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More than (where the target) meets the eyes: Disrupted visuomotor transformations in optic ataxia

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Abstract

Visually-guided reaching entails multiple coordinate frame transformations between retina-centered target location and body-centered limb location. Reaching errors in optic ataxia (OA) may be caused by disruptions to these transformations.

Consistent with this proposal, previous studies report that reaching errors in OA depend primarily on the location of a target relative to the patient's gaze regardless of its location relative to the head or body midline. We attempted to replicate this finding by testing KE, a patient with OA following bilateral parietal and left premotor lesions (as well as significant non-specific white matter disease) on a reaching task that varied the orientation of his head and torso while holding the gaze-relative position of the target constant (always foveated). In contrast to previous reports, we observed that rotating the head or body away from the midline led to decreased reaching accuracy. Further analyses showed that multiple visuomotor transformation steps may have been disrupted in KE. These results suggest that gaze-relative target position is not the sole determinant of reaching errors in all OA patients.

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A central challenge to understanding the control of visually guided actions is the well-known problem that target information enters the perceptual-motor system specified in gaze-centered coordinates but the movement to reach that target must ultimately be specified in arm-centered coordinates. In order to resolve this so-called visuomotor transformation problem, the perceptual-motor system must combine multiple sources of information to transform information between coordinate frames. For example, gaze-centered target coordinates can be combined with

from fast visuomotor to slow cognitive control.

[Neuropsychologia. 2005]

Review Oculocentric frames of reference for limb movement.

[Arch Ital Biol. 2002]

Review There may be more to reaching than meets the eye: re-thinking optic ataxia.

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proprioceptive information about where gaze is directed to form a representation of the target location in head-centered coordinates. Such a head-centered representation would be useful to create a stable target representation across saccades. Similar transformations have been proposed to represent target locations in shoulder-centered and hand-centered reference frames. Although it is debated whether the transformation problem is solved by transforming the visual target location into arm-centered coordinates (Flanders, Helms-Tillery, & Soechting, 1992), transforming the location of the arm into gaze-centered coordinates (Buneo, Jarvis, Batista, & Andersen; 2002; Buneo & Andersen, 2006), or by maintaining multiple movement-related representations in different reference frames (Battaglia-Mayer, Archambault, & Caminiti, 2006; Desmurget et al., 1998), it is clear that visuomotor transformations are required for the execution of visually guided reaching.

The process of visuomotor transformation occur within the parietal (Buneo & Andersen, 2006) and premotor (Batista et al., 2007) areas. Consistent with this claim, large errors are produced during visually-guided reaching by patients with optic ataxia (OA), a disorder typically observed after damage to the superior parietal lobe (Buxbaum & Coslett, 1997; Goodale & Westwood, 2004) or the parieto-occipital junction (Karnath & Perenin, 2005) and less frequently with damage to the premotor cortex (Nagaratnam, Grice, & Kalouche, 1998). In order to better understand this disorder, several studies have explored where within the transformation process disruption occurs by manipulating a target's location relative to the patient's gaze, head, and body position. These studies report that movement endpoint

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accuracy in patients with optic ataxia is primarily dependent on the location of the target relative to the patient's gaze at the time of reaching regardless of where the target was located relative to the head or body (Buxbaum & Coslett, 1997, 1998; Dijkerman et al., 2006; Khan et al., 2005). This pattern suggests that optic ataxia patients primarily plan movements based on target location information within gaze-centered coordinates because their errors are most consistent within this reference frame[1].

Owing to the relative scarcity of patients with optic ataxia, combined with the heterogeneity of deficits across patients (for a review, see Glover, 2003; Jax & Coslett, in press), the general trend of null effects for head and body rotations in previous work need not imply that this is true for all optic ataxia patients. OA patients are known to vary in the conditions under which their errors occur. For example, reaching errors in OA patients are observed primarily when reaching to targets outside of foveal vision (Buxbaum & Coslett, 1997, 1998; Jackson, Newport, Mort, & Husain, 2005). Comparably few patients also exhibit reaching deficits to foveated targets. These two patient subtypes have been referred to as non-foveal and foveal optic ataxia, respectively (Buxbaum & Coslett, 1997).

Previous reports of OA errors depending on gaze-relative target locations have come exclusively from the more common non-foveal subtype of OA. In this study, we report an analysis of the reaching errors made by KE, a patient with foveal optic ataxia. Because his reaching was inaccurate even to foveated targets, we were able to systematically vary the position of the torso or the head while keeping the gaze-relative position of the target constant (always foveated). If the primary determinant of reaching errors in all OA patients

is the gaze-relative target location, KE should be equally good in all conditions because his eyes were always directed at the target.

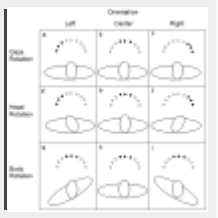
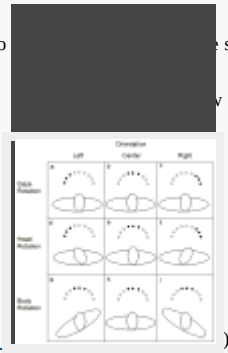
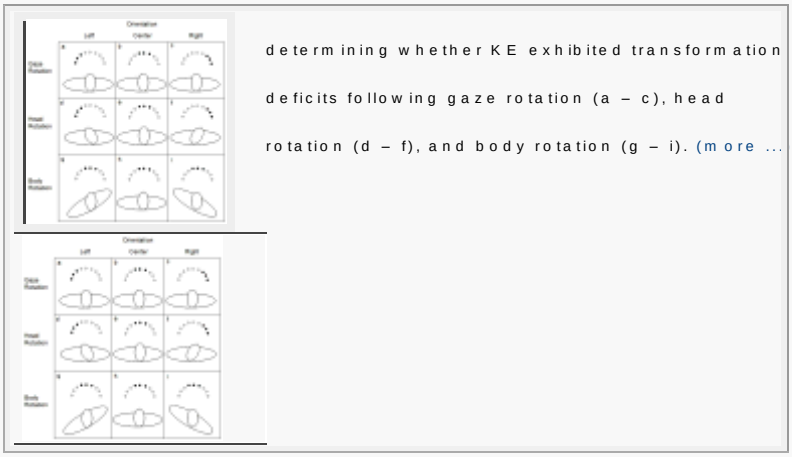
In addition to the primary aim of testing whether KE's reaching accuracy was equivalent when targets fell in the same gaze-relative location, we also tested whether KE's errors could be explained by a disruption of one or more visuomotor transformations. Identifying which specific transformations were disrupted in KE was d[redacted] examining the effects of manipulating the p[redacted] eyes (that is, gaze), head or torso (Figure 1 ). We reasoned that if reaching accuracy was unaffected by these manipulations, the corresponding transformations were intact. For example, if KE could accurately transform target information between gaze-centered and head-centered coordinates, reaching accuracy would not be affected by manipulations of gaze orientation. However, a change in errors following gaze rotation would suggest a disruption in this transformation. To avoid any confounding factors of additional transform atio[redacted]est was limited to conditions in which the [redacted]were oriented the same way (Figure 1a–c ).

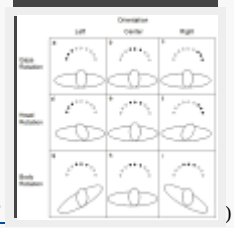
Figure 1

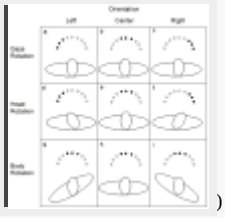
Diagram of critical test conditions, which were a subset of all movement conditions, for



determining whether KE exhibited transformation deficits following gaze rotation (a – c), head rotation (d – f), and body rotation (g – i). (more ...

The nature of these potential errors is predictable by assuming the perceptual-motor system maintains information about a "default" body configuration. Given its typicality during everyday reaching, we propose that this default configuration is when gaze, head, and body are aligned. Following a rotation, if the perceptual-motor system fails to register the degree of rotation and is overly dependent on the default orientation, rotating gaze counter-clockwise (CCW) should produce errors that are biased in the clockwise direction (CW), that is, toward the default configuration. Similarly, when gaze is rotated CW, errors should be biased in the CCW direction.

Identifying other transformation deficits involves similar logic. If KE's perceptual-motor system could accurately transform target information between head-centered and shoulder-cent[redacted]s, accuracy should be unaffected w[redacted]otated to the left or right (Figure 1d–f ). However, if this transformation step was disrupted, errors should increase when the head is rotated away from the default

configuration. Finally, if the transformation between shoul[redacted]d hand-centered coordinates was intact, accur[redacted]milar when the body is rotated (Figure 1g–i ). If this transformation was disrupted, rotating the body away from the default configuration should lead to an increase in errors. Like the gaze example, rotating the head and body should bias errors in the direction opposite of the rotation. By independently manipulating the position of gaze, head and torso, we tested the degree to which KE's reaching impairment reflected impairments in these three visuomotor transformations.

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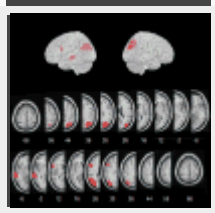
Method

Patient Description

The patient (KE) was a 58 year-old factory worker with a high school education. Three years prior to the investigations reported here KE suffered an infarction of the left hemisphere causing minor language problems and c[redacted]e right hand. He suffered a second stroke o[redacted] this testing. An MRI scan (Figure 2 ) obtained 8 months after the second stroke

revealed small areas of infarction in the left middle temporal gyrus, left middle frontal gyrus as well as a larger infarction of the left posterior parietal lobe and residual changes from a right parieto-occipital hemorrhage. Increased signal in the subcortical white matter of both hemispheres was also noted. KE's symptoms had persisted without significant change since the second stroke.

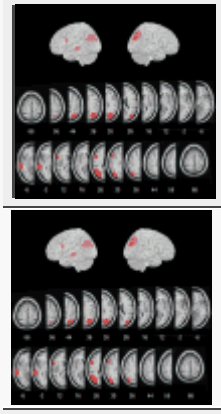


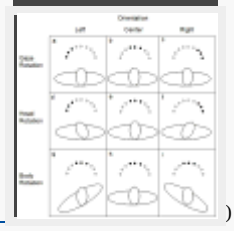
Figure 2

Locations of KE's lesions. Numbers below each slice indicate the z-value for that slice.

At the time of the present evaluation, KE was unable to accurately direct his hands to a target; on several occasions, he started fires when attempting to snuff out cigarettes in an ashtray. Neurologic examination revealed him to be fully oriented. He manifested pyramidal clumsiness with both hands but no significant weakness. Gait was slow with short steps. There was no tactile extinction. Assessment of visual processing revealed a visual acuity of 20/30 OU. When instructed to look at the examiner's face without focusing attention, visual fields were full to confrontation; when asked to focus attention on the examiner's nose, visual fields were restricted to approximately 30° concentrically with no evidence of a scotoma or asymmetry. Ocular movements to command as well as smooth and saccadic pursuit were normal in all directions.

KE also exhibited profound simultanagnosia, as described in detail in Coslett and Lie (in press a; b). For example, when shown two pictures or words for an unlimited period of time he correctly named both items on only 30% of trials. With vertically arrayed items, he reported the top item on approximately 60% of trials. With horizontally arrayed items, KE reported the right item on approximately 62% of trials. Although his simultanagnosia prevented the administration of traditional tests of neglect, KE showed a slight asymmetry to favor reporting items in his right hemispace.

Procedure

KE provided informed consent for his participation in the study, which was approved by the Temple University Institutional Review Board. KE was seated comfortably at a table and was told that on all trials he was to reach and touch a red target with his index finger. He held a small pencil in his hand such that the tip of the pencil was adjacent to the distal tip of the index finger. With this arrangement KE's movement endpoints were recorded on the surface of the table when he left a barely discer[redacted]t at the location his finger contacted the t[redacted]itions there were 9 target locations (Figure 1 ) arrayed in a semicircle with a 30 cm radius (targets at 0°, 22.5°, 45°, 67.5°, 90°, 112.5°, 135°, 157.5°, and 180°). The origin of the semicircle was located at the edge of a table 10 cm anterior to the midline of KE's body. The target was a red circle 1 cm in diameter that was placed, in full view of KE, at 1 of the 9 target locations before each trial. No effort was made

to conceal the target placement from KE because the task contained no speed requirement nor was initiation time measured.

KE completed 20 blocks of 54 trials (9 targets × 6 repetitions). Target sequence was random within a block. Two right hand blocks and two left hands blocks were completed in each of the following five conditions: (1) head centered and body centered, (2) head 30° left and body centered, (3) head 30° right and body centered, (4) head centered and body 30° left, and (5) head centered and body 30° right. In all conditions, KE gazed directly at the target. There were 6 testing sessions, each at least one week apart. Each session included between 3 and 5 blocks in a pseudo-random sequence with the restriction that the same condition was never administered twice in a single day.

Accuracy of reaching was scored by measuring the distance from KE's mark for each trial to the edge of the target. Trials on which KE touched any part of the red circle were scored as a 0 cm error. Accuracy was measured from the subject's final resting place. That is, if KE made initial contact with the score sheet 10 cm from the target but subsequently moved his finger closer to the target, the location at which he stopped was scored as his response.

Comparison data from age-matched neurologically intact participants were not completed because a pilot study with these control participants demonstrated that performance in this paradigm (full vision of hand and target; no speed constraint; error corrections allowed) was almost entirely at ceiling for all conditions. High accuracy (2–3 mm errors) for control participant under similar testing conditions has been reported in Buxbaum and Coslett (1998). As we will show,

KE's errors were an order of magnitude greater than these 2–3 mm errors even under conditions in which he was most accurate.

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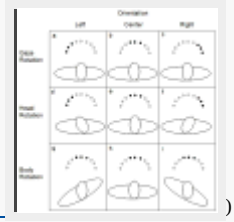
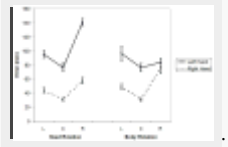
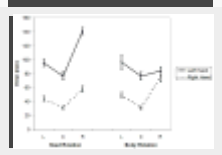
Results

The first set of analyses focused on the primary aim of the study, which was to test whether KE's errors would be equivalent when targets fell in the same gaze-relative location, as would be predicted based on previous studies of OA patients. To test this prediction, we first analyzed KE's absolute accuracy across all conditions and all targets to examine the overall effects of rotating the head and body. The second set of analyses focused on a subset of conditions and targets that allowed us to determine whether disrupted visuomotor transformation [redacted] for KE's performance (the logic of [redacted] nted in the Introduction and Figure 1 ).

Absolute accuracy

Endpoint error analyses were used to determine whether rotating KE's head or body caused a change in his reaching errors. To do so, absolute error on each trial (distance between endpoint and target center) served as the dependent variable for 2 (hand: left, right) × 3 (orientation of head and

trunk: left, center, right) × 3 (target side: 3 left targets, 3 center targets, 3 right targets) ANOVAs, performed separately for the head and body rotation conditions. Post-hoc analyses were Bonferroni-corrected for multiple comparisons with overall α = .05. Separate ANOVAs rather than a single ANOVA including a rotation type factor (head or body) were performed because data from the head centered/body centered condition would need to be included in the single ANOVA twice (once as the center condition of the body orientation manipulation and once as the center condition of the head orientation manipulation). However, effects of rotation type were analyzed within each of the four hand/orientation combination (e.g., comparing left hand/*head* rotated left to left hand/*body* rotated left).

M[redacted]rror data are shown in Figure 3  . Overall, absolute errors were greater for the left hand than the right hand and increased as the body or head was rotated away from the midline, especially when rotated to the rig[redacted] rotation conditions (left side of Figure 3 ), there was a main effect of hand (LH > RH; $F(1,6) = 475.2$, $p < .001$), a main effect of head orientation (HR > HL > HC; $F(2,12) = 63.82$, $p < .001$), and an interaction between hand and head orientation ($F(2,12) = 15.55$, $p < .001$). In this interaction, HR > HC was the only significantly different pairwise comparison for right hand whereas all pairwise comparisons were significantly different for the left hand (HR > HL > HC). All other effects, including effects of target side or interactions between target side and other factors, were not statistically

significant ($p > .23$).

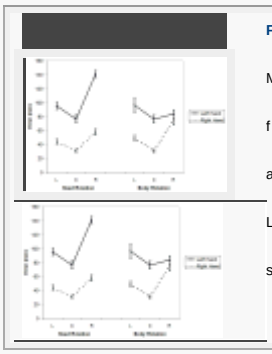


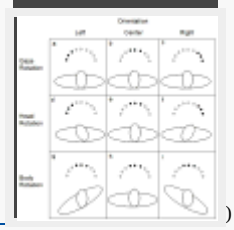
Figure 3

Mean absolute reaching errors (±1 SE), in mm, for the head rotation conditions (left side of figure) and body rotation conditions (right side of figure). L, C, and R refer to the orientation of the segment.

In the head rotation condition (right side of Figure 3) there was a main effect of hand (LH > RH; $F(1,6) = 95.17$, $p < .001$), a main effect of body orientation (BR = BL > BC; $F(2,12) = 23.77$, $p < .001$), and an interaction between hand and body orientation ($F(2,12) = 25.92$, $p = .001$). In this interaction, the effect of orientation was only marginally significant for the left hand ($p = .07$) but significant for the right hand ($p = .004$), with all pairwise differences being significant (BR > BL > BC). All other main effects and interactions were not significant ($p > .19$).

When comparing the effects of rotation type (body or head) within each of the four hand/orientation combination (right hand/right rotation, right hand/left rotation, left hand/right rotation, left hand/left rotation), the effect of rotation type depended on the direction of rotation and the hand used. Leftward rotations of the head and body resulted in equivalent levels of error within both the left ($p = .888$) and right ($p = .382$) hand. However, rightward rotations of the head and body had distinct effects for the left and right hands (body > head for left hand, $p < .001$; head > body for right hand, $p < .001$).

Identifying transformation deficits

The preceding analysis showed that KE's errors were minimized when the head [redacted] ligned and centered. Next, we analyze[redacted] conditions (see Introduction and Figure 1 ) to identify which transformations were disrupted. In these analyses we quantified errors three ways. The first error measure was *absolute error*, the same measure used in the preceding analyses, which allowed us to determine if overall error magnitude increased across conditions. The second error measure quantified the directional bias in the average endpoint location (across repeated trials; done separately for each target) relative to the target location. This *direction error* was measured as the angular disparity between the start-to-average-endpoint direction and the start-to-target direction. Positive direction errors indicated a clockwise (rightward) bias in the average endpoint and negative direction errors indicated a counter-clockwise (leftward) bias in the average endpoint. The third error measure was *variable error*, which quantified the consistency, or precision, of endpoint locations across trials regardless of absolute accuracy. Variable error was calculated by first finding the average location of the endpoints for a single target within a block and then calculating the average distance (in mm) each endpoint fell from that average endpoint. Larger average values of variable error indicate greater variability in endpoint position. All three error measures were analyzed separately with 2 (hand: left, right) × 3 (orientation of rotated segment: left, center, right)

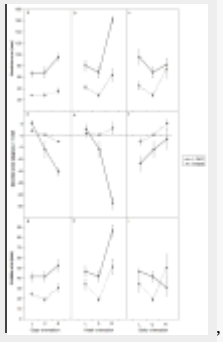
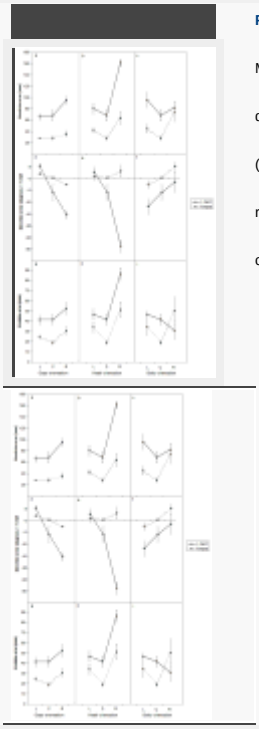
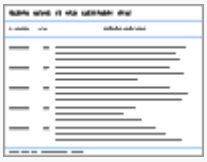
ANOVAs. [redacted]es for these analyses are shown in Figure 4  , and the F-values, p-values, and details of follow-up comparisons for all ANOVAs are reported in Table 1.

Figure 4



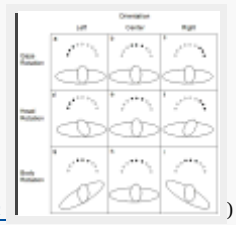
Mean (±1 SE) absolute error (in mm; a–c), direction error (in degrees; d–f), and variable erro (in mm; g–i) for tests of the effects of gaze rotation (left column), head rotation (center column), and body rotation (right (more ...)

Table 1



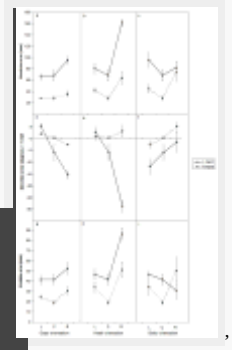
ANOVA results for transformation analyses.

By examining the effects of rotating gaze to the left or right while maintaining a constant head and body configuration

(Figure 1a – c ), we were

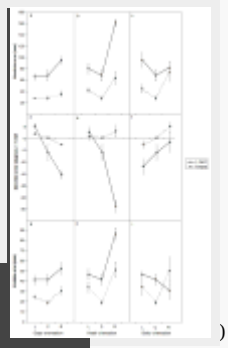
whether KE exhibited transformation def ze-

and head-centered coordinates. The resul ses



are shown in the left colu ,

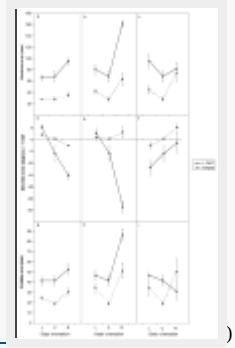
and indicated that this tran disrupted in KE.



Absolute error (F) increased for

both hands when d to the right but not the

left. Bias in endp s measured by direction



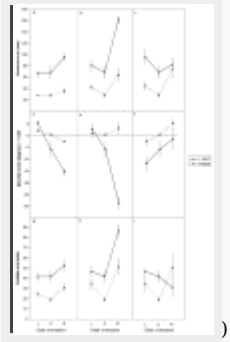
error (Figure 4d), was also affected by

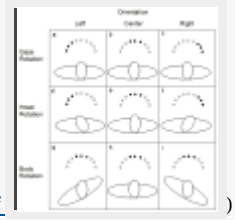
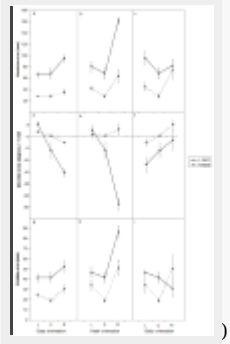
rotations of gaze, especially for the left hand. The direction

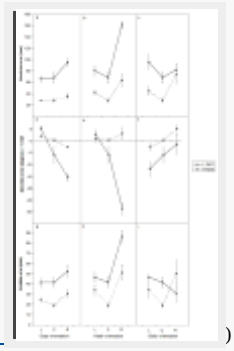
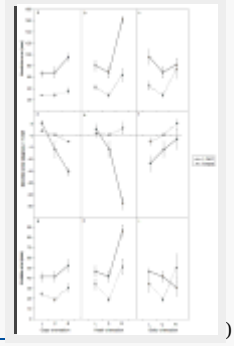
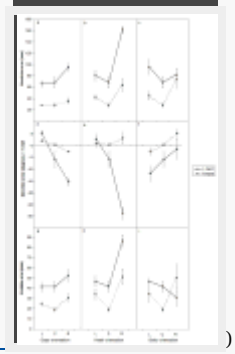
error analysis showed that errors were biased towards the

default, gaze forward, configuration. That is, leftward gaze

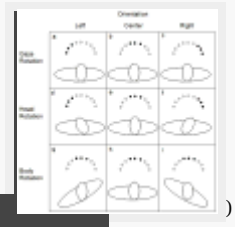
rotation led to endpoints falling to the right (CW, or having

more positive direction errors) of the target as compared to when gaze was directed centrally. Similarly, rightward gaze r[redacted]dpoints falling more to the left (CCW, or h[redacted]ative direction errors) of the target as c[redacted]n gaze was directed centrally. Finally, gaze r[redacted]used endpoint variability (Figure 4g ) to increase in both hands when gaze was rotated to the right but not the left.

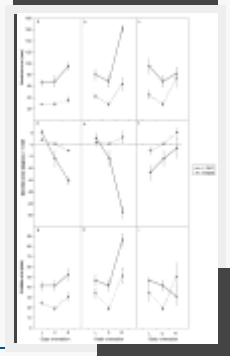
By examining the effects of r[redacted] to the left or right while maintaining a cor[redacted]body c[redacted]gure 1d – f ), we were able t[redacted]E exhibited transformation deficits between h[redacted]er-centered coordinates. The observed t[redacted]eficits (middle column of Figure 4 ) were similar to those observed following

gaze rotations. Absolute error (Figure 4b ) significantly increased when t[redacted]ted to the right but not the left, although [redacted]otations also led to a small but non-statistic[redacted]increase in error for both hands. Head rot[redacted]d the bias in endpoint locations (Figure 4e ) such that they were biased towards the default, head-forward, configuration, but only for left handed reaches. That is, left hand reach[redacted]biased to the right when the head was rotated [redacted]biased to the left when the head was rotated [redacted]ad rotations also led to increased endpoint va[redacted]ally for rightward head rotations (Figure 4h ).

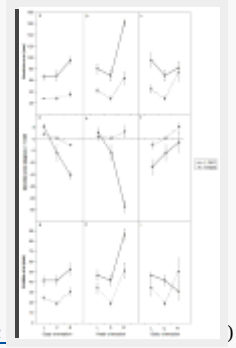
Finally, by examining the effects of rotating the body to the left or right while maintaining a constant gaze and head



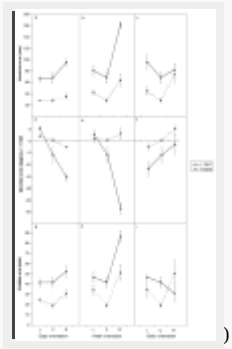
configuration (Figur), we were able to test whether KE e rmation deficits between shoulder-centered a d coordinates. Significant effects o were observed (right



column of Figure 4 ough with a slightly different pattern th d for the previous two transformations. Like transformations,



absolute errors (Figure 4c) increased for both hands when the body was rotated to the right but not to the left, although there was a non-statistically-significant trend towards absolute error increasing with leftward body rotations as well. Unlike the previous two transformation steps, however, endpoint locations (Figure 4f



) were biased *away from* the default configuration rather than towards it. That is, as compared to the body c direction errors were biased leftward f rotations and biased rightward for rightward A lso unlike the previous two transform oint variability (variable error;

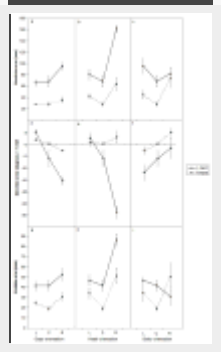


Figure 4i) did not increase following rotations of the body, although a trend towards this effect was observed for the right hand.

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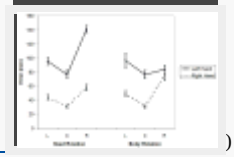
Discussion

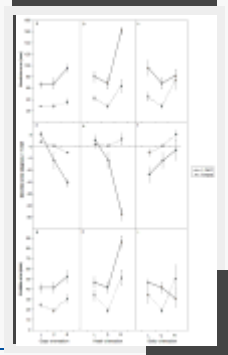
The primary aim of this study was to replicate previous studies reporting that reaching endpoint accuracy in optic ataxia (OA) patients depends primarily on gaze-relative target locations (Buxbaum & Coslett, 1997, 1998; Carey, Coleman, & Della Sala, 1997; Dijkerman et al., 2006; Jackson et al., 2005; Khan et al., 2005). In contrast to these

previous reports, KE's errors were significantly affected by rotations of the head and body even when the gaze-relative position of the target was constant (always foveated). For both hands, KE's reaching errors generally increased as his head or body was rotated away from [redacted]dy forward configuration (see Figure 3 ). Thus, it is clear that reaching errors in optic ataxia patients are not *universally* determined by a target's gaze-relative location. The second aim of this study was to determine whether KE's errors resulted from the disruption of one or more visuomotor transformations. Owing to his somewhat variable performance, the results of the present study partially, but do not fully, support this claim. However, as we will describe below in more detail, other theories of optic ataxia are also unable to account for his performance.

In the remainder of the discussion section, we will first describe in more detail the aspects of KE's performance that can and cannot be explained by visuomotor transformation deficits. Second, we will discuss how other theories of optic ataxia are unable to account for the results we observed and the implications our results have for those theories. Third, we will discuss why KE's performance may have differed from that of previous OA patients. Finally, we will discuss the implication of our results to one theory of the visuomotor transformation process and suggest areas in which future research is needed.

As described above, the proposal that KE's errors were caused by disruption to visuomotor transformations received mixed support. The data that most clearly support this claim come from the left handed reaches following manipulation

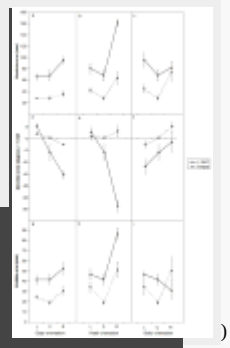
of gaze and head orientation [redacted] the left and



center columns of Figure 4 [redacted]

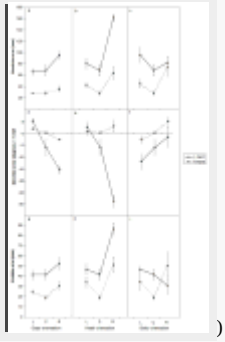
conditions, absolute error generally in [redacted] e

segment was rotated away from the ce [redacted] for



rightward rotations (Figure 4a and 4 [redacted]).

These errors were biased in the dire [redacted] at of the



segment rotation (Figure 4d and 4e [redacted]), with

leftward rotations causing errors to have a greater rightward

(CW) bias and rightward rotations causing errors to have a

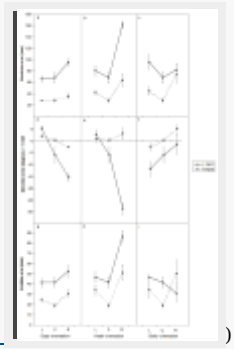
greater leftward (CCW) bias. Although absolute error did

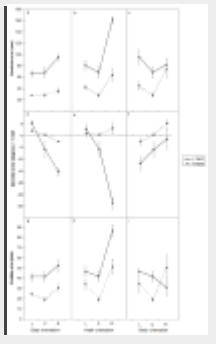
not significantly increase for the left hand following leftward

rotation of gaze, it did significantly shift the bias in these

errors from a 5° counter-clockwise (CCW) bias in the gaze-

centered condition to a 5° clockwise (CW) bias in the gaze-

left condition (Figure 4d ). Thus, the lack of a significant change in absolute accuracy was the results of the two conditions having similar error magnitudes but opposite directional biases.

Other aspects of KE's performance are less easily explained by deficits in visuomotor transformations. For example, although endpoint accuracy for the right hand showed the same general pattern of increasing absol[redacted] variable error as segments were rotated [redacted]r (although sometimes in weaker, non-sta[redacted]cant ways), these errors showed less consiste[redacted]he default configuration (Figure 4d and 4e ). These smaller effects may have been masked by the overall higher accuracy with the right hand than the left hand. Such hand differences have been previously reported in other foveal and non-foveal OA patients with unilateral damage (Perenin & Vighetto, 1988) and non-foveal OA patients with bilateral damage (Jackson et al., 2005; Khan et al., 2005). KE's differing accuracy across hands was likely explained by the more extensive damage to his right parietal region than left parietal region. Two other aspect of KE's performance are not easily explained by visuomotor

transformation deficits. The first is why there was a greater decrement in performance following rightward rotations of gaze and head than leftward rotations. Any transformation deficit should seemingly affect rotations in both directions equally. The second is that rotation of the body produced errors that were biased in the opposite direction as the biases in errors following gaze and head rotations. That is, rather than errors being biased towards the default configuration, they were biased away from it.

Although deficits in visuomotor transformations could not explain all aspects of KE's performance, it is unclear how other current theories of optic ataxia would account for our findings. For example, Jackson and colleagues (2005) claim that patients with optic ataxia cannot effectively decouple reach direction from gaze direction. In this study, however, there was no requirement to decouple the eye and limb systems. Thus, this theory in its stated form can not explain the results of our foveal OA patient even though it may explain the results of other non-foveal OA patients (Buxbaum and Coslett, 1997, 1998; Jackson et al, 2005). Although KE's deficit was not in decoupling reach and gaze direction, his performance can be partially understood as a more general deficit of decoupling the orientation of multiple segments (gaze, head, body) away from a default configuration. From this perspective, a more general form of Jackson and colleague's claim that allows for many forms of deficits in decoupling may have significant explanatory power for both foveal and non-foveal OA patients.

Other theories of OA (Glover, 2003, 2004; Rossetti et al, 2003) have claimed that the disorder is characterized by a disruption in online movement control (and relatively intact movement planning abilities). Because we did not measure

the kinematics of KE's movements, our analyses can not identify whether his errors were present at movement initiation, indicating a movement planning deficit, or whether they emerged later in the movement, indicating an online control deficit. As judged by our clinical observation of KE, however, his errors appeared to be present even early in the movement, a finding consistent with other kinematic analyses of OA patients (Roy et al., 2003; Milner et al., 2003). Regardless of whether or not KE exhibited errors during early reaching, it is unclear how a theory proposing that OA is a disruption of online control could explain why rotating gaze, head, or body orientation away from the midline would often increase endpoint errors. Such effects would seem to be most easily understood as a disruption in visuomotor transformations.

Critically, explanations of OA as a disruption in online control need not be seen as being in complete opposition to explanations of OA as a disruption in visuomotor transformations. The problem of target position and body position information being initially specified in different coordinates (gaze- and arm-centered, respectively) occurs when the arm is stationary prior to movement initiation (during planning) as well as when moving (during online control). If visuomotor transformations are more difficult and errorful during online control when limb positions are changing quickly (as compared to planning when limb positions are more static), disrupting visuomotor transformations may more strongly disrupt online control than movement planning. Thus, the two explanations of deficits in OA may not be as contradictory as previously reported. Admittedly, other findings in the optic ataxia literature are not clearly explained by a visuomotor transformation deficit, such as their increased accuracy when

grasping familiar objects than unfamiliar objects (e.g. lipstick container or similarly-sized dowel; Jeannerod, Decety, & Michel, 1994; see Glover, 2003, for other examples). Clearly, which specific perceptual-motor processes are deficient in optic ataxia is poorly understood, and more research on the behavioral deficits of these patients is needed.

Another question raised by our data is why KE's performance differed from other OA patients whose errors depended primarily on gaze-relative target locations (Buxbaum & Coslett, 1997, 1998; Carey et al., 1997; Dijkerman et al., 2006; Jackson et al., 2005; Khan et al., 2005). This behavioral difference may be explained in some patients by the difference between unilateral damage (e.g., both patients reported by Dijkerman et al., 2006, and one patient in Khan et al., 2005) and bilateral damage (as KE had). Unilateral patients may have been able to rely on transformations within the intact hemisphere, thus possibly reducing or eliminating the effects of head or body rotations. However, other studies (Buxbaum & Coslett, 1997, 1998; Carey et al., 1997; Jackson et al., 2005; Khan et al., 2005) have reported patients with bilateral lesions and non-foveal optic ataxia who produce errors that primarily depend on gaze-relative target locations.

Alternatively, differences in lesion location may also explain the variability across patients. In addition to his bilateral posterior parietal damage. KE also had damage to the left premotor area. The premotor cortex is known to be involved in visually guided reaching (Lacquaniti et al., 1997) and visuomotor transformations (see Batista et al., 2007, for a recent review), although KE's lesion was slightly more inferior than regions identified in a few papers as being most

critical for visually guided reaching (Astafiev et al, 2003; Prado et al., 2005). Like KE, however, patients in previous studies also had frontal damage to one hemisphere. Unfortunately, it is not possible to provide a thorough comparison of these frontal lesions across studies as detailed, whole-brain, lesion information has rarely been reported. Thus, we can only speculate that the damage to KE's left premotor area may have been responsible for the additional disrupted transformations not previously reported in other papers. Consistent with this proposal, single-cell recordings in monkeys suggest that neurons in the premotor cortex may involve greater coding of information in body-centered coordinate than the parietal lobe, with generally codes information in eye-centered coordinates (Pesaran, Nelson, & Andersen, 2006). This finding may explain why errors in other OA patients (with damage primarily to the parietal lobe) have depended mainly on gaze-relative target locations while errors for KE (who also had premotor damage) depended on the target's location relative to his head and body. One finding that is inconsistent with our proposal is that one would predict greater deficits in the right hand than the left hand following left premotor damage, the opposite pattern that KE exhibited. Critically, any neuroanatomic explanation of KE's behavioral deficits is further complicated by his non-specific white matter disease. Because of this, future work using more neuroanatomically precise methods, such as TMS, will be required to clarify the possible sites of neuroanatomic damage that could lead to behavioral deficits similar to KE's.

In addition to neuroanatomic differences between KE and other OA patients, KE's reaching performance may have been influenced by his simultanagnosia. Previous studies have not reported that their OA patients exhibited profound

simultanagnosia, although more subtle forms of simultanagnosia may have been present but not identified in these patients. This perceptual disorder may have limited KE's ability to perceive his moving limb and the target at the same time. Thus, reaching for KE with visual feedback may have been similar to neurologically-intact participants reaching without visual feedback, and reaching under these conditions with the head or body rotated is known to cause a shift in the perceived midline (Biguer, Donaldson, Hein, & Jeannerod, 1988; Karnath, Christ, & Hartje, 1993). Any effects of misperceived midline or other perceptual problems would not seem to explain KE's hand difference, or interactions between hand and body segment rotation, because perceptual deficits would be predicted to affect both limbs equally (or at least in a non-interacting way).

Another possible difference between the present study and previous studies reporting gaze-relative errors in OA is that in the present study KE was allowed to correct his end position whereas other studies have instructed patients to reach ballisticly (although data confirming that patients followed these instructions have not been reported). By allowing corrections, KE may have tried to correct his end position by looking back and forth between the location of his finger and the target. These perception-based corrections would have been errorful in KE since his simultanagnosia prevented him from perceiving his finger and the target at the same time. Two informal observations argue against a significant influence of perception-based corrections. First, as reported above, KE's errors appeared to be present even early in the movement, before correction based on perceptual comparison was possible. Second, given the total number of reaches he performed (over 1000 across the 6 testing sessions), and the difficulty such perceptual

comparisons were for him, KE rarely made the effort to significantly correct the end position of his movements. Thus, we feel our results are not significantly influenced by allowing KE to correct his end position.

Beyond the implications they have for understanding OA, the present results also have implications for one theory of visuomotor transformations (Buneo et al., 2002) which states that there is a direct transformation between eye- and hand-centered coordinates, bypassing the need for target representations within the intermediate coordinate frames (e.g. head- or body-centered). If these intermediate transformations are not needed, it is unclear why altering the orientation of KE's head and body affected his accuracy. Therefore, this theory may need to be qualified so that reaching is done primarily through direct transformations between eye- and hand-centered coordinates, but that the intermediate representations are created and can be used when needed, such as when the direct transformations are disrupted following damage.

In conclusion, the results from the current study show that reaching errors in optic ataxia patients are not universally determined by the target location relative to the patient's gaze. When areas outside of the posterior parietal region are damaged, such as the premotor area in KE, reaching errors can depend on the target location relative to the patient's head and body midline. Thus, many steps within the visuomotor transformation process can be disrupted in OA, especially as damage to motor-related areas is more extensive. Future work involving additional OA patients and similar manipulations of multiple body segments will be required to better understand the prevalence, and neural underpinnings, of these multiple transformation deficits.

Acknowledgments

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Footnotes

[1]The one exception to this finding is patient DP (Buxbaum & Coslett, 1997, 1998), who exhibited two patterns of reaching deficits that depended on the target location relative to both head position and gaze direction. DP's first reaching deficit was a significant directional hypometria (Coslett, Bowers, Fitzpatrick, Haws, & Heilman, 1990), such that he typically failed to reach to targets on the right side of his head midline. When tested with targets to the left of the head midline, DP exhibited a second reaching deficit such that he produced large errors when reaching to non-foveated targets. Thus, his errors also depended on the location of the target relative to his gaze. As noted by the authors, the relationship between these two deficits is unclear. Given that directional hypometria has not, to our knowledge, been reported in other cases of optic ataxia, this deficit may have had an independent but additive influence on his reaching errors.

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