

# Unilateral resection of both cortical visual pathways in a pediatric patient alters action but not perception

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## ABSTRACT

The human cortical visual system consists of two major pathways, a ventral pathway which subserves perception and a dorsal pathway which primarily subserves visuomotor control. Previous studies have found that children with cortical resections of the ventral visual pathway retain largely normal visuo-perceptual abilities. Whether visually guided actions, supported by computations carried out by the dorsal pathway, follow a similar pattern of preservation remains unknown. To address this question, we examined visuo-perceptual and visuomotor behaviors in a pediatric patient, TC, who underwent a cortical resection that included portions of the left ventral and dorsal pathways. We collected kinematic data when TC used her right and left hands to perceptually estimate the width of blocks that varied in width and length, and, separately, to grasp the same blocks. TC's perceptual estimation performance was comparable to that of controls, independent of the hand used. In contrast, relative to controls, she showed reduced visuomotor sensitivity to object shape and this was more evident when she grasped the objects with her contralesional right hand. These results provide novel evidence for a striking difference in the competence of the two visual pathways to cortical injuries acquired in childhood.

## 1. Introduction

The cortical visual system is comprised of two anatomically and functionally distinct pathways. The ventral pathway projects from the occipital lobe to the temporal lobe and supports vision-for-perception, while the dorsal pathway projects from the occipital lobe to the parietal cortex and processes information that is utilized to support vision-for-action (Mishkin et al., 1983; Goodale and Milner, 1992). Over several decades now, accumulating evidence has shown that the dissociation between the two pathways (and functions) is not binary but, rather, is relative and more graded (Franz et al., 2000; Freud et al., 2016b, 2020; Schenk and McIntosh, 2010). Nevertheless, the functional specialization of the two pathways is still considered a fundamental organizational principle of the visual system.

The dissociation between the two visual pathways and their corresponding functions has been highly informed by neuropsychological investigations of adult patients with acute damage (due to a stroke or traumatic brain injury) to one of the pathways. Patients with lesions to

the ventral pathway have been shown to have a deficit in visual object perception, termed visual agnosia, but nevertheless have relatively intact visually guided behaviors (Ganel and Goodale, 2019; Goodale et al., 1991; Karnath et al., 2009; Whitwell et al., 2014; but see Himmelbach et al., 2012; Rossit et al., 2018; Schenk, 2006, 2012). In contrast, individuals with posterior parietal lobe lesions (dorsal pathway) specifically with lesions in the superior parietal lobule (SPL) and areas around the intraparietal sulcus (IPS), suffer from 'optic ataxia', an impairment in reaching and grasping objects in their contralesional visual field but, nonetheless, have minimal perceptual deficits (Jakobson et al., 1991; Karnath and Perenin, 2005; Rossetti et al., 2019; but see Medina et al. (2020) who documented mild perceptual deficits in these patients).

Interestingly, the remarkable deficits in object perception observed after a lesion sustained to the ventral pathway are not always evident. A striking demonstration comes from pediatric pharmaco-resistant epilepsy patients who underwent a cortical surgical resection to manage their seizures (Liu et al., 2018, 2019). Although a large portion of the

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ventral visual pathway was compromised, these children typically demonstrated mostly normal visuo-perceptual abilities. In particular, post-surgery, visuo-perceptual performance was within the normal range across a series of mid-level (for example, Glass patterns) and high-level (for example, face recognition) visual tasks (Liu et al., 2019). The normality in behavioral profile was accompanied by normal topography, magnitude, and representational structure of category-selective organization in the non-lesioned hemisphere, as demonstrated using functional MRI. This conclusion was corroborated by a longitudinal study of a single child whose resection, at age 6 years and 9 months, resulted in the removal of the right occipital and posterior temporal lobes. Despite a persistent left homonymous hemianopia, the patient exhibited preserved intermediate- and high-level visual abilities suggesting a normal developmental trajectory following the resection (Liu et al., 2018).

Importantly, the preserved visuo-perceptual behaviors described by these recent studies only examined computations carried out by the ventral visual pathway. However, the question remains whether visuo-motor behaviors, mediated by the dorsal visual pathway (Goodale and Milner, 1992), display a similar pattern of resilience, and follow a normal developmental trajectory post-resection. Notably, behavioral (Atkinson, 2017), neuroanatomical (Vinci-Booher et al., 2021) and animal (Smith et al., 2017) studies have argued that the two pathways are subject to distinct developmental trajectories, and as such, might display differential levels of susceptibility to injuries acquired early in life.

To determine whether the development of visuo-motor behavior is disrupted following an occipital-parietal resection, we characterized the behavior of patient TC who had undergone a unilateral cortical resection that included portions of both the left ventral and dorsal pathways for the clinical management of drug-resistant epilepsy (see Methods for more details about the etiology of the lesion). Clinical neuropsychological assessments had already identified a possible deficit in visuo-motor coordination (see Methods) suggesting that, in contrast with perceptual functions (Liu et al., 2019), TC's visuo-motor behaviors might be adversely impacted. Importantly, the plausible dissociation in the restoration profile of the two pathways can shed light on the developmental and plasticity profiles of different portions of the human cortical visual system and can also provide insights to clinicians who work with epileptic pediatric patients.

To explore and characterize this dissociation, we evaluated TC's visuo-perceptual and visuo-motor competence using Efron blocks. The Efron blocks are rectangular 3D objects that are matched in their overall surface size, color and depth but differ in their height and length (aspect ratio). Thus, discrimination between these blocks relies on deriving a precise representation of shape (Efron, 1969; Freud et al., 2016a; Goodale et al., 1991). TC and matched control participants completed the task with each of the right and left hands, allowing us to compare performance not only between TC and the control participants but also between TC's contralesional (right) and ipsilesional (left) hands.

Similar to previous studies that investigated grasping behaviours in typical observers (Jeannerod, 1984, 1986) and neuropsychological patients (Goodale et al., 1991; Jakobson et al., 1991), we focus our analysis on the maximum grip aperture (MGA). The MGA, which occurs approximately two-thirds into the reaching kinematic trajectory, is an established measure of sensitivity to object size in visually guided grasping experiments. The MGA is reached before the hand has any contact with the target object, and therefore, it is not 'contaminated' by the physical interaction with the object itself.

To quantify visuo-perceptual representations, we asked participants to manually estimate the size of the Efron blocks using their thumb and index finger. This task provides a continuous perceptual measure that is directly comparable to the grip calibration measure (Haffenden and Goodale, 1998), and it has been used widely and successfully under different tasks and conditions (Freud et al., 2016a; Ganel and Goodale, 2003; Goodale et al., 1991; Haffenden and Goodale, 1998; Westwood et al., 2002). Past research has confirmed that the manual estimation

task is comparable to other perceptual estimation methods and yields similar results (Hartle and Wilcox, 2016, but see Franz, 2003 for a different view). Adopting the manual estimation task here has the advantage of being closely matched with the grasping task in terms of motor control (i.e., move the hand from the initiation point, scale the fingers to the size of the object), but still mainly recruits perceptual (rather than visuo-motor) mechanisms. Thus, the elaborated motor demands of the manual estimation task allowed us to validate that any deficit observed for the grasping task in patient TC could not be attributed to deficits in motor control per-se.

## 2. Methods

### 2.1. Participants

#### 2.1.1. Patient TC

TC is a right-handed female who was 16 years old when this testing took place. TC reached all normal developmental milestones till the age of 6. The onset of epilepsy was at the age of 7 and she was diagnosed with perinatal stroke with medically intractable focal epilepsy and multifocal encephalomalacia consistent with remote ischemic injury (Fig. 1A – pre-surgical scan, 13 years old). She underwent a left parieto-occipital lobectomy at the age of 13 years (Liu et al., 2019) (Fig. 1B–C).

We delineated the extent of the resected region using a T1 MRI scan (resolution - 1 mm<sup>3</sup>, Liu et al., 2019) obtained after the surgery and a detailed anatomical atlas (Mai et al., 2016). Close scrutiny of the anatomical scans revealed that most left occipital structures were removed in the course of the surgery, including the posterior calcarine sulcus and Occipital gyri. Additionally, regions of the inferior temporal lobe (ventral pathway) such as the Fusiform and Lingual gyri and Superior Temporal Sulcus (STS) are atrophied when compared against the homologue right hemisphere STS. The resection also includes regions adjacent to the approximate location of area MT that projects to the parietal cortex, the parieto-occipital junction and posterior parietal cortex (i.e., Angular gyrus, posterior IPS) (i.e., posterior dorsal pathway). The more anterior portions of the intraparietal sulcus, known to be involved in visuo-motor computations (Culham et al., 2003; Freud et al., 2018), are preserved.

Neuropsychological assessments were conducted shortly following the surgery (age 13 years) and were administered in English (See Table 1). However, as TC is not a native English speaker (and was not fluent in English at that time), these assessments likely underestimate her abilities. We also add the behavioral results from Liu et al. (2019) that were administered several months after the surgery.

#### 2.1.2. Control participants

We recruited a control group of 14 typically developing participants (10 female, average age 18.4 ± 1.6 years, all right-handed). Control participants were tested using the same experimental setup (see Apparatus and Stimuli for details) at York University, Toronto. Participants older than 18 years of age provided informed consent to the experimental protocol approved by the York University Human Participants Review Committee. Minor participants provided assent and their parents provided informed consent. Participants received course credit or \$15 as compensation for their participation.

### 2.2. Data availability

Raw data as well as the analysis code are distributed under the terms of the Creative Commons Attribution License, which permits unrestricted use and redistribution provided that the original author and source are credited. [https://osf.io/c4qky/?view\\_only=91dcd53067284a298ee7b9a056532f06](https://osf.io/c4qky/?view_only=91dcd53067284a298ee7b9a056532f06).



**Table 1**  
Patient TC's neuropsychological evaluation test performance after the surgery.

Cognitive Function	Test	Academic skills/ performance
Vision (neuropsychological assessment)	Visual Field Testing	Right superior quadrantanopsia
	Visual Spatial Index	3rd percentile
	Visuoperception	1st percentile
	Judgement of Lines and Angles	
Vision (Liu et al., 2019)	Visual Memory	1st – 2nd percentile
	Glass Pattern	Normal range (controls = 39.4 ± 7.74, TC = 45)
	Recognition Threshold	Normal range (controls = 94.86 ± 3.08%, TC = 89%)
	Object Matching Score	Normal range (controls = 88.22 ± 11.55%, TC = 83.3%)
	Face Perception	Normal range (controls = 74.04 ± 3.53, TC = 77.27)
Visuomotor Skills	Contour Integration Threshold	Normal range (controls = 74.04 ± 3.53, TC = 77.27)
	Graphomotor Cognitive Flexibility	<1st percentile
	Speeded Graphomotor Tasks	<2nd percentile
	Fine Motor Skills	<1st percentile
	Visuomotor Integration	1st percentile
Intelligence and higher cognitive abilities	WIAT-III: Reading	1st grade <sup>a</sup>
	WIAT-III: Spelling	2nd grade <sup>a</sup>
	Peabody Picture Vocabulary Test	1st percentile <sup>a</sup>
	Working Memory and Speed	1st percentile
	Single Word Receptive Language	1st percentile
	Fluid Reasoning Index	3rd percentile
	Verbal Learning	1st – 5th percentile
	Attention and Executive Functioning	1st – 2nd percentile
	Planning and Problem Solving	2nd percentile
	Hearing	Hearing

WIAT-III, Wechsler Individual Achievement Test.

<sup>a</sup> Could not be reliably obtained due to language barrier.

### 2.3. Apparatus and Stimuli

Participants sat in front of a small table on which the target objects were presented. The target objects were a set of four Efron blocks (1969) that all had the same surface area, texture, and color, but varied in width and length. The width of the blocks ranged from 20 to 35 mm in gaps of 5 mm and lengths were adjusted accordingly (see Fig. 2A). Grasping movements and manual estimations were recorded using an Optitrack system (Natural Point DBA OptiTrack, USA). The system included four Prime 13 W cameras and three active infrared-light emitting diodes attached to the participant's hand in such a way that permitted complete freedom of movement of the hand and fingers (Fig. 2B). The system tracked the 3D trajectory of the participants' index, thumb and wrist movement using a 100 Hz sampling rate and the resultant data permit the calculation of the aperture between the fingers at any given time point.

### 2.4. Procedure

Participants completed two tasks, a grasping (Fig. 2C) and a manual estimation task (Fig. 2D). In each task, on every trial, participants started with their thumb and index finger grasping a permanently stationary block placed immediately in front of them. This was referred to as the "home" position. On each trial, one of the four target objects was placed in front of the participant with the width parallel to the left-right orientation of participant, within arm's reach (approximately 40 cm). In the grasping task, the participants were required to reach for the

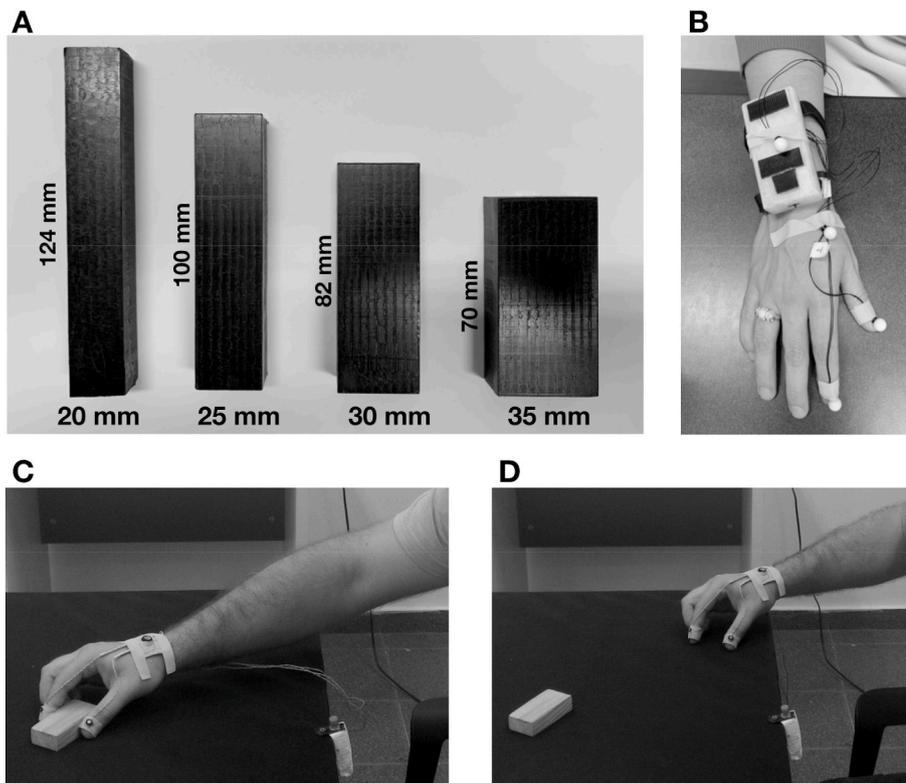
target object with the thumb and index finger across its width (thumb more proximal to the viewer and index finger more distal) and to lift it off the table (approximately 15 cm) before setting it down and then returning to the "home" position. In the manual estimation task, participants were required to indicate the perceived width of the object by extending their thumb and index finger at a height of approximately 15 cm from the table surface to estimate the corresponding width. They were instructed to hold the finger posture for roughly 2 s before returning to the "home" position. Each task was completed separately with each hand, resulting in four experimental blocks. In each block, each of the four target objects was presented 15 times in a randomized order resulting in a total of 60 trials per block. All participants completed the experiment in the following order: grasping using the right hand, manual estimation using the right hand, grasping using the left hand, manual estimation using the left hand to mirror the same order as used for TC.

### 2.5. Data analysis

For each trial, the 3D trajectory of the index finger and thumb was analyzed using in-house code written in Python. The starting point of the grasping movement was defined as the frame following five consecutive frames that had a velocity greater than 10 mm/s. The endpoint of the grasping movement was defined as the point during three consecutive frames in which the change in grasping aperture (i.e., the distance between the thumb and the index finger) relative to the previous frame was smaller than 0.2 mm. An additional condition was that the Z (superior-inferior) location of the fingers was smaller than 80 mm, which indicated that the fingers were positioned along the same plane as the target object. The Maximum Grip Aperture (MGA) was calculated for each trial as the frame that reached the maximum distance between the index finger and the thumb following the movement onset and prior to the end of the movement. For the estimation task, the aperture between the thumb and index finger that was held constant over 10 consecutive frames was taken to be the perceived width of the object (Freud et al., 2016a). All trials were visually inspected, and the analysis was manually refined for a small number of trials in which the algorithm did not accurately detect the end point of the movement.

In addition to comparing the MGA to the controls, we included other dependent measures, as well. The JNDs were measured by analyzing the standard deviation in the MGA for each object in each task (Freud et al., 2016a; Ganel et al., 2008). The JND measures the minimum detectable increment in stimulus magnitude and therefore reflects the sensitivity, which is the size resolution in this case, of the task of interest (Marks and Algom, 1998). The deviation from the ideal slope was calculated as followed. First, we calculated the linear slope between the hand aperture and object width for each pair of objects (i.e., 20 mm–25 mm, 25 mm–30 mm and 30 mm–35 mm). We then measured the absolute deviation from the slope of 1 that indicates an ideal scaling of the hand aperture to object width. Finally, we averaged across the different comparisons. Smaller values (closer to 0) reflect smaller deviation from the ideal slope and, accordingly, better perceptual or visuomotor resolution. Note that a simple slope analysis (across all four objects) was not employed as it gives more weight to the grasping aperture directed to the largest and smallest objects.

Finally, we also employed the deviation from the ideal slope analysis across the movement trajectory to permit a description of shape sensitivity that does not rely solely on the MGA. Similar to previous studies (Ganel et al., 2012; Freud et al., 2016a; Heath et al., 2012), we sampled the grip aperture at 11 normalized time points from movement initiation (defined as 0%) to the final grasping of the object (defined as 100%) in 10% steps, and the deviation from the ideal slope was calculated for each of these 11-time points. To compare statistically between the data from TC and the controls (considering the number of comparisons), we first averaged the deviation from the ideal slope in each third of the movement (i.e., 10%–30%, 40%–60%, 70%–90%), and then applied the



**Fig. 2.** (A) Experimental stimuli - target objects used in the experimental set-up were a set of four Efron blocks that all had the same surface area, texture, and color, but varied in width and length, with their width indicated below the block. Using their index finger and thumb, in separate blocks of trials, participants were asked either to grasp the blocks or manually estimate the width of the blocks. (B) Location of diodes - three active infra-red-light emitting diodes were attached to the participant's hand during the experiment for tracking the grasping and estimation trajectories. (C) Grasping trial - example of a grasping trial, in which the participant reached and grasped one of the target objects (D) Manual estimation trial - example of a manual estimation trial, in which the participant indicated the width of the target objects with their thumb and index finger.

single-case statistical analysis (Crawford and Garthwaite, 2002). Last, to account for the problem of multiple comparisons, we applied a Bonferroni correction.

## 2.6. Statistical analysis

We applied a modified single-subject *t*-test to examine whether TC's scores across the different variables deviated from the performance of the control groups across the different conditions (hand x task) (see above) (Crawford and Garthwaite, 2002). Finally, we also used the Revised Standardized Difference Test (RSDT) (Crawford and Garthwaite, 2005) to measure whether the difference between TC's standardized score on two conditions (e.g., grasping with the contralesional right hand and grasping with the left ipsilesional hand) was significantly different from the difference between the two hands measured for the control participants.

## 3. Results

To examine whether TC was impaired in her perceptual and/or grasping abilities, we examined her performance in the two tasks, each completed with her ipsilesional left and contralesional right hands. We tested both of TC's hands to observe the effect of the unilateral lesion on each hand and with the prediction that the contralesional hand would be more affected.

### 3.1. Average aperture

We analyzed the final aperture across the different object sizes for the manual estimation task and the MGAs for the grasping task. For the manual estimation task, TC exhibited final apertures that fell within the normal range (Fig. 3B, left), as verified by single-case statistical comparisons [contralesional (right) hand:  $t_{(13)} = 1.63$ ,  $p > 0.1$ ,  $Z_{-CC} = 1.68$  (95% CI 0.84 to 2.05); ipsilesional (left) hand:  $t_{(13)} < 1$ ,  $Z_{-CC} = 0.41$  (95% CI = -0.14 to 0.95)]. However, for the grasping task, her maximum grip

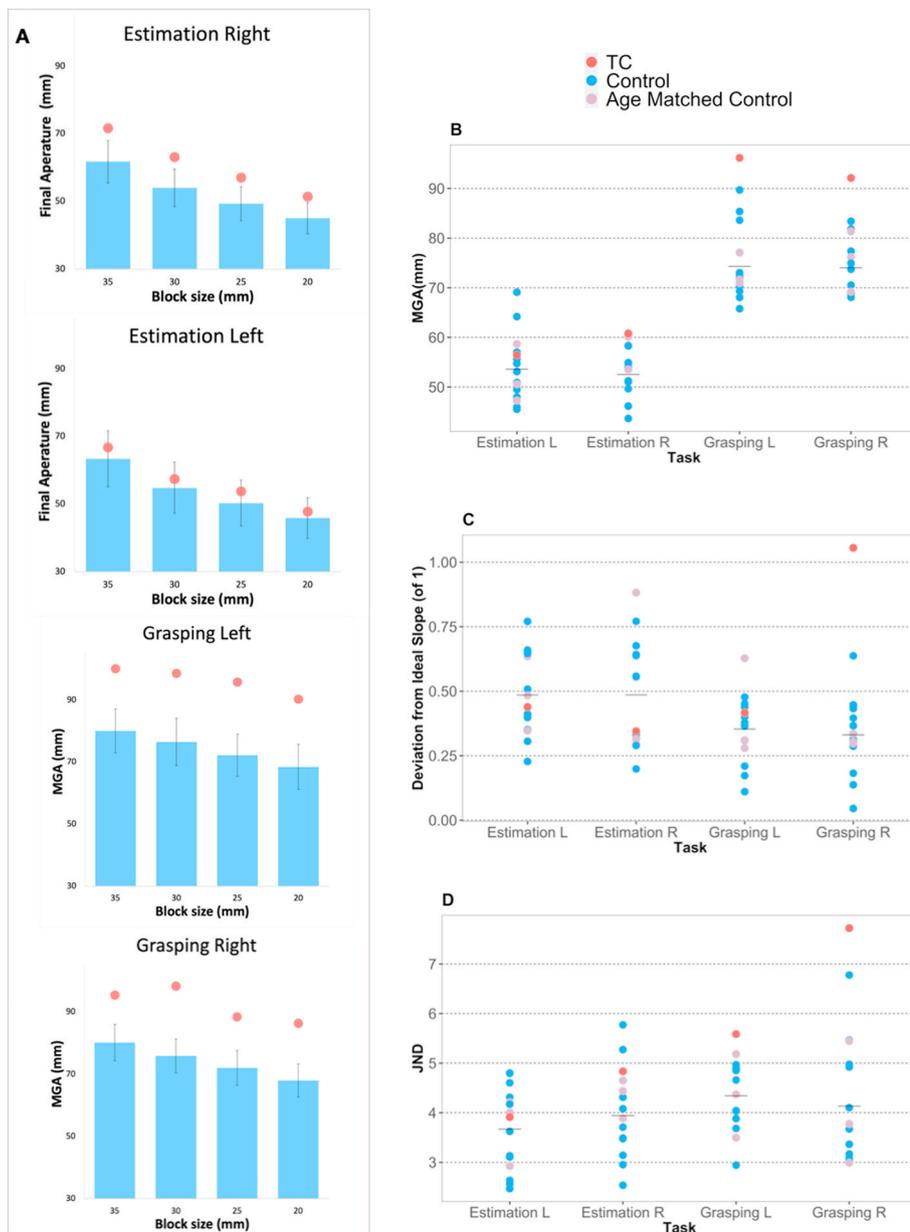
apertures for both her contralesional and ipsilesional hands fell outside of the normal range (Fig. 3B, right, grasping ipsilesional left: 92.11 mm, grasping contralesional right hand: 96.16 mm): her MGA was, on average, ~20 mm larger than that of control participants, and, single-case statistical comparisons confirmed this exaggerated MGA for both the contralesional (right) [ $t_{(13)} = 3.24$ ,  $p < 0.05$ ,  $Z_{-CC} = -2.099$  (95% CI = -1.97 to 4.73)] and ipsilesional (left) [ $t_{(13)} = 2.816$ ,  $p < 0.05$ ,  $Z_{-CC} = 2.91$  (95% CI = -1.68 to 4.12)] hands. This finding is consistent with previous reports from optic ataxia patients that reported disproportionately large aperture as indicative of a visuomotor deficit (Jakobson et al., 1991).

We used the RSDT (Crawford and Garthwaite, 2005) to determine whether the difference between TC's grasping performance was different between the two hands and observed no difference between her ipsilesional left and contralesional right hand [ $t_{(13)} < 1$ ,  $Z_{-DCC} = -0.238$  (95% CI = -1.780 to -1.266)].

Notably, the exaggerated grasping apertures were evident across all object sizes (Fig. 3B) and were accompanied by a reduced sensitivity to object size (see next section for a detailed analysis). TC's apertures displayed a very clear separation between the two large target objects (the 35 and 30 mm blocks) and the two smaller target objects (the 25 and 20 mm blocks), but then a reduced separation within each pair of objects.

### 3.2. Slope analysis

Next, to characterize sensitivity to object shape, we computed the linear relationship between object width and hand aperture, where a slope value of 1 indicates an ideal fit between object width and hand aperture (Fig. 3C). We report each individual's deviation from a slope of 1, with a higher deviation reflecting a poorer size resolution (See Methods for details). In accordance with previous research (Liu et al., 2019), for the perceptual task, we found comparable sensitivity to that of controls regardless of hand used by TC [contralesional right hand  $t_{(13)} < 1$ ,  $Z_{-CC} = -0.658$  (95% CI = -1.228 to -0.067); ipsilesional left hand [ $t_{(13)} < 1$ ,  $Z_{-CC} = -0.283$  (95% CI = -0.812 to 0.257)]. In contrast, for



**Fig. 3. Results from grasping and manual estimation tasks.**

Across all figures, TC's value is represented as the dark red dot. Each blue (control) or purple (age-matched control) dot represents the value of a single participant's data. The mean value of the control group is indicated by the horizontal black line. R stands for right hand and L stands for left hand. (A) **MGA plots by target object size.** TC's value is represented in red and the average of all control data is represented in blue with standard error bars. The average results of the MGA or final aperture in mm are plotted for each target object size ranging from the largest (35 mm) to the smallest (20 mm) block size. TC exhibited final apertures that fell within the normal range for each of the target object sizes when completing the manual estimation task. TC exhibited exaggerated maximum grip apertures for each of the target objects. (B) **The average results of the MGA (grasping) or final aperture (estimation) in mm for each task.** TC exhibited normal final apertures for the manual estimation task but showed exaggerated maximum grip apertures for the grasping task. (C) **The reported deviation from an ideal slope of 1 between the true object size and hand aperture for all tasks.** Higher values indicate reduced sensitivity to object size. TC showed a higher deviation from a slope of 1 than the controls just for the grasping task and only in her contralesional (right) hand. (D) **The JND values representing the average within-subject variability to each Efron block.** Higher values represent reduced sensitivity to object size. TC was found to have impaired resolution in the grasping task (contralesional hand), but not in the manual estimation task. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

the grasping task, TC's sensitivity to object size was significantly impaired but only with her contralesional (right) hand [ $t_{(13)} = 4.775$ ,  $p < 0.001$ ,  $Z_{-CC} = 4.943$  (95% CI = 2.989 to 6.884)]. The results from TC's ipsilesional hand fell within the normal range [ $t_{(13)} < 1$ ,  $Z_{-CC} = 0.508$  (95% CI = -0.059 to 1.057)].

Next, we employed the RSDT (Crawford and Garthwaite, 2005) to validate statistically the dissociation between grasping and estimation performance for her contralesional hand [ $t_{(13)} = 3.382$ ,  $p < 0.005$ ,  $Z_{-CC} = 3.636$  (95% CI = 2.106 to 5.428)]. In contrast, for the ipsilesional hand, there was no difference between the two tasks  $t_{(13)} < 1$ , one-tailed,  $Z_{-CC} = 0.440$  (95% CI = -0.110 to 0.994)]. Finally, we found a significant difference between TC's performance for grasping with greater deviation for her contralesional compared to her ipsilesional hand [ $t_{(13)} = 2.872$ ,  $p < 0.05$ ,  $Z_{-CC} = 3.120$  (95% CI = 1.614 to 4.940)], providing further within-subject evidence for a dissociation between TC's performance for grasping with her contralesional compared to her ipsilesional hand.

### 3.3. JNDs

The average within-subject variability of responses to each Efron block was used as an additional indicator of sensitivity to the objects' width (Freud et al., 2016a; Ganel et al., 2008). Similar to the above analysis, smaller values reflect finer resolution for object size.

Consistent with the slope analysis results (see above), analysis of the JND values indicated that TC's performance for the manual estimation tasks was comparable to the control group mean, confirming that she exhibited normal sensitivity to object shape in perceptual estimation when using either her contralesional [ $t_{(13)} < 1$ ,  $Z_{-CC} = -0.247$  (-0.775 to 0.290)] or ipsilesional hand [ $t_{(13)} < 1$ ,  $Z_{-CC} = 0.273$  (-0.266 to 0.802)] (Fig. 3D, left). Whereas TC's variability was greater than that of controls for the grasping task (Fig. 3D, right) for her contralesional hand [ $t_{(13)} = 2.923$ ,  $p < 0.05$ ,  $Z_{-CC} = -2.099$  (-3.041 to -1.133)], TC's JND for her ipsilesional hand was numerically large, but the difference from the control group was not significant [ $t_{(13)} = 1.7891$ ,  $p = 0.09$ ,  $Z_{-CC} = 1.851$  (0.961-2.715)].

The RSDT test confirmed the existence of a dissociation between

grasping and estimation performance with the contralesional hand [ $t_{(13)} = 2.272, p < 0.05, Z_{\text{-DCC}} = 2.472$  (95% CI = 1.346 to 3.785)]. In contrast, no significant difference between the perceptual and action tasks was observed for the ipsilesional hand [ $t_{(13)} = 1.40, p > 0.05, Z_{\text{-DCC}} = -1.121$  (95% CI = -1.946 to 0.376)]. Finally, the RSDT (Crawford and Garthwaite, 2005) did not provide evidence for a dissociation between TC's performance for grasping with her contralesional right hand compared to her ipsilesional left hand [ $t_{(13)} < 1, Z_{\text{-DCC}} = 0.861$  (95% CI = -0.225 to 2.061)].

### 3.4. Movement trajectory

Next, we analyzed the movement trajectories of each hand for the grasping task. Sensitivity to object size is usually observed early in the movement (e.g., Freud et al., 2016a), and can serve as an additional

indicator of the integrity of visuomotor representations. Note that for the estimation task, similar to previous studies (e.g., Freud et al., 2016a; Ganel et al., 2008; Goodale et al., 1991), only the final aperture was used to analyze sensitivity to object size and therefore the movement trajectory analysis was not employed.

Fig. 4A–D illustrate TC's exaggerated grasping apertures observed for both hands, as well as the reduced sensitivity to object size observed for the contralesional right hand. Notably, this reduced sensitivity was observed not only in the MGA but also in earlier stages of the movement trajectory. To quantify these modulations, we analyzed the size sensitivity at different time points along the grasping trajectory by normalizing the movement trajectory and then calculating the deviation from the ideal slope for each timepoint. We then averaged the slopes in each third of the movement (to reduce the number of statistical comparisons—early: 10%–30%, mid: 40%–60%, late: 70%–90%), and applied the

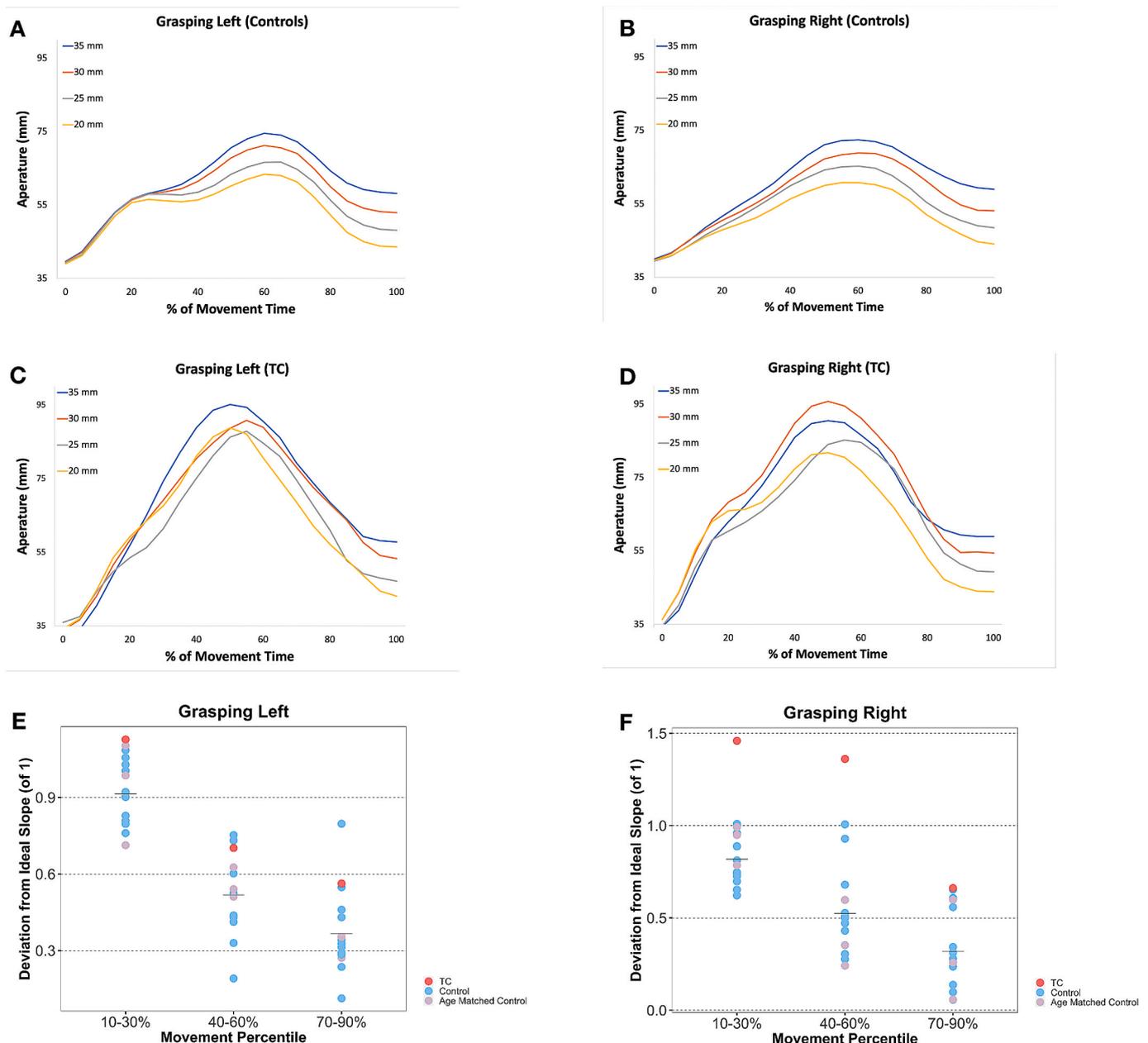


Fig. 4. Grip apertures along the movement trajectory for each target block size and hand. (A, B) Grip aperture was averaged across all control participants for the left hand and for the right hand. (C, D) Grip apertures of TC for her left and right hand. The graphs demonstrate that TC does not scale her hand appropriately when grasping with her right hand. (E, F) TC's slope analysis results at three intervals along her movement trajectory for her right and left hand. Lower values reflect greater sensitivity.

Crawford single-case test to compare between TC’s performance and that of the controls (Crawford and Garthwaite, 2002) (see Table 2).

We found comparable size sensitivity between TC and controls when TC grasped with her ipsilesional (left) hand. This was evident across all segments of movements (Table 2). In contrast, for the contralesional (right) hand, we found reduced size sensitivity in the early and mid-segments of the grasp (Table 2), reflecting TC’s visuomotor deficits. For the last portion of the movement (70–90%), no differences were observed between TC and controls, suggesting that she may still be able to utilize visual feedback to better refine her aperture near the termination of the grasp.

3.5. Results summary

As shown in Table 3 below, TC demonstrates normal perceptual estimation abilities irrespective of the hand used for response. On the grasping task, for trials with the contralesional (right) hand, TC’s performance is not normal on any of the four dependent measures. For trials with the ipsilesional (left) hand, performance is largely, although not entirely intact: her average aperture deviates from that of the controls and her JND scores are marginal. Nevertheless, the difference in grasping between the right and left hands is measurable and marked.

4. Discussion

The current study was designed to elucidate possible dissociable effects of unilateral cortical lesion of the dorsal and ventral pathways sustained during childhood on visuomotor and perceptual behaviors. We examined shape sensitivity in TC, an adolescent who has a left lateralized cortical resection that affects both visual pathways. Notwithstanding the ventral resection, TC displayed preserved perceptual sensitivity to object shape even when she used her right, contralesional hand. In contrast, her visuomotor sensitivity was profoundly impaired when she used her right, contralesional hand and, to a lesser extent, when she used her left, ipsilesional hand. This deficit was observed across different dependent measures including aperture size, variability of the grasping aperture and sensitivity to object size (see Table 3 for a summary of TC’s performance).

The results from the estimation tasks are consistent with previous investigations that documented retained perceptual functions in pediatric patients with cortical resections even when the resection compromised a large portion of the ventral visual pathway (Liu et al., 2019). The novel findings from the current study pertain to the deficit observed for visuomotor behaviors presumably mediated by the lesion to the dorsal pathway which emerged during childhood. In particular, the visuomotor deficit observed for TC resembles deficits found in adult patients with acute lesions to the dorsal pathway (Perenin and Vighetto, 1988). Thus, the current study provides evidence for dissociable post-injury profiles of behaviors associated with the two visual pathways. These dissociable recovery profiles are assumed to reflect the differential developmental trajectories of the two cortical pathways (Atkinson, 2017; Smith et al., 2017; Vinci-Booher et al., 2021).

The possible reasons for the dissociable effects of the cortical resection on visuomotor and perceptual behaviors are complicated, primarily because of the complex developmental profile of the patient. TC suffered

**Table 2**  
Summary of TC’s slope analysis results at various points along her movement trajectory.

Hand	Movement Segment		
	Early (10–30%)	Mid (40–60%)	Late (70–90%)
Left Hand	t = 1.61 p > 0.12	t = 1.04 p > 0.31	t = 1.17 p > 0.26
Right Hand	t = 4.69 p < 0.00042*	t = 3.61 p < 0.003*	t = 1.75 p > 0.1

**Table 3**  
Summary of TC’s performance compared to controls on behavioral tasks.

Measure	Task (Hand)			
	Grasp		Estimation	
	LH	RH	LH	RH
Average aperture	×	×	✓	✓
Slope	✓	×	✓	✓
Just Noticeable Difference	*	×	✓	✓
Movement trajectory	✓	×	✓	✓

Note: Checks (✓) indicate that TC’s performance was comparable to that of the controls for that measure. An impairment of each hand (left/right) for each task (grasp/estimate) is indicated by a cross (×). \* The JND for left hand grasping was higher in TC compared with controls, but this difference did not reach statistical significance.

from three related neurological incidents. First, she was diagnosed with perinatal stroke. Second, she suffered from medically intractable epilepsy with an onset of seizures at the age of seven; it’s likely that the epilepsy is related to the stroke but the temporal interval between the two events is rather long. Third, she had a cortical resection at the age of 13 years although her presurgical anatomical profile was not normal either. As such there is no concrete way of knowing to what degree each of these incidents resulted in her performance in the current study which was conducted three years after the cortical resection surgery. Because the presurgical scan (Fig. 1A) showed extensive anatomical alterations that preceded the cortical resection surgery, it is reasonable to assume that the observed visuomotor deficits emerged prior to the surgery. The underlying basis of her deficit might, therefore, be attributed to the perinatal stroke and/or to the early-onset epilepsy although no evidence is available from those time periods, and we also know that the surgery extended the existing pre-surgical lesion so that might also be a relevant factor.

If TC’s visuomotor impairment truly resulted from her early-onset epilepsy and/or her perinatal stroke, the dissociation between perception and action might be attributable to the differential susceptibility of the two visual pathways to developmental abnormalities with the ventral, but not the dorsal, cortex evincing some resilience or imperviousness to early insult. This hypothesis is compatible with studies that demonstrated that dorsal pathway functions, such as motion processing and visuomotor control, are more likely to be affected by neurodevelopmental (e.g., developmental dyslexia, Williams Syndrome) and ophthalmological (e.g., early cataract) disorders (Atkinson et al., 1997; Atkinson and Braddick, 2005; Atkinson, 2017) than is the case for ventral pathway functions. This interpretation is also consistent with recent studies in mice reporting that the ventral pathway shows greater plasticity over the course of development compared with the dorsal pathway (Smith et al., 2017).

The development of the dorsal pathway relies, at least in part, on a transient pathway between the pulvinar and area MT (Bridge et al., 2016). Recent research in non-human primates demonstrated that lesions to this pathway (either to the rostral lateral medial pulvinar nuclei or to area MT) sustained early in-life lead to alterations in the development of dorsal pathway structures and to deficits in visuomotor behaviors (Kwan et al., 2021; Mundingano et al., 2018). It is worth noting that the proximal location of area MT was partially resected in TC. Given that TC suffered from an early stroke, it is possible that this region was comprised early in life and that the observed visuomotor deficits specifically reflect the absence of necessary input from this region to parietal structures. This question might be partially addressed in future studies with patient TC that will utilize fine-grained neuroimaging tools to characterize the functional and connectivity properties of area MT in the two hemispheres.

An alternative explanation for the dissociable effect on perception and action might be that TC’s dorsal lesion was more extensive than her

ventral lesion, and included more critical regions for visuomotor control. Note, however, that careful delineation of the lesion does not support this account (Fig. 1). In particular, multiple structures along both pathways were affected. Notably, for the ventral pathway, the lateral occipital cortex, which is known to be critical for shape perception (Grill-Spector et al., 2001), was resected, while the anterior portion of the left IPS, which plays a critical role in visuomotor control (e.g., Culham et al., 2003; Freud et al., 2018) was not resected. It is unlikely then that the dissociation is simply a result of greater dorsal than ventral cortex damage.

Another plausible explanation is that TC's difficulty in grasping is not a function of dysfunctional visuomotor computations per se but that her impaired performance reflects a downstream motor deficit. However, the anatomical and behavioral data do not support this notion. In particular, the anatomical scans do not show any lesion to the motor cortex which is far more anterior than the edge of the parietal resection. Moreover, TC's performance for the manual estimation was normal even though this task requires the execution of a motor plan and this execution is roughly similar to that engaged in the grasping task.

Finally, another interesting question is whether limb apraxia can account for TC's performance. Limb apraxia is often characterized by the inability to use common tools or to imitate simple movements (Ambron et al., 2015). We did not formally examine tool use in TC, but she was able to use a pen to sign her consent form and she did not report any issues with regards to tool use. In terms of imitating simple movements – TC was able to imitate the manual estimation movement, and in fact her performance was similar to controls, challenging the notion that she had problems with downstream motor control. In contrast, optic ataxia is characterized by a deficit in reaching and grasping movements, which better describes TC's behavior. However, most cases of optic ataxia are mostly evident for grasping/reaching movements directed to objects that are presented in the peripheral visual field, while, for TC, we found the deficit in grasping stimuli in central vision. Thus, TC deficit's can not be clearly categorized as limb apraxia or optic ataxia, but her behavior is more consistent with the clinical description of optic ataxia.

#### 4.1. Bilateral deficit after a unilateral lesion

An additional unique property of the current study is the characterization of visuomotor behaviors across the two hands. The comprehensive testing approach allowed us to reveal that despite the clear left lateralization of TC's lesion, her visuomotor deficit is also evident when she grasped with her left, ipsilesional hand, albeit to a lesser extent. There are two possible neural mechanisms, which are not mutually exclusive, that might account for the bilateral nature of TC's visuomotor deficit, namely hemispheric specialization within the dorsal pathway or an inter-hemispheric inhibition process.

Hemispheric specialization refers to the dissociable contribution of each hemisphere to different functions. This specialization is not strictly dichotomous, but is reflected on a continuum of functions between the hemispheres (Bradshaw and Nettleton, 1981). For example, in most people, both right- and left-handed, language is more lateralized to the left hemisphere (Knecht et al., 2000; Ojemann, 1991), despite a contribution of the right hemisphere to different aspects of language (Ross and Mesulam, 1979; Vigneau et al., 2011).

The notion of hemispheric specialization has also been demonstrated for the dorsal visual pathway (i.e., parietal cortex) in that there is general consensus that the left hemisphere plays a greater role than the right hemisphere in visuomotor computations even among left handed individuals (Gallivan and Culham, 2015; Gonzalez et al., 2006). Homologue regions in the right hemisphere contribute more to attentional mechanisms (Bowen et al., 1999; Ringman et al., 2004; Becker and Karnath, 2007) and spatial transformations (Gauthier et al., 2002; Harris et al., 2000; Warrington and Taylor, 1973).

This specialization is also supported by neuropsychological investigations. For example, patients with right-hemisphere injuries

displayed a dissociation between action and perception, which is not evident for patients with left-hemisphere lesions (Radoeva et al., 2005). Additionally, greater severity of optic ataxia (Perenin and Vighetto, 1988) has been observed in patients with left hemisphere injuries. In particular, most patients with optic ataxia after a left hemisphere lesion have displayed a hand effect (errors when pointing with their contralesional hand) as well as a contralateral field effect (errors when pointing to stimuli in the contralesional visual hemifield) (Vindras et al., 2016), whereas patients with a right hemisphere lesion showed a milder version of optic ataxia with only a field effect (Perenin and Vighetto, 1988). TC's deficit is consistent with the non-dichotomous specialization of the left hemisphere in visuomotor computations. In particular, despite the unilateral nature of her lesion, her grasping behaviors were altered when she used her right contralesional hand, and, albeit to a lesser extent, when she used her left ipsilesional hand.

A second possible mechanism that could have contributed to this bilateral decrement is inter-hemispheric inhibition of the non-lesioned right parietal cortex. Inter-hemispheric inhibition refers to the process by which one perturbed hemisphere of the brain inhibits the function of the opposite hemisphere (van Meer et al., 2010). This phenomenon was described in a case of visual agnosia after a lesion sustained to the right ventral pathway; despite the unilateral nature of the lesion, reduced visual as well as object-related and -selective responses obtained from fMRI were apparent in homologous locations in the intact left hemisphere, pointing to remote effects or diaschisis from the affected to preserved hemisphere (Konen et al., 2011; Freud and Behrmann, 2020). Importantly, inter-hemispheric inhibition has also been described in the context of motor behaviors (Murase et al., 2004), and this inhibition can be ameliorated using TMS and can contribute to motor training (Williams et al., 2010).

The bilateral nature of TC's deficit is consistent with the inter-hemispheric inhibition account, such that the unilateral left lesion adversely affected activation in the non-lesioned, right parietal cortex. It is not exactly clear why inter-hemispheric inhibition would affect only one pathway and not the other and this warrants further exploration. To test this hypothesis, future studies, with cortical resection patients, might utilize a neuroimaging approach to describe better the visuomotor and perceptual representations across the two hemispheres and their behavioral manifestations, and to evaluate further the cross-hemispheric connectivity patterns.

#### 4.2. Limitations

The current study provides important insights into the effect of a unilateral cortical lesion on visuomotor and visuo-perceptual behaviours in a paediatric/teenage individual. However, several limitations should be noted and addressed in future experiments.

First, as discussed above, the developmental course of the injury is complicated and hinders our ability to reach firm conclusions about the neurological event that led to the observed visuomotor deficit. Second, the current study is based solely on TC's behavioral performance. As such, it is impossible to conclude whether the retained perceptual behaviors rely on the intact right hemisphere, or alternatively on remaining tissue in the left hemisphere. Importantly, however, previous investigations of TC's neural profile using functional MRI confirmed that her affected left hemisphere ventral pathway showed no activation in response to any of the tested visual categories (faces, objects, words, and scenes), while normal sensitivity was observed along the right ventral pathway (Liu et al., 2019). Hence, it is reasonable to assume that the retained perceptual abilities observed in this patient were mediated by computations carried out by the intact right occipitotemporal cortex.

Finally, we have utilized two well-established tasks (manual estimation and grasping) to estimate the perception versus action dissociation in TC. These measurements have been used extensively in the past, but it is plausible that other aspects of TC's visuomotor behavior are preserved, while some perceptual abilities may even be impaired (but

see Liu et al., 2019 that demonstrated the TC perceptual abilities are preserved across a range of tasks). Thus, we cannot definitively infer from our results that the perception-action dissociation would be evident across all perceptual and visuomotor abilities. Future research and more diverse testing can further evaluate this point.

## 5. Conclusion

The goal of the current study was to explore the effect of a unilateral lesion affecting both visual pathways on perception and action. We found that perceptual behaviours, presumably mediated by the ventral pathway, were retained, while visuomotor behaviours, presumably mediated by the dorsal pathway, were selectively impaired. These results provide novel evidence for fundamental differences in the reorganization profiles of the two visual pathways in children.

## Author contributions

ZA, MB, CP, and EF developed the study concept and contributed to study design. ZA, MB, and EF collected the data. ZA and EF analyzed the data. ZA drafted the first version of the manuscript. MB, CP and EF edited the manuscript.

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