hand position drift across time (Brown et al., 2003a; Cameron et al., 2015; Patterson et al., 2017). The distance between the hand and the target was progressively increased after the removal of hand vision and then seemed to reach a plateau after about 20 trials. As previously reported, drift orientation and distance considerably differed across

Figure 5
Intertrial Drift Distance Variability

Note. Intertrial drift distance variability (in mm) for right and left hands in the three gaze fixation conditions. Variability was calculated across all 45 trials without vision, in each condition. The light gray area corresponds to the standard deviation of the mean across control participants.

participants (Brown et al., 2003a; Patterson et al., 2017; Smeets et al., 2006). However, we found that control participants systematically drift back to the same spatial position across the three different blocks performed for a given hand and eye fixation condition, thus highlighting the idiosyncratic nature of hand position drift. This suggestion is further supported by the fact that we found strong correlations between the orientation of the initial drift (on the first trial following vision removal) and the final drift orientation observed during the 5 last trials of the block. More interestingly, the systematic initial drift distance happened to be a fairly good predictor of the final drift distance, and this was found for all three gaze fixation conditions. On average, the magnitude of the final drift was about 3.5 times larger than that of the initial drift (inverse regression slopes averaged across all conditions, Figure 6B).

Our findings, in line with those of Smeets et al. (2006), confirm that movement drift is subject-specific and therefore cannot be explained by accumulation of random execution errors. Although not tested in this study, we suspect this idiosyncratic drift in hand position to be extremely stable across time. Indeed, others have shown that visuo-proprioceptive matching errors are also subject-dependent and very consistent, both in direction and magnitude,

over days (Kuling et al., 2016). Hand position drift following multiple movements in the dark has been proposed to result from a misalignment between vision and proprioception, which both nevertheless remain accurate (Patterson et al., 2017; Smeets et al., 2006). This explains why proprioceptive information is correctly used to maintain reach trajectories throughout movement drift (Brown et al., 2003a) and why, following drift, movement direction to a new target is determined by visual inputs (i.e., last-seen hand position; Patterson et al., 2017). As repetitive movements are made without vision, the visual hand estimate centers at the initial start location—corresponding to the visual target—while the proprioceptive hand estimate is aligned with the actual hand position.
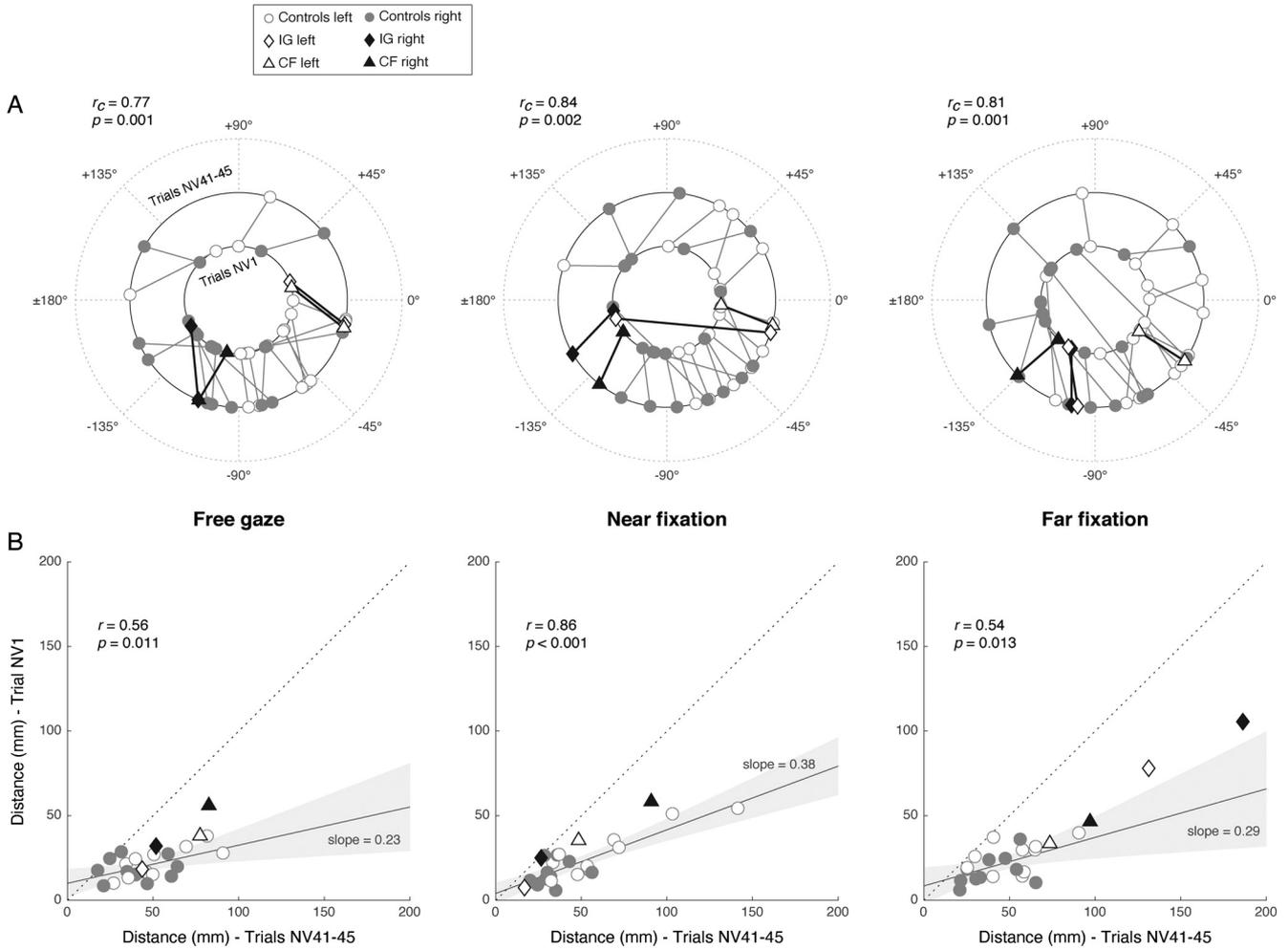
Aside from the inherent misalignment between visual and proprioceptive modalities, an alternative, not mutually exclusive, hypothesis about the mechanisms underlying hand position drift points to errors in sensorimotor transformations. Motor planning requires sensory information to be converted into motor commands, a process referred to as sensorimotor transformation. Interestingly, it has been shown that matching the unseen hand with visual or proprioceptive targets results in subject-specific errors (Kuling et al., 2017). Furthermore, the authors found that matching errors differed when moving the hand to a visual target or when moving the visual target to the hand.

Table 1
Final Hand Positions Between Different Blocks in Control Participants

Blocks	Variables	Free gaze	Near fixation	Far fixation
Block 1 vs 3	X position	$p = .018$ [−4.87, 9.25]	$p = .022$ [−9.94, 3.34]	$p = .008$ [−4.42, 8.35]
	Y position	$p = .005$ [−7.11, 6.94]	$p = .023$ [−8.91, 7.22]	$p < .001$ [−8.31, −0.15]
Block 1 vs 2	X position	$p < .001$ [−5.32, 5.91]	$p = .001$ [−6.82, 3.89]	$p = .006$ [−3.17, 8.58]
	Y position	$p = .012$ [−9.62, 2.04]	$p = .047$ [−10.48, 5.80]	$p = .002$ [−6.43, 5.14]
Block 2 vs 3	X position	$p = .006$ [−7.99, 4.62]	$p < .001$ [−2.91, 6.58]	$p < .001$ [−4.39, 5.86]
	Y position	$p = .030$ [−10.41, 3.14]	$p = .064$ [−10.70, 7.70]	$p = .014$ [−2.48, 9.65]

Note. Results of the equivalence tests for x and y final hand positions across the three blocks performed in the free gaze, near fixation and far fixation conditions. Numbers in brackets correspond to the 90% confidence interval from the two one-sided tests procedure. X and Y positions were averaged across the last 5 trials without vision (NV41-45). *p* values reported are Bonferroni-corrected.

Figure 6
Initial Versus Final Drift Orientation and Distance

Note. Data was averaged across the 3 blocks performed in each gaze fixation condition. (A) Circular correlations of drift orientations (in degrees) between trial NV1 and trials NV41-45. Negative and positive values correspond to drift toward and away from the body, respectively, and 90° represents the straight-ahead direction. (B) Linear correlations of drift distances (in mm) between trial NV1 and trials NV41-45. Pearson's correlation coefficients are reported. The black dotted line represents the line of unity, the gray line is the line of best fit (regression) based on controls' left and right data and the light gray area is the 95% confidence interval for the regression fit.

This provides evidence for the importance of the direction of sensorimotor transformations and the reference frame, or coordinates, in which sensory information is encoded. In the case of visually-guided movements, the hand position and the target location need to be transformed into common coordinates, which are usually oculocentric or gaze-centered (Batista et al., 1999; Henriques et al., 1998).

Our results cannot fully dissociate between these two explanations of movement drift (visuo-proprioceptive misalignment or sensorimotor transformation errors). However, both of them imply a major role of the PPC, which is known to be a sensorimotor interface. The activity in PPC neurons has been shown to be modulated by visual, eye position, and limb position signals (Andersen et al., 1997; Graziano et al., 2000). Moreover, the PPC is thought to mediate the alignment of visual and proprioceptive representations of space and limb position (Bolognini & Maravita, 2007; Ghilardi et al., 2000; Gregoriou &

Savaki, 2003). Note that sensory modalities other than vision have been found to be represented in gaze-centered coordinates (Blangero et al., 2005; Jones & Henriques, 2010; Pouget et al., 2002), and there is compiling evidence suggesting that the parietal cortex encodes hand position and target location in an oculocentric reference frame (Buneo et al., 2002; Colby et al., 1995; Medendorp et al., 2003; 2005).

Previous research about optic ataxia supports these observations. Indeed, when targets are presented in the space contralateral to their PPC lesion, patients with OA show large mislocalization errors that are modulated by eye movements and strongly biased toward gaze fixation point. This so-called field effect has been demonstrated not only for visual but also proprioceptive targets and is thought to reflect impaired spatial integration in oculocentric coordinates (Blangero et al., 2007; 2010; Khan, Pisella,

Vighetto, et al., 2005). This view is supported by our results showing that both OA patients we tested did not exhibit larger hand position drift than control participants when eye movements were not constrained. However, in near and far fixation conditions, unilateral patient CF showed a drift more important with his ipsilesional (healthy) hand compared to his contralesional (ataxic) hand. The explanation for this rather counterintuitive result is that CF was moving his healthy hand within the contralesional space, and his ataxic hand within the ipsilesional space. This provides evidence that the transformation of proprioceptive information about the effector in oculocentric coordinates is disrupted by PPC damage. This echoes a previous study, which reported that, when reaching to a foveated target aligned with midline, patient CF showed larger errors when the initial position of his healthy hand was seen in the contralesional visual field (Khan et al., 2007). In addition, we found that larger movement drift was accompanied by greater intertrial drift variability, which suggests that the proprioceptive hand estimate is noisier following PPC damage.

In this study, the fixation on the far target represents a particular condition in which participants' hands moved in the lower visual field. It has previously been shown that the PPC overrepresents the lower visual field (Fattori et al., 2017; Pitzalis et al., 2013; Previc, 1990; Rossit et al., 2013). More specifically, electrophysiological recordings in macaques demonstrated that the inferior contralateral quadrant was the most represented, followed by the inferior ipsilateral and the superior contralateral quadrants (Galletti et al., 1999). As a consequence, following PPC damage in both hemispheres, we would expect larger movement drift in the lower visual field but similar errors across left and right visual fields or left and right hands. Consistent with these predictions, we observed that bilateral patient IG was specifically impaired and showed extensive drift in the far fixation condition, irrespective of the hand tested. In contrast, her performance with either hand was similar to that of control participants when fixating on the near target. This particular behavior is likely to be attributable to the perceptual and motor deficits exhibited by IG when processing hand-to-target distances within the lower visual field, in the absence of hand visual feedback (Bartolo et al., 2018). These findings provide further evidence for an oculocentric representation of proprioceptive hand estimate, which is mediated by the parietal cortex.

As mentioned above, it seems that hand position drift in the dark results from small systematic errors that accumulate during repetitive movements. These errors are subject-specific and can predict the magnitude of the final movement drift in different gaze fixation conditions. On average, the final drift distance was about 3.5 times larger than the initial error on the first trial without vision. Data from OA patients suggests that similar mechanisms are involved, although larger initial errors and thus larger (but consistent) drift is observed. Moreover, these systematic initial errors in patients with OA appear to be dependent on the eye fixation position and the location of the moving hand. Altogether, these findings confirm the influence of gaze fixation on the proprioceptive estimate of hand position. This process is disrupted as a result of parietal damage, inducing a biased and noisier representation of proprioceptive hand position relative to the eyes. This suggests that the PPC is involved in the multisensory representation of hand location in the oculocentric reference frame, over the course of multiple movements.

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