THE EMERGENCE OF THE FUNCTIONAL DISSOCIATION BETWEEN ACTION AND PERCEPTION

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Abstract

Humans rely on their visual system to navigate and interact with the world, utilizing two functionally distinct cortical pathways: the ventral pathway, responsible for visual perception, and the dorsal pathway, which supports visuomotor actions. While the functional dissociation between these behaviours has been extensively studied in adults, its developmental trajectory and susceptibility to neurodevelopmental conditions is not as well-understood. This dissertation investigates the dissociation between perception and action in pediatric and adult populations with atypical neurodevelopment, focusing on three experimental studies. The first study examines a pediatric patient, TC, who underwent a unilateral cortical resection impacting both the dorsal and ventral pathways. Despite intact perceptual abilities, her visuomotor behaviors were markedly impaired, highlighting differential developmental trajectories of the two pathways and the dissociation between perception and action. The second study investigates children with amblyopia, a developmental visual disorder, and finds a reduced perception-action functional dissociation compared to neurotypical controls. This suggests that atypical visual experience disrupts the functional specialization of the pathways early in life. The final study focuses on adults with Autism Spectrum Disorder (ASD) and reveals reduced perception-action dissociation in two different contextual conditions. Together, these studies provide a detailed examination of how neurodevelopmental conditions influence the emergence of perceptual behaviors, visuomotor behaviors and the dissociation between these functions. These investigations confirm the sensitivity of visuomotor behaviours to atypical development and show that the dissociation between perceptual and visuomotor functions is disrupted under a range of neurodevelopmental conditions.

Dedication

I dedicate this dissertation to my Papa,
who planted the seed of knowledge in my mind,
and to my Mama, who nurtured it.

Acknowledgments

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CHAPTER 1: INTRODUCTION

Introduction

Humans rely on their visual system to navigate and interact with the world around them. Whether recognizing a face in a crowd or reaching out to grab a cup of coffee, the brain seamlessly processes visual information to serve different goals. While some visual processes focus on understanding and interpreting the environment, others are dedicated to guiding precise actions. This multifaceted ability of the visual system is fundamental to daily life**.**

One of the most important conceptualizations regarding the human visual system is the idea of the division of labour between the dorsal and ventral visual pathways, known as the Two-Visual Pathway Hypothesis. This conceptualization postulates that there are two functionally distinct visual processing pathways, the ventral (mainly responsible for visuoperceptual behaviours) and the dorsal pathway (mainly responsible for visuomotor behaviours) (Goodale & Milner, 1992; Mishkin & Ungerleider, 1982). The functional separation between the two pathways is linked to their anatomical distinction, as each pathway is localized to different cortical areas. The dorsal pathway begins from the primary visual cortex (V1) and stretches from the occipital lobe into the parietal lobe. The ventral pathway also begins from V1 and extends to the temporal lobe. This distinction between the dorsal (i.e., the parietal lobe) and the ventral pathway (i.e., the temporal lobe) has been the cornerstone for understanding the principles of visual processing.

This distinction in the human visual system builds upon earlier work by researchers such as Schneider (1969), whose studies using selective lesioning in rodents first highlighted the presence of functionally distinct visual systems. His findings revealed that impairments in visually guided behaviors, such as orienting towards or locating visual stimuli, were closely linked to damage in the superior colliculus, which is part of the subcortical pathway. Conversely, impairments in object recognition tasks were more strongly associated with cortical lesions, particularly in the geniculostriate pathway. These insights not only elucidated the hierarchical organization of visual processing but also paved the way for Ungerleider and Mishkin's (1982) identification of two cortical visual pathways.

Ungerleider and Mishkin (1982) made significant strides in characterizing these pathways by proposing a “where” versus “what” distinction. Instead of focusing on sub-cortical and cortical pathways, they focused on two cortical pathways originating from V1. Their study investigated the roles of the dorsal and ventral pathways in non-human primates. They employed lesion studies as their primary methodology, in which specific areas of the monkey brain were surgically lesioned to observe the resulting behavioral effects. Through a series of experiments, they demonstrated that lesions in the ventral pathway impaired the ability to recognize objects (visual object discrimination tasks), while lesions in the dorsal pathway disrupted spatial processing abilities, such as locating objects or navigating spatial environments (landmark discrimination tasks). Their work, rooted in these anatomical and behavioral studies, mapped the dorsal and ventral pathways cortically, laying the groundwork for subsequent research into their distinct functional roles. The distinction they proposed (the “what” versus “where” pathways) was a transformative idea that shaped the understanding of visual processing and its division of labor within different cortical systems.

Building on this work, Milner and Goodale (1992) redefined the functional distinction between these two pathways. The key innovation in Milner and Goodale’s model was their emphasis on output requirements (that is function) rather than object qualities. They disagreed that the two pathways simply evolved to process separate types of visual information for perception. They demonstrated that the dorsal pathway is not simply concerned with “where” objects are located in space but plays a critical role in transforming visual inputs into motor commands to guide actions in real time. Milner and Goodale’s work was groundbreaking because it provided a functional account of the visual pathways that went beyond spatial distinctions. By emphasizing the temporal dynamics and real-world utility of visual information, they reframed the dorsal pathway as a critical mediator of action, highlighting its role in moment-to-moment visual guidance. This conceptualization remains a cornerstone of visual neuroscience today, inspiring a wide array of research into perception, action, and their dissociation.

The idea of the differential functional roles of the two pathways was supported by neuropsychological investigations of adults 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 (Himmelbach et al., 2012; Rossit et al., 2018; Schenk, 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 & Perenin, 2005; but see Medina et al., 2020, who documented mild perceptual deficits in these patients).

One seminal patient was DF, who exhibited a dissociation between perception and action following extensive damage to the ventrolateral regions of her occipital lobe. This injury resulted in severe visual form agnosia, leaving her unable to identify or describe visual characteristics of objects, such as the orientation of a mailbox slot (Goodale et al., 1991; Milner et al., 1991). Remarkably, despite these perceptual deficits, DF could still use visual information to guide her actions accurately, for example, placing a letter into the slot. Neuroimaging studies confirmed that her bilateral lesions corresponded to the lateral occipital complex, a region critical for object recognition in healthy individuals (James et al., 2003). These neuropsychological findings, such as those observed in DF, demonstrated a clear dissociation between vision for action (dorsal pathway) and vision for perception (ventral pathway).

The dissociation between action and perception can also be observed in neurotypical individuals through studies involving visuomotor behaviors and perceptual judgments. Notably, visual illusions serve as effective tools for examining this phenomenon, as they manipulate perceptual judgments while minimally influencing visuomotor actions. For instance, research on the Ponzo illusion has consistently demonstrated that while perceptual estimations are significantly distorted, grasping trajectories remain largely unaffected, emphasizing the distinct processing roles of the dorsal (action-oriented) and ventral (perception-oriented) visual pathways (Freud et al., 2021; Ganel, Tanzer, et al., 2008; Gonzalez et al., 2008; Whitwell et al., 2016). These findings, although sometimes debated (Aglioti et al., 1995; Franz et al., 2000, 2003; Haffenden et al., 2001), highlight the differential processing roles of the ventral and dorsal pathways.

Neuroimaging and neurophysiological data in humans are generally in agreement with these functional and anatomical distinctions between the two pathways. The lateral occipital complex, a region of the occipitotemporal cortex in the ventral pathway, is active in object recognition (Grill-Spector et al., 2001). In the dorsal pathway, areas centred around the intraparietal sulcus are active during visually guided actions. For instance, the anterior intraparietal (AIP) region has been implicated specifically in grasping (e.g., Gallivan & Culham, 2015; Monaco et al., 2014; Murata et al., 2000)

Over several decades, 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., 2016, 2020; Schenk & McIntosh, 2010). It has been demonstrated that the ventral and dorsal pathways are not entirely independent systems but interact to support complex visuomotor tasks. For instance, evidence from patients with extensive lesions to the ventral pathway suggests that they still generate object representations in the dorsal pathway, and evince perceptual sensitivity to object structural information (Freud, Plaut & Behrmann, 2016). A similar study found evidence that the dorsal pathway contributes uniquely to the perception of a range of visuospatial attributes such as 3D geometric shape, orientation, and size (Freud et al., 2020). Such findings challenge earlier notions of strict segregation and emphasize a graded, interactive functional specialization.

The perception-action dissociation has been a cornerstone of research in adult cognitive neuroscience, outlining distinct pathways responsible for perception and action. However, the developmental trajectory of this dissociation remains poorly understood. Investigating how and when this dissociation emerges during development is essential, as it provides critical insights into the maturation of the two cortical systems, their interactions, and the development of both perceptual and visuomotor functions.

Studies on the perception-action dissociation in children yielded mixed results. For instance, children aged 5–8 exhibit susceptibility to the Ponzo illusion in perceptual tasks but not in grasping tasks, suggesting an early dissociation between perception and action. However, this dissociation becomes less evident when children are presented with more complex objects that require the integration of multiple dimensions (Freud et al., 2019, 2021; Schum et al., 2012). These findings imply that while basic dissociations are observable early in life, task complexity can blur these distinctions during development.

While research on the emergence of the dissociation between the two functions is limited, several behavioural and imaging studies investigated the maturation rate of the two pathways. For example, Kovács et al. (2000) demonstrated that younger children are slower and less precise in tasks mediated by the dorsal pathway, such as motion detection and spatial localization, while tasks presumably processed by the ventral pathway like color and shape discrimination exhibit adult-like performance at much earlier stages. They suggested that the dorsal pathway’s reliance on spatial and temporal integration contributes to its delayed maturation compared to the ventral pathway. Findings such as these highlight distinct developmental timelines for the two visual pathways.

Neuroplasticity can also provide important insights into the developmental trajectory of perception and action systems. Particularly during early life, the brain demonstrates a remarkable capacity for reorganization (Kolb & Gibb, 2011), which significantly influences the dissociation between perception and action. Children with early cortical lesions, such as those caused by perinatal stroke or epilepsy, often retain perceptual abilities, suggesting robust compensatory mechanisms in perceptual systems. In contrast, visuomotor functions remain impaired, emphasising the dorsal pathway’s greater susceptibility to early disruptions. This vulnerability may arise from its reliance on multisensory and motor integration to refine visuomotor coordination, resulting in a more protracted developmental timeline (Liu et al., 2019; Smith et al., 2017).

Neuroimaging studies offer further insights into the differential developmental rates of the two pathways, revealing uneven reorganization of visual pathways following early brain injuries. Functional MRI studies (Ciesielski et al., 2019; Vinci-Booher et al., 2022) show, by comparing ventral pathway-related perceptual abilities and dorsal pathway-mediated visuomotor processes, an earlier maturational course of the dorsal pathway. The idea that the dorsal pathway matures after the ventral pathway is supported by findings from Vinci-Booher et al. (2021), who modeled the development of major white matter pathways within and between the ventral and dorsal pathways. Their findings suggest that the ventral pathway, with its early-maturing pathways, is better equipped to support perception-related functions early in life. Similarly, findings from Ciesielski et al. (2019) reveal that the ventral pathway reaches structural and functional maturity earlier than the dorsal pathway, which relies on more protracted development due to its dependence on multisensory and motor integration. These insights reinforce the distinct plasticity profiles and critical developmental windows of each system.

Interestingly, examining atypical developmental patterns provides insights into the origins of the maturational trajectory of perceptual and visuomotor function. For example, children with Williams syndrome, a genetic developmental disorder associated with profound spatial impairments, exhibit greater delays in visuomotor behaviors compared to perceptual behaviors. In one study by Dilks et al. (2008), children with Williams syndrome were assessed on tasks requiring spatial navigation and visuomotor coordination, such as object placement and target reaching. These tasks revealed pronounced deficits in spatial and action-related tasks, while their performance on perceptual tasks, like object recognition, remained relatively preserved highlighting the uneven developmental trajectories of the dorsal and ventral pathways. Neurodevelopmental conditions like these can alter not only the cortical organization of visual regions but also the nature of visual experiences, offering unique perspectives on the interplay between perception and action.

The dorsal pathway, and functions associated with this pathway, appears to be more vulnerable to developmental disruptions compared to the ventral pathway, a phenomenon often termed “dorsal stream vulnerability” (Braddick et al., 2003). The increased vulnerability of the dorsal pathway may be due to its prolonged maturation timeline, as it develops later and relies on complex processes such as multisensory integration and spatial computations. Studies have shown that conditions such as periventricular leukomalacia (PVL), which is commonly observed in preterm infants, disproportionately affect the white matter tracts associated with the dorsal pathway. This vulnerability leads to impairments in visuospatial processing and visuomotor control, while object recognition abilities mediated by the ventral pathway remain relatively preserved (Atkinson & Braddick, 2012). Additionally, evidence from individuals with developmental dyslexia and autism spectrum disorder (ASD) further supports the dorsal pathway’s susceptibility, as these populations often exhibit deficits in motion perception and spatial awareness, both of which rely heavily on dorsal pathway processing (Braddick et al., 2003; Hay et al., 2020). These findings stress the critical role of the dorsal pathway in supporting visuomotor behaviors and highlight how disruptions in its development can have far-reaching consequences for spatial and motor functions.

Despite these foundational insights, the emergence of the dissociation between action and perception remains an open question. This dissertation will specifically explore the susceptibility of the action and perception dissociation through the lens of neurodevelopmental conditions, focusing on diverse patient populations. By investigating how disorders such as amblyopia, autism spectrum disorder, and early cortical lesions impact the visuomotor and perceptual behaviours, as well as the dissociation between these behaviours, this work aims to provide a deeper understanding of how perception and action systems evolve and interact during development.

The first experimental chapter of this dissertation [Chapter 2] focuses on a pediatric patient, TC, who underwent a unilateral cortical resection affecting both the ventral and dorsal pathways. This study uniquely investigates how simultaneous lesions to both pathways influence the development of perceptual and visuomotor behaviors. By examining visuoperceptual performance alongside visuomotor tasks such as grasping, this research highlights the dissociable effects of such injuries and finds that while perceptual abilities remained intact, presumably supported by the unaffected hemisphere, visuomotor behaviors showed marked impairments, particularly when relying on the contralesional hand. These findings contribute novel evidence regarding the differential developmental trajectories of the ventral and dorsal pathways as well as more information about the dissociation between perception and action following childhood cortical injuries. This chapter was published in the journal Neuropsychologia in 2022 (Ahmad et al., 2022).

The second experimental chapter [Chapter 3] transitions to studying children with amblyopia, a developmental visual disorder characterized by reduced acuity in one eye. By utilizing grasping and perceptual tasks, this study investigates whether atypical visual development in amblyopia alters the functional dissociation between perception and action, offering a comparative analysis with neurotypical controls. The results of this study found a reduced dissociation between perception and action behaviours in children with amblyopia compared to typically developing children. A unique aspect of this study is its focus on young children with otherwise typical development, excluding their visual experience. Given that their visual experience is atypical from an early age, even with treatment, this population provides a distinctive opportunity to examine the role of visual experience in the emergence of the perception-action dissociation. This chapter was published in Neuropsychologia in 2023 (Ahmad et al., 2023).

Finally, the third experimental chapter [Chapter 4] investigates the perception-action dissociation in adults with Autism Spectrum Disorder (ASD) through two complementary experiments. Autism Spectrum Disorder is associated with atypical sensory processing and motor behaviors, making it an ideal population for examining how these differences affect the functional dissociation between perception and action. The results of this study indicate that individuals with ASD exhibit reduced specialization in cortical processing, supporting the reduced specialization account as a potential underlying mechanism mediating perceptual and motor alterations in autism. By examining this population, the study contributes novel evidence of a diminished functional dissociation between perception and action, offering insights into the neurodevelopmental mechanisms of ASD. This chapter was submitted for publication and is currently under review.

Together, these studies provide a detailed examination of how neurodevelopmental conditions influence the emergence of perceptual behaviors, visuomotor behaviors and the dissociation between these functions. These investigations confirm the sensitivity of visuomotor behaviours to atypical development and also show, for the first time, that the dissociation between perceptual and visuomotor functions is disrupted under a range of neurodevelopmental conditions.

CHAPTER 2: UNILATERAL RESECTION OF BOTH CORTICAL VISUAL PATHWAYS ALTERS ACTION BUT NOT PERCEPTION

Ahmad, Z., Behrmann, M., Patterson, C., & Freud, E. (2022). Unilateral resection of both cortical visual pathways in a pediatric patient alters action but not perception. *Neuropsychologia*, *168*, 108182.

2.1 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 visuoperceptual 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 visuoperceptual 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.

2.2 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 travels from the occipital lobe to the posterior parietal cortex and processes information that is utilized to support vision-for-action (Mishkin & Ungerleider, 1982; Goodale & Milner, 1992; for a revised view see Freud, Plaut & Behrmann, 2016; Freud, Behrmann & Snow, 2020).

The dissociation between the two visual pathways and their corresponding functions has been highly informed by neuropsychological investigations of adults' 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 Himmelbach et al., 2012; Rossit et al., 2018). In contrast individuals with posterior parietal lobe lesions (dorsal pathway) specifically lesions in the superior parietal lobule (SPL) and areas around the intraparietal sulcus (IPS), suffer from a disorder termed optic ataxia, and display an impairment in reaching and grasping objects with their hands in their contralesional visual field but nonetheless have minimal deficits to their perceptual abilities (Jakobson et al., 1991; Karnath & Perenin, 2005; Rossetti et al., 2019; but see Medina et al., (2020) that documented mild perceptual deficits in these patients).

Interestingly, the remarkable deficits in object perception observed after a lesion sustained to the ventral pathway is not always evident. A striking deomonstration comes from pedatric pharmaco-resistant epilepsy patients who undergone a cortical surgical resction to reduce the frequency of the sezuires (Liu et al., 2018, 2019). Recent studies found that pediatric patients with resections that compromised a large portion of the ventral visual pathway typically demonstrate mostly normal visuoperceptual abilities. In particular, post-surgery visuoperceptual performance was found to be normal 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 pattern 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 visuoperceptual behaviors described by these recent studies only examined computations carried out by the ventral visual pathway. However, the question remains whether visuomotor behaviors, mediated by the dorsal visual pathway (Goodale & 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 adjudicate between these two competing conjectures, 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 visuomotor coordination (see Methods) suggesting that, in contrast with perceptual functions (Liu et al., 2019), TC's visuomotor 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 important insights to clinicians who work with epileptic pediatric patients.

To explore and characterize this dissociation, we evaluated TC's visuoperceptual and visuomotor 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., 2016; 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 & Goodale, 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 visuoperceptual representations, we asked participants to manually estimate the size of the Efron blocks using their thumb and index figure. This task provides a continuous perceptual measure that is directly comparable to the grip calibration measure (Haffenden & Goodale, 1998), and it has been used widely and successfully under different tasks and conditions (Freud et al., 2016; Ganel & Goodale, 2003; Goodale et al., 1991; Haffenden & Goodale, 1998; Westwood et al., 2002). Past research has validated that the manual estimation task is comparable to other perceptual estimation methods and yields similar results (Hartle & 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 visuomotor) 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.

2.3 Methods

2.3.1 Participants

2.3.1.1 Patient TC

TC is a right-handed female. She was 16 years old when this study took place. She reached all normal developmental milestones till the age of 6. Onset of epilepsy was at the age of 7. She was diagnosed with perinatal stroke with medically intractable focal epilepsy and multifocal encephalomalacia consistent with remote ischemic injury (Figure 1A – pre-surgical scan, 13 years old). She underwent a parieto-occipital craniotomy and left parieto-occipital lobectomy at the age of 13 years (Liu et al., 2019). Her surgery resulted in a left posterior parietal and occipitotemporal lobectomy (Figure 1 B-C).

We delineated the extent of the resected region using a T1 MRI scan (resolution - 1mm^3, Liu et al., 2019) obtained after the surgery and a detailed anatomical atlas (Mai, Majtanik & Paxinos, 2016). Close scrutiny of the anatomical scans revealed that most occipital structures were removed in the course of the surgery, including the posterior calcarine sulcus and Occipital gyri. Resected regions also include regions of the inferior temporal lobe (ventral pathway) such as the Fusiform and Lingual gyri. Additionally, the left Superior Temporal Sulcus (STS) is atrophied compared with the homologue right hemisphere sulcus. For the dorsal pathway, the resection includes posterior temporal cortex (adjacent to the proximate location of area MT) and posterior parietal cortex (i.e., Angular gyrus, posterior IPS). The more anterior portions of the intraparietal sulcus, known to be involved in visuomotor 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.

For the current study, TC was tested at her home and provided assent, and her parents provided informed consent for her participation.

2.3.1.2 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.

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 Judgement of Lines and Angles	1st percentile
	Visual Memory	1st – 2nd percentile
Vision (Liu et al., 2019)	Glass Pattern Recognition Threshold	Normal range (controls = 39.4 ± 7.74, TC = 45)
	Object Matching Score	Normal range (controls=94.86 ± 3.08%, TC = 89%)
	Face Perception	Normal range (controls = 88.22 ± 11.55%, TC = 83.3%)
	Contour Integration Threshold	Normal range (controls = 74.04 ± 3.53, TC = 77.27)
Visuomotor Skills	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[a]
	WIAT-III: Spelling	2nd grade[a]
	Peabody Picture Vocabulary Test	1st percentile[a]
	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	Normal range

WIAT-III, Wechsler Individual Achievement Test.

[a] Could not be reliably obtained due to language barrier.

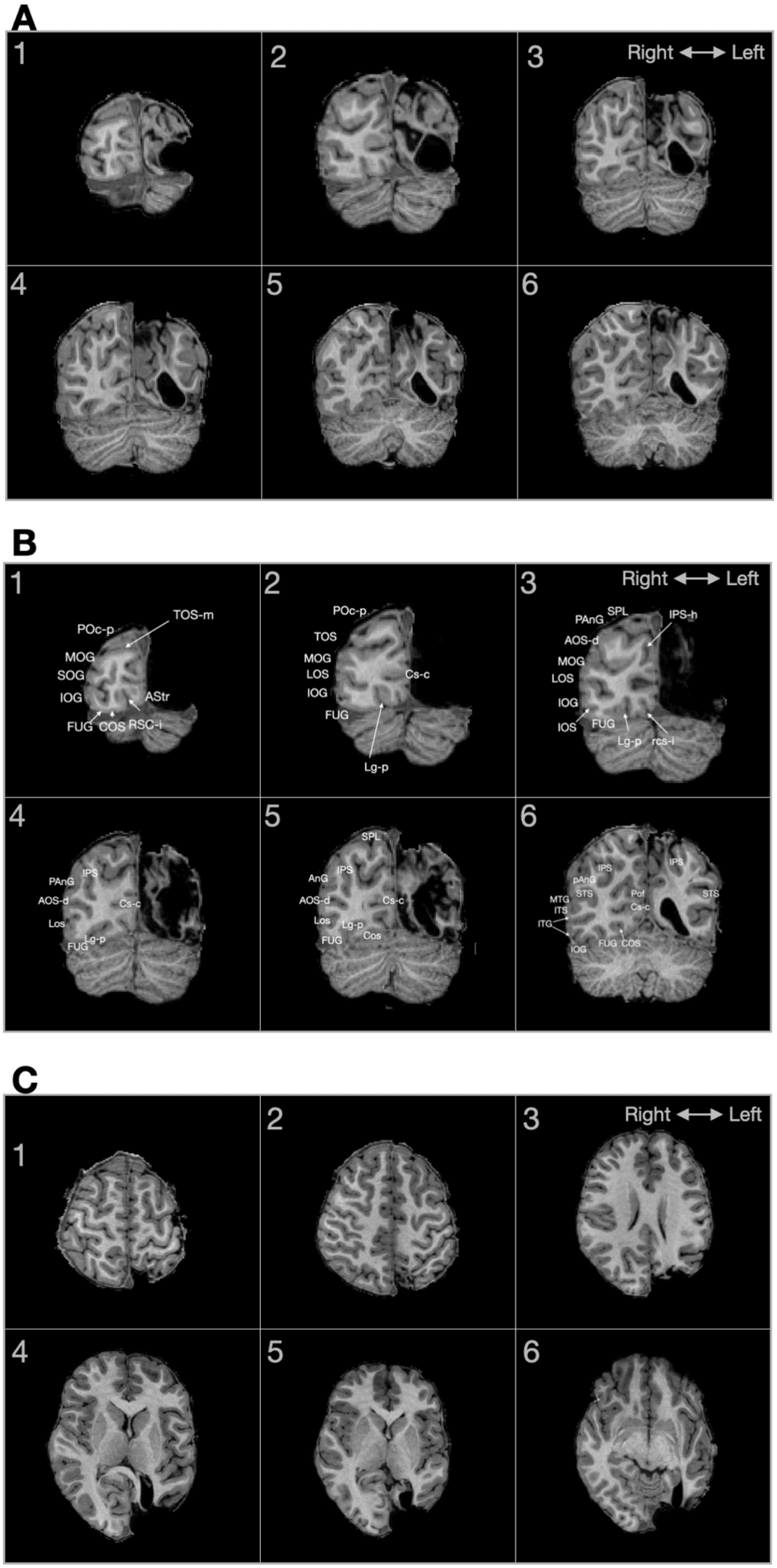
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Figure 1: TC Scans (age 13 years)

(A) TC pre-surgical scans. Representative coronal slices (posterior-A.1 to anterior-A.6) from the presurgical MRI scan of TC. Prior to TC's cortical resection, lesions to parts of the ventral and dorsal pathways of the left were evident (and could be attributed to the prenatal stroke and/or to the early-onset epilepsy). **(B) TC post-surgical scans.** Representative coronal slices (posterior-B.1 to anterior-B.6) from the MRI scan of TC. The resection included the posterior parts of the ventral and dorsal pathways of the left hemisphere. The regions homologous to the resected hemisphere were delineated using a detailed anatomical atlas (Mai, Majtanik & Paxinos, 2016). The resection extends to inferior and posterior parts of the temporal cortex. The resection includes all occipital structures, posterior temporal cortex (adjacent to the proximate location of area MT), and posterior parietal cortex (i.e., angular gyrus, posterior IPS). Identified areas include the anterior occipital sulcus, dorsal segment (**AOS-d**); striate area (**AStr**); collateral sulcus (**COS**); calcarine sulcus (**Cs-c**); fusiform gyrus (**FUG**); inferior occipital gyrus (**IOG**); inferior occipital sulcus (**IOS**); intraparietal sulcus (**IPS**); intraparietal sulcus, horizontal segment (**IPS-h**); inferior temporal gyrus (**ITG**); inferior temporal sulcus (**ITS**); lingual sulcus, posterior ramus (**Lg-p**); lateral occipital sulcus (**LOS**); middle occipital gyrus (**MOG**); middle temporal gyrus (**MTG**); posterior angular gyrus (**PAnG**); posterior-occipital arc, posterior part (**POc-p**); parietooccipital fissure (**Pof**); retrocalcarine sulcus, inferior branch (**RSC-i**); superior occipital gyrus (**SOG**); superior parietal lobule (**SPL**); superior temporal sulcus (**STS**); transverse occipital sulcus (**TOS**); transverse occipital sulcus, medial ramus (**TOS-m**). **(C) TC post-surgical scans.** Representative axial slices (superior-C.1 to inferior-C.6) from the post-surgical MRI scan of TC.

2.3.2 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

2.3.3 Apparatus and Stimuli

Participants sat in front of a 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 - 35 mm in gaps of 5mm and lengths adjusted accordingly (see Figure 2A). Grasping movements and manual estimations were recorded using an Optitrack system (Natural Point DBA OptiTrack, USA). The system included four Prime 13W 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 (Figure 2B). The system tracked the 3D trajectory of the participants’ index, thumb and wrist movement using a 100 Hz sampling rate and allows to calculate the aperture between the fingers at any given time point.

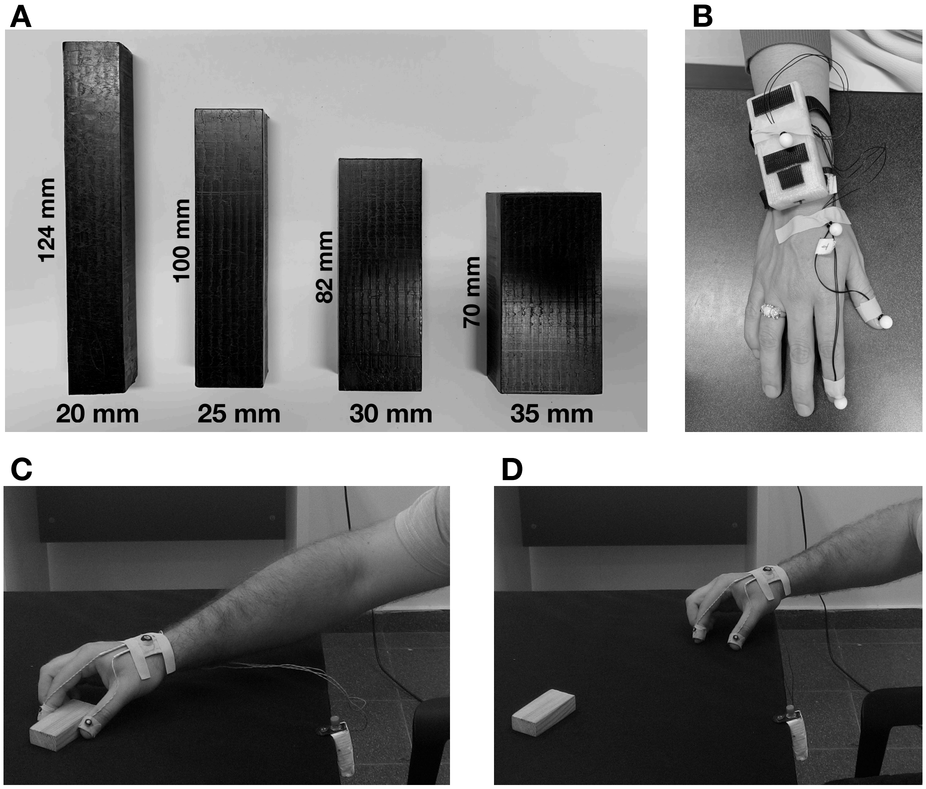


Figure 2: (A) Experimental stimuli - target objects used in the experimental set-up were a set of four Efron blocks that all had the same surface area, texture, mass, and color, but varied in width and length, with their width indicated below the block. Using their index finger and thumb, in separate 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 grasping trial, in which the participant reached and grasped one of the target objects **(D)** Manual estimation trial - example of manual estimation trial, in which the participant indicated the width of the target objects with their thumb and index finger.

2.3.4 Procedure

Participants completed two tasks, a grasping (Figure 2C) and manual estimation task (Figure 2D). In each task, participants began with their thumb and index finger grasping a permanently stationary block 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 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 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 two seconds 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.

2.3.5 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 10mm/sec. 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 0.2mm. An additional condition was that the Z (superior-inferior) location of the fingers was smaller than 80mm, 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 determined to reflect the perceived width of the object (Freud et al., 2016). 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., 2016; 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 & 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., 20mm-25m, 25mm-30mm and

30mm-35mm). 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 at 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., 2016), 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 single-case statistical analysis (Crawford & Garthwaite, 2002). Lastly, to account for the problem of multiple comparisons, we applied the Bonferroni correction.

2.3.6 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 & Garthwaite, 2002). Finally, we also used the Revised Standardized Difference Test (RSDT) (Crawford & 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.

2.4 Results

To examine whether TC was impaired in the perceptual and/or grasping task, 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.

2.4.1 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 (Figure 3B, left), as verified by single-case statistical comparisons [contralesional (right) hand: $t_{(13)} = 1.63$, $p>.1$, 1.68 (0.84 to 2.05); ipsilesional (left) hand: $t_{(13)} < 1$, 0.41 (-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 (Figure 3B, right, grasping ipsilesional left: 92.11 mm, grasping contralesional right hand: 96.16 mm): her MGA was, on average, ~20mm larger than that of control participants, and, single-case statistical comparisons confirmed this exaggerated MGA for both the contralesional (right) [$t_{(13)} = 3.24$, $p < 0.05$, $Z\text{-}_{CC} = -2.099$ (1.97 to 4.73)] and ipsilesional (left) [$t_{(13)} = 2.816$, $p < 0.05$, $Z\text{-}_{CC} = 2.91$ (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 & 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 (Figure 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.

2.4.2 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 (Figure 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 a comparable sensitivity to that of controls regardless of hand used by TC [contralesional right hand $t_{(13)} < 1$, $Z\text{-}_{CC} = -0.658$ (95% CI = -1.228 to -0.067); ipsilesional left hand [$t_{(13)} < 1$, $Z\text{-}_{CC} = -0.283$ (95% CI = -0.812 to 0.257)]. In contrast, for the grasping task, TC's sensitivity to object size was significantly impaired but only with her contralesional (right) hand [$t_{(13)} = 4.775$, $p < 0.001$, $Z\text{-}_{CC} = 4.943$ (95% CI = 2.989 to 6.884)]. The results from TC's ipsilesional hand fell within the normal range [$t_{(13)} < 1$, $Z\text{-}_{CC} = 0.508$ (95% CI = -0.059 – 1.057)].

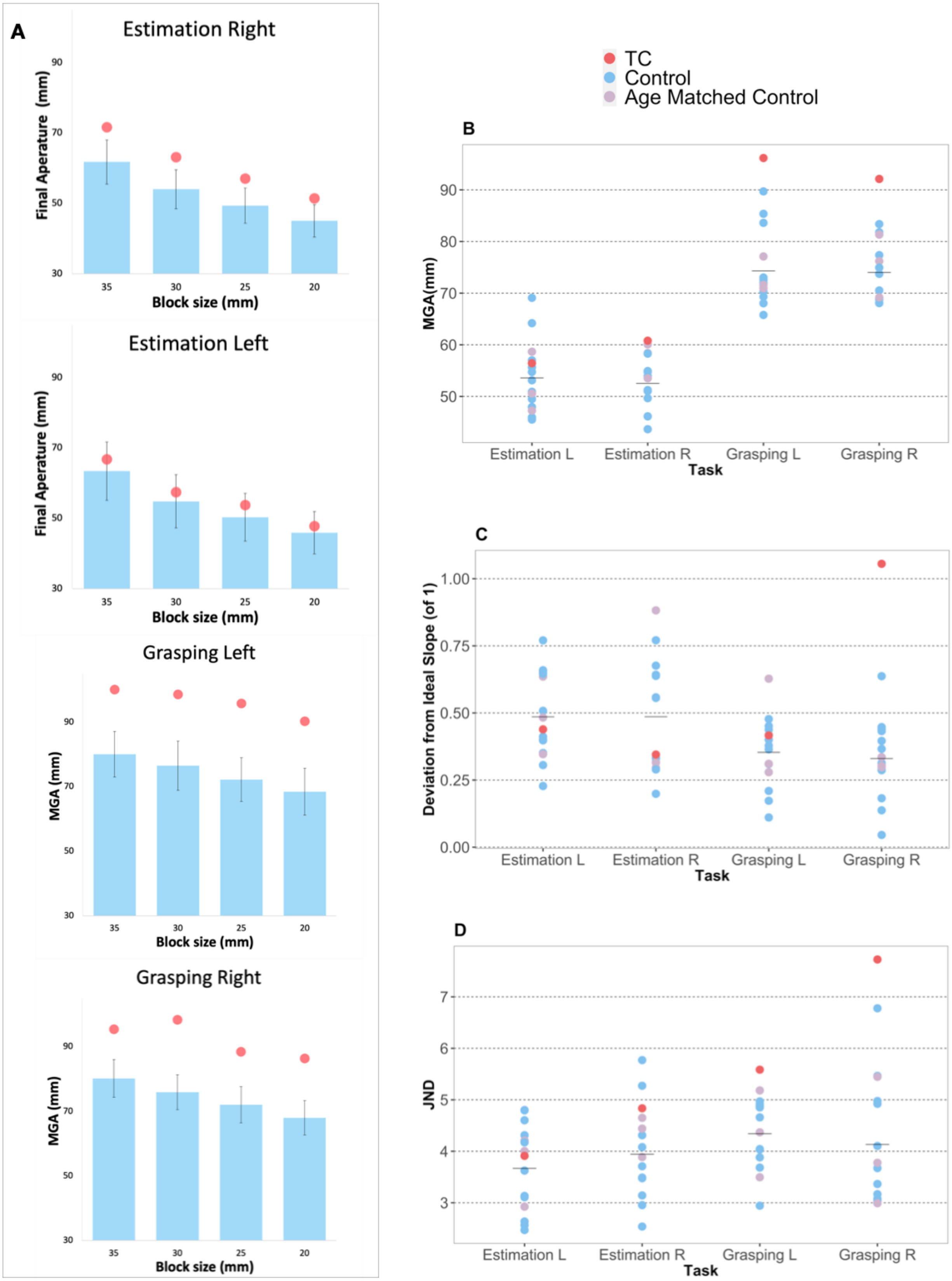
Next, we employed the RSDT (Crawford & Garthwaite, 2005) to validate statistically the dissociation between grasping and estimation performance for her contralesional hand [$t_{(13)}$ = 3.382, $p < 0.005$, Z-$_{CC}$ = 3.636 (95% CI = 2.106 to 5.428)]. In contrast, for the ipsilesional hand, there was 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 more deviation for her contralesional hand 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.

2.4.3 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., 2016; 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)] (Figure 3D, left). Whereas TC's variability was greater than that of controls for the grasping task (Figure 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 to 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-$_{DCC}$ = 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-$_{DCC}$ = -1.121 (95% CI = -1.946 to 0.376)]. Finally, the RSDT (Crawford & 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-DCC = 0.861 (95% CI = -0.225 to 2.061)].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Estimation Right
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Estimation L
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Figure 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 (35mm) to the smallest (20mm) 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.

2.4.4 Movement trajectory

Next, we analyzed the movement trajectories of both hands for the grasping task. Sensitivity to object size is usually observed early in the movement (e.g., Freud et al., 2016) 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., 2016; 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.

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

We found comparable size sensitivity between TC and controls when she 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.

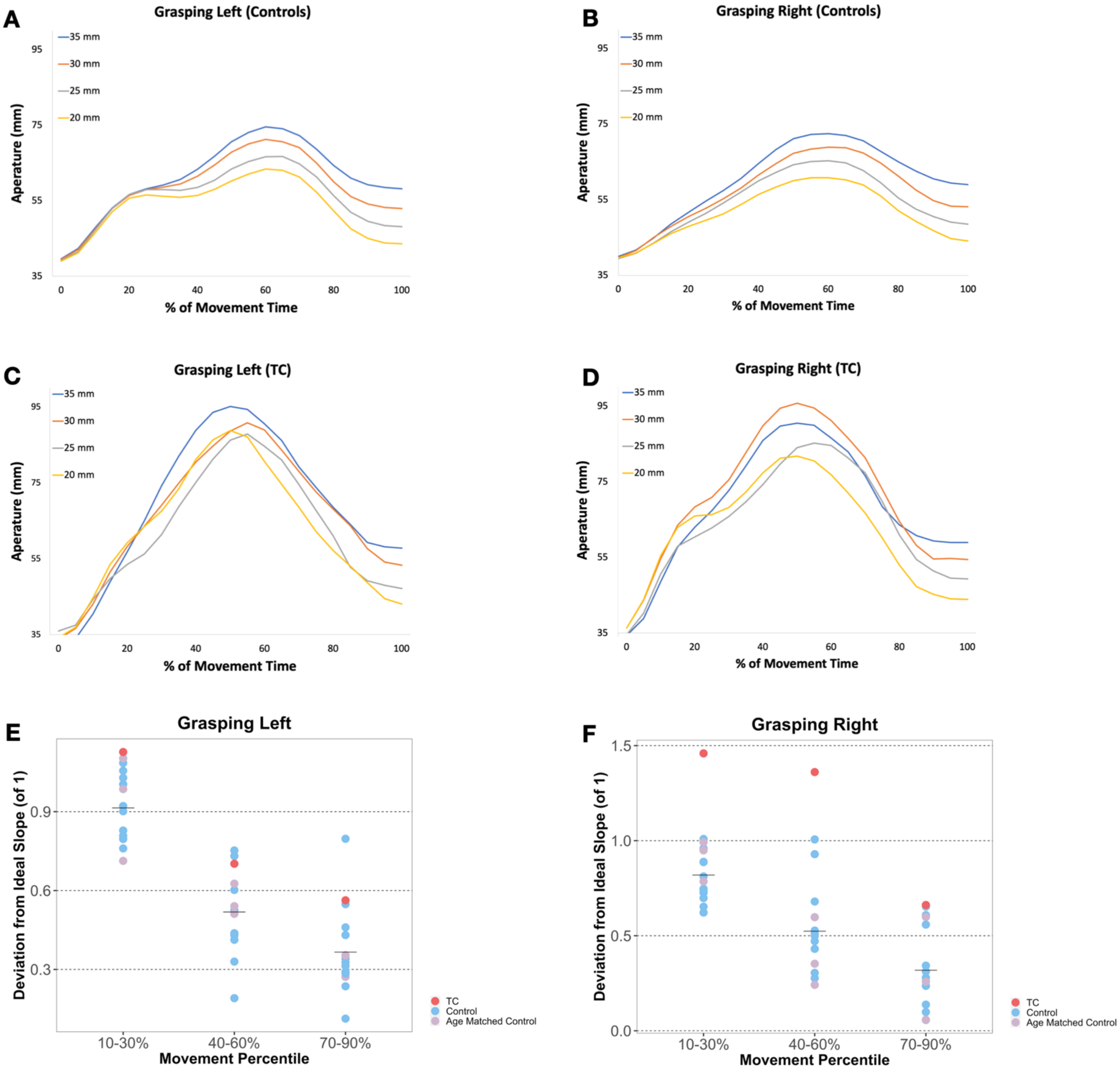

Figure 4: Grip apertures along the movement trajectory for each target block size and hand. **(A&B)** Grip aperture was averaged across all control participants for the left and right hand. **(C&D)** Grip apertures of TC for her left and right hand. The graphs demonstrate that TC does not scale her hand appropriately when grasping with her right hand. **(E&F)** TC's slope analysis results at various points along her movement trajectory for her right and left hand.

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

Hand	Portion of Movement		
	Early (10-30%)	Mid (40-60%)	Late (70-90%)
Left Hand	$t = 1.616$ $p > 0.12$	$t = 1.035$ $p > 0.31$	$t = 1.171$ $p > 0.26$
Right Hand	$t = 4.689$ $p < 0.00042$	$t = 3.607$ $p < 0.003$	$t = 1.748$ $p > 0.1$

Note: TC has a comparable performance to the controls in all portions of her movement with her left hand and during the late portion of her grasping trajectory with her right hand. During the early and mid-portions of movement with her right hand, her grasping performance is significantly different than the controls.

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.

Table 3: Summary of TC's performance compared to controls on behavioural tasks.

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

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.

2.5 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 & 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 suggested 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 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 (Figure 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 & Braddick, 2005; Atkinson, 2017) than 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; Mundinano 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 and included more critical regions for visuomotor control. Note, however, that careful delineation of the lesion does not support this account (Figure 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 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 that this execution is roughly similar to that engaged in the grasping task.

Finally, another interesting question is whether limb apraxia can account for TC 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 deficit in reaching and grasping movements, which better describes TC's behavior. Notably, 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 central vision grasping. Thus, TC deficit's cannot be clearly categorized as limb apraxia or optic ataxia, but her behavior is more consistent with the clinical description of optic ataxia

2.5.1 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 & 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 & 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 & Culham, 2015; Gonzalez et al., 2006). Comparatively, homologue regions in the right hemisphere contribute more to attentional mechanisms (Bowen et al., 1999; Ringman et al., 2004; Becker & Karnath, 2007) and spatial transformations (Gauthier et al., 2002.; Harris et al., 2000; Warrington & 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 & Vighetto, 1988) has been observed in patients with left hemisphere injures. 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 & 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 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 & 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-hemispherical connectivity patterns.

2.5.2 Limitations

The current study provides important insights into the effect of a unilateral cortical lesion on visuomotor and visuoperceptual 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 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.

2.6 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.

CHAPTER 3: REDUCED PERCEPTION-ACTION DISSOCIATION IN CHILDREN WITH AMBLYOPIA.

Ahmad, Z., Kelly, K. R., & Freud, E. (2023). Reduced perception-action dissociation in children with amblyopia. *Neuropsychologia*, *191*, 108738.

3.1 Abstract

The functional distinction between vision-for-perception and vision-for-action is a key aspect of understanding the primate visual system. While this dissociation has been well-established in adulthood, its development and dependence on typical visual experience remain unclear. To address these questions, we examined two groups of children: typically developed children and those with amblyopia, who presumably have a sub-optimal visual experience. The Ponzo illusion, known to impact perception but not visuomotor behaviors across age groups, was employed to assess the extent of dissociation. Participants engaged in two tasks involving the Ponzo illusion: a grasping task (vision-for-action) and a manual estimation task (vision-for-perception), with objects placed on the "close" and "far" surfaces of the illusion. Typically developed children displayed grasping movements that were unaffected by the illusion, as their grasping apertures were scaled based on object size, independent of its location.

In contrast, children with amblyopia exhibited a clear susceptibility to the illusion, showing larger apertures for objects placed on the 'far' surface of the illusion, and smaller apertures for objects placed on the 'close' surface. Interestingly, both groups of children demonstrated similar susceptibility to the illusion during the perceptual task, with objects placed on the far surface being perceived as longer compared to objects placed on the close surface. These findings shed light on the impact of atypical visual development on the emergence of the dissociation between perception and action, highlighting the crucial role of typical visual experience in establishing this distinction.

3.1. Introduction

According to the Two Visual Pathway Hypothesis, the cortical visual system is segregated into two anatomically and functionally distinct pathways: the ventral pathway and the dorsal pathway. This division of labor was originally articulated based on the visual qualities represented by each pathway (Mishkin & Ungerleider, 1982). However, Goodale and Milner (1992) revised this framework and redefined the functions of the two pathways by their output requirements. According to this influential view, computations carried out by the ventral pathway support perceptual processes (i.e., “what”), while computations carried out by the dorsal pathway promote visually guided actions (i.e., “how”).

Over the years, visual illusions have been found to be an efficient tool to explore the nature of the dissociation between perception and action in healthy neurotypical individuals. Visual illusions are perceptual phenomena where the brain misinterprets visual stimuli, leading to a perception that differs from objective reality. Interestingly, across different studies, visual illusions were found to have a reduced effect on visuomotor behaviors relative to their effect of perceptual behaviors. While some of these findings are subject to a scientific debate (Aglioti et al., 1995; Franz et al., 2000, 2003; Haffenden et al., 2001), findings on certain illusions, such as the Ponzo illusion (Ganel et al., 2008, Gonzalez et al., 2008, Whitwell et al., 2016, Freud et al., 2021) consistently show that perceptual estimations are heavily influenced by the illusions, while grasping trajectories can mostly escape illusory effects.

Although the nature of the perception-action dissociation has been extensively studied in adults, a crucial outstanding question regarding the maturation and developmental trajectory of this well-established specialization still stands (Atkinson, 2017; Smith et al., 2017). Various studies have shown inconsistent results when comparing the developmental rates of the two visual systems. While some studies indicate that the functions controlled by the ventral pathway mature earlier than those controlled by the dorsal pathway, other studies suggest the opposite (Ciesielski et al., 2019; Kovács et al., 2000). Similarly, the evidence regarding the development of the dissociation between the functions mediated by the two systems are mixed.

Several studies have documented early emergence of the dissociation, such that in both 5-year-old children and adults, adherence to Weber's law (a psychological principle stating that the ability to perceive a difference between two stimuli is proportional to the relative change in their intensity, not their absolute difference) was observed for a perceptual task but not for visuomotor task (Hadad et al., 2012). Additional evidence for the early emergence of the perception-action dissociation comes from a recent study that demonstrated that similarly to adults (Ganel, Chajut, et al., 2008), children (5-8 years old) are susceptible to the Ponzo illusion under a perceptual task, but not under a grasping task (Freud et al., 2021). Notwithstanding, this early dissociation was evident only when children were presented with simple objects in which only the relevant object dimension was manipulated and not when children were presented with more complex objects where the perceived magnitude is influenced by the relationship between two different dimensions, such as the width and length of a rectangle (Freud et al., 2019 and also see: Schum et al., 2012). These findings suggest that although visual functions become more specialized during development, the computations that support these dissociable functions may still overlap to a greater extent during childhood.

It should be emphasized that the aforementioned developmental studies focused on neurotypical participants. Nevertheless, examining atypical developmental patterns can provide complementary insights that will shed light on the origins of this dissociation. Accordingly, it was demonstrated that in children with Williams syndrome (WS), a genetic developmental disorder which results in profound impairments in spatial abilities, there is a greater delay in development of visuomotor behaviours compared to perceptual behaviours (Dilks et al., 2008).

Notably, neurodevelopmental conditions can alter not only the cortical organization of regions within the visual system but also the nature of visual experiences. However, the role of early visual experience in shaping the functional dissociation is yet to be determined. To bridge this gap, the current study investigates whether the emergence of the perception-action dissociation is altered following an atypical, sub-optimal, visual experience in childhood from amblyopia ("lazy eye"). Amblyopia is a common neurodevelopmental disorder clinically defined as reduced visual acuity in one eye that cannot be immediately corrected using optical refraction (Wallace et al., 2018). The most common causes of amblyopia are strabismus (misalignment of the visual axis) and anisometropia (unequal refractive error) (Birch, 2013). Recent findings have frequently connected the effects of amblyopia on visuomotor control to its related impairments in binocular vision rather than to visual acuity in the affected eye (Birch, 2013; Hou et al., 2022; Kelly et al., 2020; Niechwiej-Szwedo et al., 2019).

Prior research has established a decrease in visuomotor performance in children and adults diagnosed with amblyopia, particularly in tasks necessitating the amalgamation of visual and motor data, such as eye-hand coordination. Amblyopic participants show poor performance on intricate shape drawing or copying (Levi & Klein, 1983; Niechwiej-Szwedo et al., 2014), a decline in manual dexterity (Kelly et al., 2020; Webber et al., 2008), imprecise reaching movements, inaccurate object grasping due to compromised stereoacuity (Birch, 2013,; Hou et al., 2022), and anomalies in the temporal sequencing of eye-hand coordination during visually guided reaching tasks (Fronius & Sireteanu, 1994; Niechwiej-Szwedo et al., 2014). Despite progress in understanding visuomotor behaviors in amblyopia, it remains an open question whether the observed visuomotor impairments in amblyopic children are indicative of a decrease in functional specialization between perception and action, or if they represent a pure motor deficit. Thus, the goal of the current investigation was to examine whether children with amblyopia also demonstrate alterations in the emergence of the perception-action dissociation.

To this end, children with amblyopia and neurotypical children were asked to perform a visuomotor ("grasping") and a perceptual ("estimation") task involving objects of different sizes placed on an illusory Ponzo background. This illusion has been shown to be an efficient tool to explore the nature of the dissociation between perception and action in healthy adults and children (Freud et al., 2021; Ganel, Tanzer, et al., 2008; Gonzalez et al., 2008; Whitwell et al., 2016). Particularly, it was found that this illusion consistently modulates perceptual estimations, while grasping trajectories can mostly escape the illusory effect. Prior investigations, such as the one conducted by Rohr et al. (2022), have employed the Ponzo illusion in studies involving children with strabismus. Their findings revealed that individuals with strabismus exhibited higher susceptibility and longer response times compared to their healthy counterparts when assessing Ponzo's illusory images. Nonetheless, the current study marks the first attempt to examine the effects of visual illusions on the dissociation in visuomotor and perceptual abilities in amblyopia. If amblyopia modulates the emergence of the dissociation, we expect that in contrast to typically developed children, children with amblyopia would be sensitive to the Ponzo illusion under both the perceptual and grasping tasks.

3.2. Methods

The research protocol was approved by the Institutional Review Board of York University and by The University of Texas Southwestern Medical Center and conformed to the requirements of the US Health Insurance Portability and Accountability Act of 1996. Written informed consent was obtained from a parent or legal guardian before testing of their child and after an explanation of the nature and possible consequences of the study. Participants over the age of 10 provided assent. Participants received monetary compensation for their participation.

3.2.1. Participants

3.2.1.1. Amblyopic participants

We recruited a group of 20 children (4 to 14 years old) diagnosed with amblyopia due to strabismus, anisometropia, or both and were referred to the Retina Foundation of the Southwest by pediatric ophthalmologists in the Dallas/Fort Worth area. Amblyopia was defined as an interocular difference in visual acuity of ≥0.2 logMAR, with best-corrected visual acuity (BCVA) in the fellow eye of ≤0.1 logMAR (20/25 or better; 0.3 logMAR [20/40] for ages 4 years) (Table 1).

3.2.1.2. Control participants

We recruited a control group of 28 typically developing children (4 to 14 years old) who had age-normal visual acuity and stereoacuity and no history of vision disorders. We also recruited an additional 8 control children (6 to 10 years old) to test monocularly with a patch over their dominant eye. To mitigate potential confounding factors related to binocular vision, this additional group (“monocular controls”) was included in this study. Seven control participants were tested at the Retina Foundation of the Southwest. The remaining (21) control participants were tested using the same experimental setup (see Apparatus and Stimuli for details) at York University, Toronto.

3.2.2 Vision Assessment:

Similar to (Kelly et al., 2020), prior to visuomotor and perceptual skills testing, we conducted a series of visual assessments on all the participants. The results of all visual assessments and group characteristics can be found on Table 1. Stereoacuity and the presences (or absence) of stereo vision was measured using the Randot Preschool Stereoacuity and Stereo Butterfly Tests converted to log arcsec for analyses (ranging from 1.3 to 3.3 log arcsec). In cases where no stereoacuity was detected, a fixed value of 4 log arcsec was assigned (Birch et al., 1997, 2008). The extent of suppression scotoma was evaluated using the Worth 4 Dot (W4D) test at seven distinct distances, quantified as the farthest distance at which the child could report four dots. These measurements were then converted into the size of the suppression scotoma in logarithmic degrees. Larger numerical values indicated the presence of larger suppression scotomas, while a value of 1.2 log degrees was assigned when no fusion was achieved at the shortest distance (33 cm). The extent of the suppression was categorized as bifoveal-macular fusion (−0.15 to 0.45 log deg) or peripheral-no fusion (0.60 to 1.2 log deg) (Kelly et al., 2018; Rosenbaum & Santiago, 1999).

3.2.3. Apparatus and Stimuli

Participants sat in front of a small table on which the illusory context and the two objects were presented (Fig. 2). The two target objects were rectangular 3D blocks matched in width (10 mm), depth (10 mm), and color (black) but differed in length by 2mm (small: 40mm &

large: 42mm). The illusionary background (a version of the Ponzo Illusion) was flipped every 20 trials to counterbalance right and left movements directed to the larger and smaller objects. Grasping movements and manual estimations were recorded using an Optitrack system (Natural Point DBA OptiTrack, USA). The system included six Prime 13W cameras and three passive reflective markers attached to the participant's hand in such a way that permitted complete freedom of movement of the hand and fingers. 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.

3.2.4 Procedure

Participants completed a grasping task and a manual estimation task. For each trial in both tasks, participants started with their thumb and index finger closed together on a sticker placed immediately in front of them (i.e., the "home" position). On each trial, one of the two target objects was placed on the illusion on either the "close" or "far" side of the illusion in front of the participant with the width parallel to the left-right orientation of participant, within arm's reach (approximately 40 cm) (Figure 1A).

3.2.4.1 Grasping

Participants were instructed to reach for the target object with the thumb and index finger across its length and to lift it off the table (approximately 15 cm) before setting it down in the same spot and then returning to the "home" position.

3.2.4.2 Manual estimation

Participants were instructed to indicate the perceived length 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 length and to hold the finger posture for roughly two seconds before returning to the “home” position.

In every block, each of the two target objects was presented 10 times in a randomized order in both locations (“close” and “far”) resulting in a total of 40 trials per block. This experimental design allows us to obtain a reliable and independent assessment of both size sensitivity to the objects and the impact of the illusion on visual perception. All participants completed the grasping task first followed by the manual estimation task. This deliberate arrangement was motivated by a greater research emphasis and priority placed on the analysis of grasping outcomes.

3.2.5 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 by a conjunction of three conditions; 1) the Z (superior-inferior) location of the fingers was at its local minimum value, which indicated that the fingers were positioned along the same plane as the target object, 2) the Y (right-left) location of the fingers was at its maximum, which indicated that the fingers were furthest away from the “home” position, and 3) the delivery velocity (the speed of the overall hand movements) reached the minimum speed, indicating that the grasping movement had come to end as the hand had made contact with 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. The MGA is known to be well correlated with the size of the goal object (Jakobson et al., 1991).

For the estimation task, the aperture between the thumb and index finger that was held constant over 10 consecutive frames was determined to reflect the perceived width of the object (Freud et al., 2016). 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.

To assess size sensitivity and average effect of the illusion for the grasping task, we first calculated the average MGA of the small object under both the far and close conditions and repeated the procedure for the large object. Size sensitivity was then determined by subtracting the average MGA for the large object (across the far and close conditions) from that of the small object (across the far and close conditions). To obtain the effect of the illusion, we subtracted the average MGA for grasping movements directed to the far surface (for both large and small objects) from the average MGA for grasping movements directed to the close surface. Values that are greater than 0 (mm) reflects an effect of the Ponzo illusion. To assess size sensitivity and average effect of the illusion for the estimation task, we employed similar calculations on the aperture values at the estimation point.

3.2.6 Statistical analysis

Statistical analyses were conducted using JASP (JASP Team, 2018). We employed mixed analysis of variance (ANOVA) on the grasping and estimation data. We compared the monocular and binocular control groups and found no difference between the two groups in either the grasping or estimation tasks. Additionally, no interaction between control groups and the effect of the illusion was found (all F's < 1). Thus, we collapsed the data across the two control groups. For transparency, we still present the monocular children separately in the result figures.

3.2.7 Data availability

The experimental data is available on OSF:

https://osf.io/v5qb9/?view_only=46af6adcce384d838cd5dc23bdf0c6e7

Table 1: Group Characteristics

	Amblyopic (n = 20)	Control (n = 20)	Monocular Control (n = 8)
Sex: F, n (%)	11 (55)	9 (45)	3 (37.5)
Age (years), n (%)			
4 – 7	5 (25)	4 (20)	3 (37.5)
8 – 9	11 (55)	10 (50)	3 (37.5)
10- 14	4 (20)	6 (30)	2 (25)
Mean ± SD [a] (years)	9.2 ± 2.2	9.3 ± 2.1	8.7 ± 1.5
Nonpreferred eye visual acuity (logMAR [b]), n (%) (Snellen equivalent)			
No amblyopia [c] −0.1–0.2 (20/16–20/32)	0 (0)	20 (100)	8 (100)
Mild to moderate amblyopia [d] 0.2–0.6 (20/32–20/80)	17 (85)	N/A	N/A
Severe amblyopia [d] 0.7–0.8 (20/100–20/125)	3 (15)	N/A	N/A
Mean ± SD	0.416 ± 0.24	-0.01 ± 0.07	0.0 ± 0.05
Preferred eye visual acuity (logMAR)			
Mean ± SD	0.05 ± 0.22	-0.025 ± 0.07	-0.02 ± 0.046
Etiology, n (%)			
Anisometropia	7 (35)	N/A	N/A
Strabismus	6 (30)	N/A	N/A
Combined mechanism	6 (30)	N/A	N/A
Unilateral Cataract	1 (5)	N/A	N/A
Stereoacuity (log arcsec)	3.407 ± 0.78	1.48 ± 0.16	1.44 ± 0.14
Present, n(%)	8 (40)	20 (100)	8 (100)
Absent, n(%)	12 (60)	0 (0)	0 (0)
Fusion (Worth 4-dot log deg)	0.48 ± 0.50	-0.15 ± 0	-0.15 ± 0
Extent of suppression			
Bifoveal-macular fusion, n(%)	13 (70)	20 (100)	8 (100)
Peripheral -no fusion, n(%)	6 (30)	0 (0)	0 (0)

[a] SD, standard deviation.

[b] logMAR, logarithm of the minimum angle of resolution.

[c] 0.1 or leslogMAR interocular difference.

[d] 0.2 or greater logMAR interocular difference.

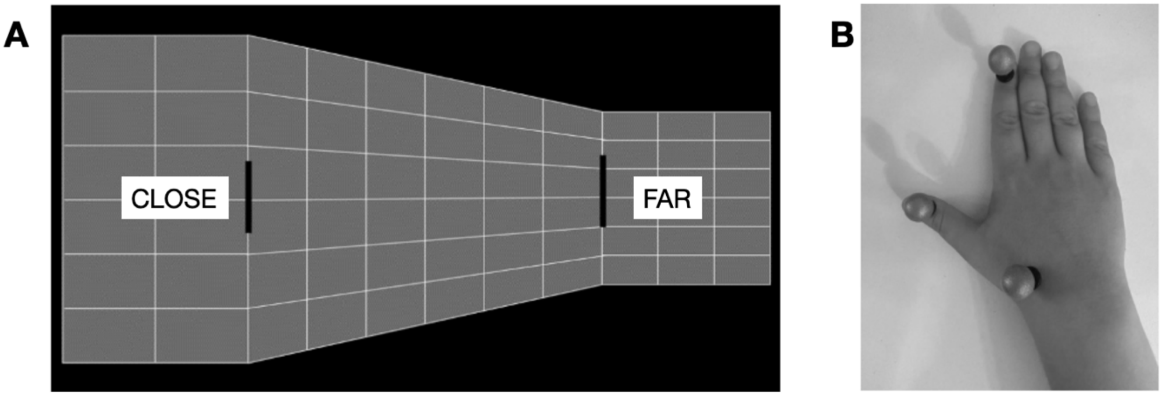

Figure 1 (**A**) Stimuli and experimental design. The figure shows the illusionary background (Ponzo Illusion) that the objects were placed on. (**B**) Distance between the fingers was measured with an Optitrack system, which tracked the 3-D position of light-reflecting diodes attached separately to each participant's index finger, thumb and wrist.

3.3. Results

3.3.1 Grasping task

First, we analyzed the MGAs to estimate the sensitivity of grasping movements to object size and the susceptibility to the effect of the illusion (Figure 2A). A mixed ANOVA with object size (small or big), perceived distance (close or far) and group (amblyopia or control) as the independent variables revealed a clear dissociation between the two groups in terms of the effect of the illusion, such that an interaction between distance (that is, the effect of the illusion) and group was found [$F_{(1, 46)} = 16.391$, $p < .001$, $\eta_p^2 = 0.263$]. Simple planned comparisons further demonstrated that for the control group, MGAs were similar across the perceived depth planes (i.e., no illusionary effect, F<1). In contrast, amblyopic children had greater MGAs for objects placed on the "far" surface and smaller MGAs for the objects placed on the "close" surface reflecting a clear adherence to the depth illusion ($F_{(1, 46)} = 13.911$, $p < .001$; Figure 2B). The effect of the illusion on grasping behaviors of children with amblyopia could not be attributed to the lack of binocular vision, as neurotypical children who completed the task under the monocular condition did not show any susceptibility to the illusion under the visuomotor task (Figure 2B).

The ANOVA also revealed a main effect of size [$F_{(1, 46)} = 18.128$, $p < .001$, $\eta_p^2 = 0.283$; Figure 2C) with no interaction between size and group (F<1), suggesting both groups were equally sensitive to object size. Hence, the effect of the illusion in the amblyopia group could not be simply attributed to a pure visuomotor deficit. These results suggest that the illusion's impact is not related to a scaling problem (as evidenced by the maintained size sensitivity), but rather it is probable that children with amblyopia are employing perceptual representation that affect their grasping behaviors as well.

Next, we analyzed additional kinematic measures such as movement time (i.e., time from movement onset to movement offset) and the time taken to reach MGA (Figure 3). While we did not find any difference between the two groups for time taken to reach MGA ($t<1$), there was a significant difference in the groups' overall movement time [$t_{(38)} = 2.936$, $p < 0.01$, Cohen's $d = 0.98$] suggesting the two groups behave differently in the post-MGA part of the grasping trajectory. Particularly, the time from the MGA to the endpoint was longer for the amblyopia group, which might reflect the need for on-flight aperture corrections to compensate for the illusory effect.

3.3.1.2 Discussion of grasping results

The analysis of the grasping data provides novel evidence that atypical and suboptimal visual experience can modulate the emergence of the perception-action dissociation. Particularly, while typically developed children were not influenced by the Ponzo illusion during the grasping tasks (similarly to the behavior reported by Freud et al., 2021), children with amblyopia exhibited a clear susceptibility to the illusion. Notably, one might suggest that the susceptibility to illusion in children with amblyopia, might not reflect a reduced perception-action dissociation, but rather an overall oversensitivity to monocular depth illusion because of their established deficit in the processing of binocular cues. Accordingly, if this alternative explanation is correct, children with amblyopia should show a greater effect of the illusion under the perceptual task. Next, we analyze the estimation data to address this concern.

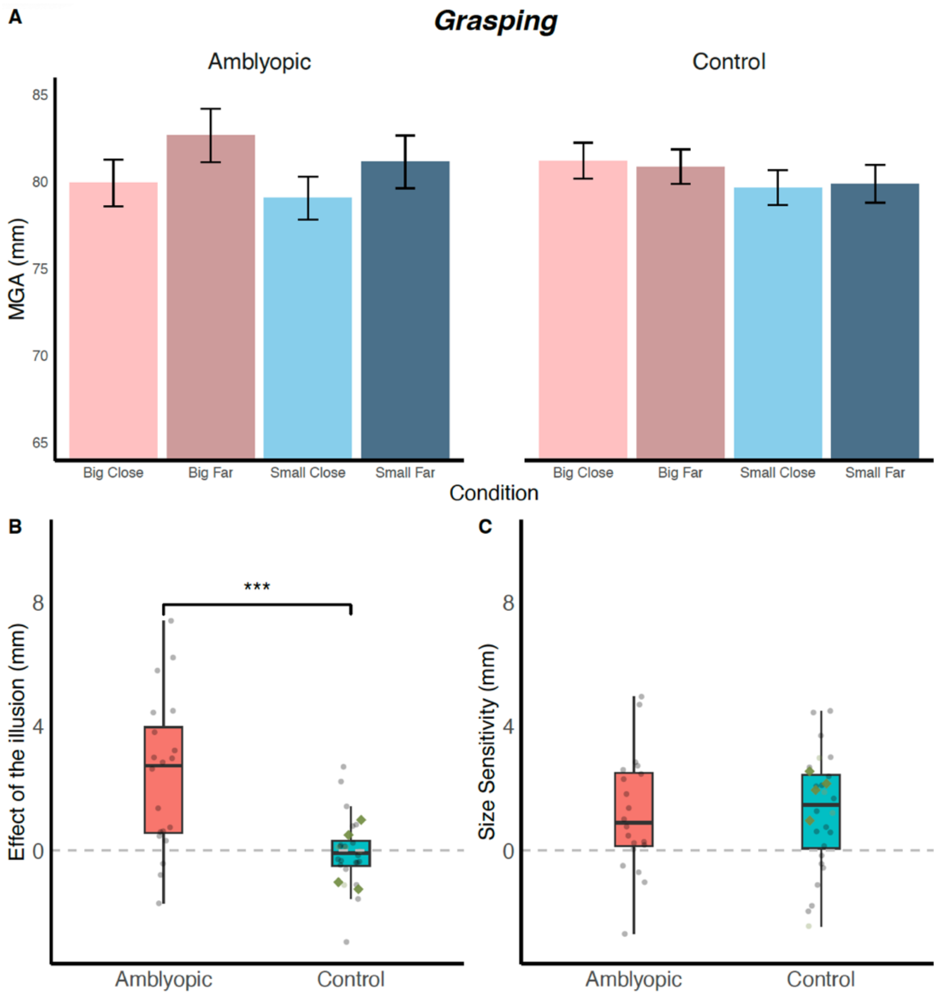

Figure 2. Grasping Task Results. **A.** The average MGAs as a function of group and conditions are plotted. Error bars reflect the standard error. The amblyopic group (left) had higher average MGAs for the "far" condition across block size and likewise smaller MGA's when the same block was placed on the "close" surface. The control group (right) had similar MGAs for the big block across the "close" and "far" surfaces and similar results for the small block. Both the results seen in panels B and C are computed from the MGA results found in panel A. **B.** The result of every individual is plotted as a singular data point for both groups. The green rhombuses reflect the results from the monocular controls**.** Across Figures B and C, the amblyopic group effect is indicated by the red boxplot whereas the control group is indicated by the blue**.** Group means are indicated by the bold black line. The lower and upper limits of the box plots correspond to the first and third quartiles (the 25th and 75th percentiles). The dotted grey line indicates the results if there was to be no effect of the illusion (0mm). The control group (right) did not exhibit susceptibility to the illusory size of the objects whereas the amblyopic group (left) did. **C.** The average size sensitivity of every individual is plotted as a singular data point for both tasks. The dotted grey line indicates the results if there was to be no sensitivity to object size (0mm). Both the amblyopic group (left) and control (right) group exhibited similar size sensitivity when grasping the blocks.

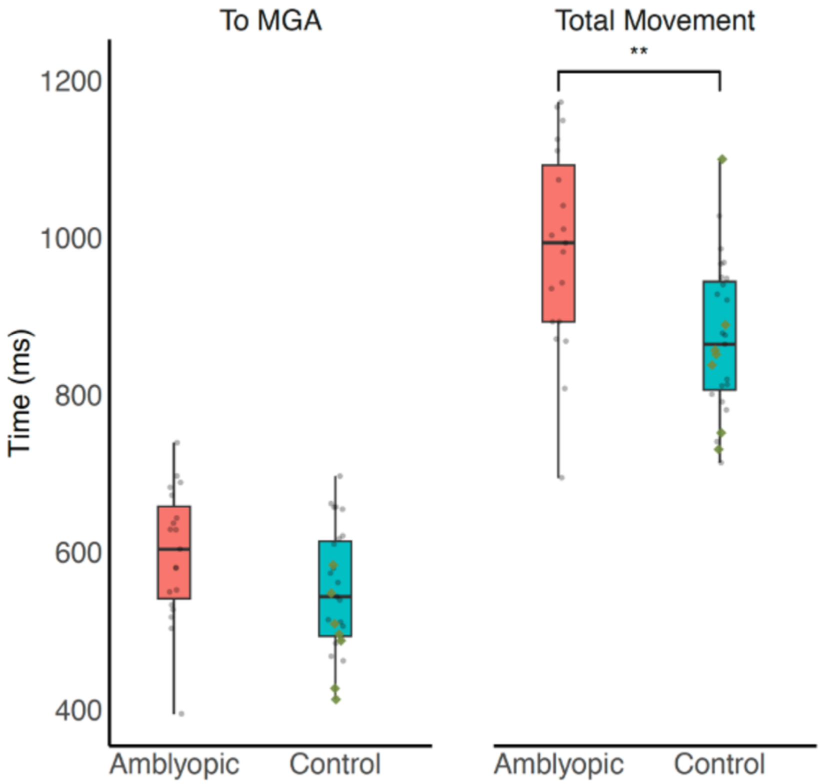

Figure 3. Movement times for grasping task. The data from every individual is plotted as a singular data point for both tasks. The lower and upper limits of the box plots correspond to the first and third quartiles (the 25th and 75th percentiles). The amblyopic group effect is indicated by the red boxplot whereas the control group is indicated by the blue. The green rhombuses reflect the results from the monocular controls. The amblyopic group and control group had no difference in the time taken to reach the MGA (left). There was a significant difference however in the groups' overall movement time (right) with longer movements times for the amblyopia group.

3.3.2 Estimation task

We examined performance in the vision-for-perception task by analyzing the perceptual estimates of the objects (Figure 4A). A mixed ANOVA with object size (small or big), perceived distance (close or far) and group as the independent variables revealed a main effect of both size [$F_{(1, 35)} = 29.171$, $p < .001$, $\eta_p^2 = 0.455$] and distance [$F_{(1, 35)} = 31.298$, $p < .001$, $\eta_p^2 = 0.472$], suggesting that participants were sensitive to object size and were influenced by the illusion. Critically, there were no interactions between group and other factors (Fs < 1), suggesting both groups were equally sensitive to object size and to the illusion (Figure 4C). Simple planned comparisons (with distance as the independent variable) further demonstrated that the amblyopic ($F_{(1,35)} = 11.403$, $p < .005$) and control participants ($F_{(1, 35)} = 21.594$, $p < .001$) modulated their endpoint estimations based on illusory effect of the Ponzo Illusion, such that the objects which were placed on the “far” surface were perceived to be longer compared with those placed on the “close” surface(Figure 4B)**.**

3.3.2.1 Discussion of estimation results

Collectively, the results from the perceptual task show similar size sensitivity and susceptibility to the illusion across both groups. Thus, the susceptibility to illusion observed under the grasping task in children with amblyopia could not be attributed to an overall oversensitivity to monocular depth cues and is more likely to reflect a reduced functional dissociation between perceptual and visuomotor representations.

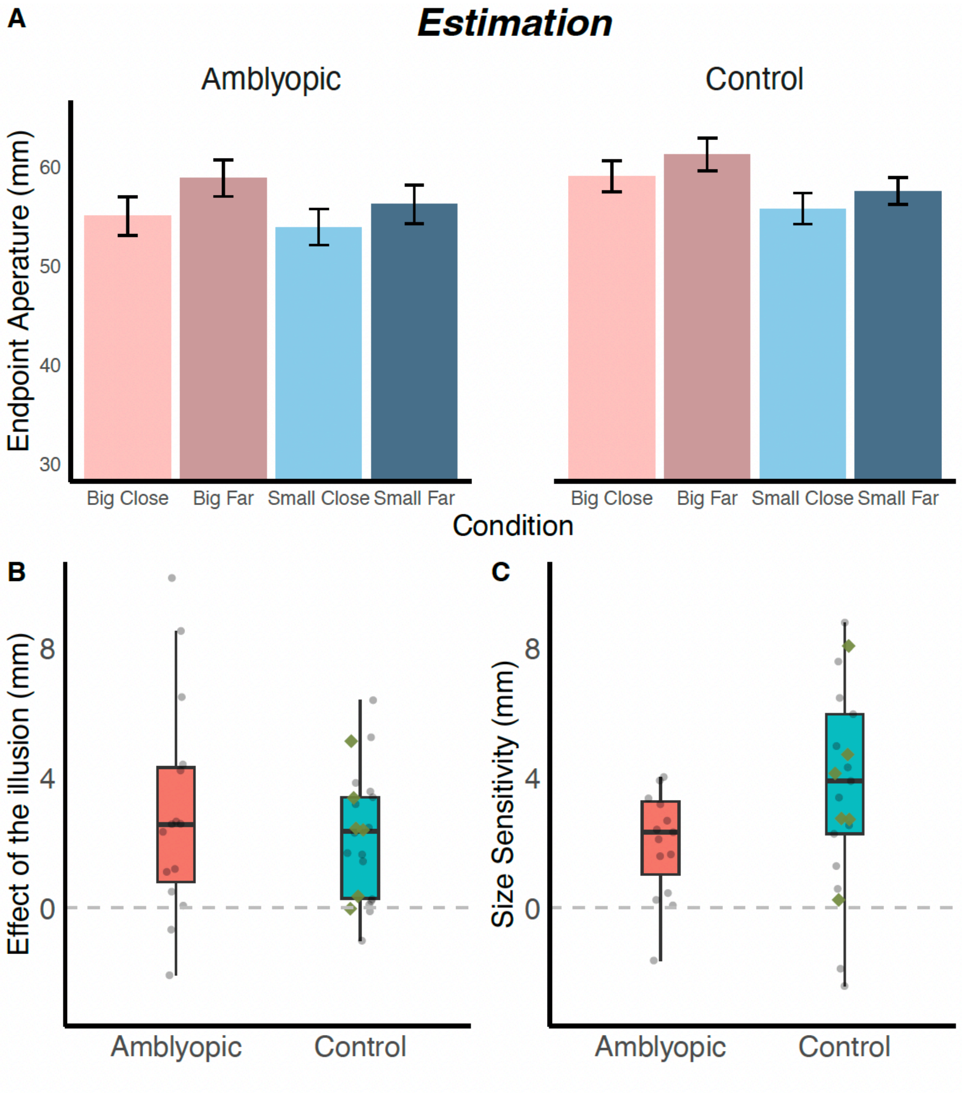

Figure 4. Estimation Task Results. **A.** The average manual estimates as function of group and conditions are plotted. Error bars reflect the standard error. Both the amblyopic group (left) and the control group (right) had higher average endpoint apertures for the "far" condition across block size and likewise, smaller endpoint apertures when the same block was placed on the "close" surface. **B.** The effect of the illusion of every individual is plotted as a singular data point for both tasks. The green rhombuses reflect the results from the monocular controls**.** Across all figures, the amblyopic group effect is indicated by the red boxplot whereas the control group is indicated by the blue**.** Group means are indicated by the bold black line. The lower and upper limits of the box plots correspond to the first and third quartiles (the 25th and 75th percentiles). The dotted blue line indicates the results if there was to be no effect of the illusion (0mm). Both the control group (right) and amblyopic group exhibited susceptibility to the illusory size of the objects **C.** The average size sensitivity of every individual is plotted as a singular data point for both tasks. The dotted blue line indicates the results if there was to be no sensitivity to object size (0mm). Both the amblyopic group (left) and control (right) group exhibited similar size sensitivity when perceptually estimating the blocks.

3.4. Discussion

The current study aimed to investigate the role of normal visual experience in the development of the functional dissociation between vision-for-perception and action. To this end, we compared perceptual and visuomotor performance in children with amblyopia and typically developed children. The results of the grasping task revealed a profound difference between the two groups in terms of the effect of the illusion. Specifically, similar to a previous study (Freud et al., 2021), neurotypical children demonstrated a dissociation between perception and action, such that the illusion modulated their perceptual estimations but not their grasping apertures. In contrast, amblyopic children were influenced by the illusion under both tasks as their perceptual estimations and their grasping apertures were modulated by the perceived size of the objects. These findings shed new light on the role of atypical visual development on the emergence of the dissociation between action and perception. In particular, the susceptibility of amblyopic children to the Ponzo illusion observed for the grasping task provides evidence for a greater association between vision-for-action and vision-for-perception in these children compared to typically developing children.

3.4.1 Development of action-perception dissociation under normal development

The longstanding functional distinction between perception and action has been predominantly studied within the context of the mature brain, leaving the developmental trajectory of this dissociation somewhat unclear. Recent behavioral (Freud et al., 2019, 2021; Hadad et al., 2012) and neuroimaging studies (James & Kersey, 2018; Vinci-Booher et al., 2022), however, have begun to elucidate the developmental processes that shape this dissociation.

The current study echoes previous findings (albeit with a slightly modified design) that school-age children can resist the influence of the Ponzo illusion during a grasping task, while still being susceptible to the illusion during a perceptual task (Freud et al., 2021). Similarly, a dissociation between perception and action has been noted in children as young as five years old who do not conform to Weber’s law only during a visuomotor task (Hadad et al. 2012). An fMRI study further revealed that children, during various visuomotor tasks, engage similar cortical regions of the dorsal visual pathway as adults, suggesting an early maturation of this pathway (James & Kersey, 2018). These findings could be interpreted as evidence for an early maturation of the perception-action dissociation. However, results from other behavioral and neuroimaging studies suggest that these two systems continue to specialize throughout development, and their computations may exhibit more overlap during this stage compared to adulthood. For instance, Freud et al. (2019) found that children, unlike adults, conform to Weber's law in their grasping trajectories when presented with more complex stimuli. Similarly, Schum and colleagues (2012) used the Garner paradigm to demonstrate a diminished perception-action dissociation in children, indicating that children process object shape holistically even when performing a grasping task that prompts a more analytical processing style in adulthood. A recent MRI diffusion study also revealed a gradual maturation of white matter tracts, with dorsal pathway tracts maturing last, following the maturation of between-pathways tracts and ventral pathway tracts (Vinci-Booher et al., 2022).

Our study further substantiates that certain aspects of the dissociation are present even in young children. However, the limited sample size in our study precludes us from investigating developmental changes across different ages within the control group. Consequently, it remains possible that the insensitivity of grasping movements to visual illusions is an emerging characteristic of the developing system. Importantly, children with amblyopia, who were age-matched with the control group, exhibited profound differences from the controls and did not display the anticipated dissociation between perception and action.

3.4.2 Visuomotor deficits in amblyopia

Over the years, individuals with amblyopia were found to have deficits in visually guided functions presumably related to dorsal pathway computations such as the processing of motion cues (Simmers et al., 2003; Thompson et al., 2008), spatial localization (Sireteanu et al., 2008) and visuomotor behaviors (Grant and Conway 2015; Kelly et al. 2020; Niechwiej-Szwedo et al. 2014; for a comprehensive review see: Niechwiej-Szwedo, Colpa, and Wong 2019). In the last two decades different studies have demonstrated consistent alterations in different types of visuomotor behaviors including reach-to-touch (Niechwiej-Szwedo et al., 2011, 2014) and reach-to-grasp (Grant et al., 2007, 2014; Niechwiej-Szwedo, Goltz, et al., 2012).

These alterations modulate both feedforward and feedback control of reaching and grasping movements (for a review see Niechwiej-Szwedo et al., 2019). For example. one of the first studies to quantify the kinematics of grasping movements in amblyopic subjects reported that while individuals with amblyopia were comparable to controls in terms of their MGA, their grasping movements were slower, less accurate and more variable even during the binocular viewing condition (Grant et al., 2007). Consistent with these findings, we showed that children with amblyopia exhibited similar size sensitivity in terms of their MGAs, but nevertheless had prolonged overall movement times. Importantly, our study sheds new light on the underlying mechanisms that modulate grasping behaviors in individuals with amblyopia. Specifically, we revealed that children with amblyopia demonstrated a clear susceptibility to the Ponzo illusion suggesting an overreliance on perceptual representations when executing grasping movements.

The reduced functional dissociation in amblyopia observed in the current work could be indicative of a reduced neural dissociation between the dorsal and ventral pathways. Notably, some neuroimaging studies have proposed abnormalities in cortical connections in individuals with amblyopia, further supporting this notion. For example, Ding et al. (2013) found altered functional connectivity between the cerebellum, inferior parietal lobule, and the primary visual area in amblyopic individuals. These findings indicate decreased functional connectivity within the dorsal pathway, particularly between the primary visual area and the inferior parietal lobule. Similarly, Li et al. (2011) examined effective connectivity in adults with amblyopia and reported diminished connectivity in both ventral and dorsal pathways, primarily implicating deficits in the extrastriate cortex. Importantly, normal action control doubtless involves cross-talk between the ventral and dorsal pathways, emphasizing the complexity of the underlying neural mechanisms that govern the integration of perceptual and motor processes.

Lastly, it is important to note that the reduced dissociation between perception and action observed here could not be attributed solely to the lack of stereovision in children with amblyopia. Due to their lack of or reduced stereovision, children with amblyopia likely rely more on monocular cues to depth. This heavier reliance on monocular depth cues may be influencing their response to the Ponzo Illusion (linear perspective as a monocular depth cue). However, previous studies have already demonstrated that impaired visuomotor behaviors are evident even when individuals with amblyopia use their healthy eye or both eyes (Grant et al., 2007). Moreover, healthy adults who used plus lenses to simulate mild amblyopia did not exhibit changes in their reaching behaviors (Niechwiej-Szwedo et al., 2012). Similarly, in the current study, the “monocular control” group completed the experiment wearing an eye-patch, removing all binocular cues, but nevertheless their grasping behaviours were similar to the “binocular vision” control group, rather than the amblyopic group.

3.4.4 Dorsal pathway vulnerability

Deficits in visuomotor skills, while maintaining relatively intact visuoperceptual skills, have been observed not only in children with amblyopia but also in various other neurodevelopmental conditions, such as developmental coordination disorder, autism, and developmental dyslexia (for review see Atkinson 2017). Interestingly, it appears that the impact on behaviors associated with the dorsal pathway is often disproportionately greater compared to abilities associated with the ventral pathway in several neurodevelopmental disorders. Hence, this phenomenon has been termed "dorsal pathway vulnerability" (Atkinson & Braddick, 2011; Braddick et al., 2003)

Accordingly, amblyopia was found to modulate other functions that are promoted by regions of the dorsal pathway. For example, individuals with amblyopia often exhibit deficits in perceiving global motion indicating compromised integration of visual motion information, resulting in difficulties in perceiving and interpreting dynamic scenes accurately (Meier et al., 2016; Simmers et al., 2003). Notably, the computation of global motion heavily relies on hMT+, a region recognized as part of the dorsal pathway and projecting to the parietal cortex (Kwan et al., 2021; Mundinano et al., 2018) as well as the intraparietal sulcus (Sunaert et al., 1999; Helfrich et al., 2013). The visuomotor and global motion processing deficits in amblyopia are thought to arise from abnormal development and functional connectivity in the visual pathways during critical periods of early visual development (Hamm et al., 2014).

We propose that the abnormal visual experience in amblyopia disrupts the development of the typical dissociation between the ventral and dorsal pathways. This in turn has a consequent impact on visuomotor behaviors unevenly compared to visual perceptual abilities and highlights the profound effect of early life suboptimal visual experience on the development of the dorsal visual pathway. It is important to note, normal action control doubtless involves crosstalk between the ventral and dorsal pathways, emphasizing the complexity of the underlying neural mechanisms that govern the integration of perceptual and motor processes.

3.4.5 Limitation

Despite the novel insights from the current investigation, we acknowledge several limitations that should be addressed in future research. First, only children were tested in this study and therefore our knowledge regarding whether the reduced dissociation between action and perception observed in amblyopic children persists into adulthood remains unanswered. One option is that the onset of this dissociation is just delayed, but nevertheless occurs later in life. Alternatively, it is plausible that there is a critical or sensitive period for the emergence of the dissociation and consequently the suboptimal visual developmental alters the dissociation between the two systems even in adulthood (Knudsen, 2004).

Another limitation of the current design is the focus on one aspect of the dissociation (i.e., the effect of visual illusions on perception and action). Further research that will utilize other established paradigms like the Garner paradigm (Ganel & Goodale, 2003) or adherence to

Weber’s law (Ganel, Chajut, et al., 2008) are needed to fully characterize which aspects of the dissociation are reduced in children (and adults) with amblyopia.

Earlier research conducted on typical adults has shown that the Ponzo illusion does not significantly impact the scaling of Maximum Grip Aperture (MGA), similar to what we observed in neurotypical children in this study. However, this illusion is known to influence the grip forces exerted on objects. Specifically, the perception that objects appear larger than their actual size leads to an increase in the grip forces applied to them, something we did not explore here. This observation aligns with the idea of an overestimation of the size-weight relationship (as demonstrated by Brenner & Smeets, 1996; Jackson & Shaw, 2000). Therefore, this raises the possibility of another dissociation to explore in future research endeavors.

One notable limitation of our study pertains to the age disparity observed among our child participants. The inclusion of children from a wide age range was necessitated by practical constraints and the inherent challenges associated with recruiting child participants with amblyopia. We recognize that the age disparity among child participants is a limitation of our study, and it may impact the generalizability of our findings to specific age cohorts. Notably, however, it is important to emphasize that control participants were age-matched to the amblyopia group, suggesting that the observed differences between the two groups could not be attributed to the wide range of ages. We encourage future research to further investigate these phenomena by recruiting more children in each age group to better elucidate age-related trends and developmental factors affecting action and perception in amblyopia.

3.5 Conclusion:

The present study offers innovative perspectives on the influence of typical visual experiences in shaping the dissociation between action and perception. We provide new evidence for a reduced functional dissociation between perceptual and visuomotor representations in children with amblyopia. The results highlight that the reduced action-perception dissociation in children with amblyopia maybe a factor in driving a compromised development of visuomotor behaviors and findings further supports the concept of dorsal pathway vulnerability in neurodevelopmental disorders.

CHAPTER 4: REDUCED DISSOCIATION BETWEEN PERCEPTION AND ACTION IN AUTISTIC INDIVIDUALS

Ahmad, Z., Hadad, BS., Mazuz,Y., Ganel, T., & Freud, E. (Under Review). Reduced Dissociation Between Perception and Action in Autistic Individuals

4.1 Abstract

Changes in perceptual behaviors are a core phenotype of autism[1], yet the underlying mechanisms remain unclear. In two experiments testing functional specialization of the visual system, we compete different hypotheses arising from two different accounts for perceptual alterations in autism. The Bayesian accounts predict an overall attenuated use of priors in perception, while the reduced functional specialization account predicts broad and underspecified tunning of functions subserving perceptual and visuomotor behaviors. We characterized the effects of spatial context (Experiment 1) and context over time (Experiment 2) of stimulus presentation, which typically affect perception but not grasping in non-autistic individuals. In each experiment, autistic and non-autistic participants completed grasping and estimation tasks. In Experiment 1, we used two objects of different sizes, placed on an illusory Ponzo background, making them appear “close” or “far” from the observer. Non-autistic individuals showed a robust illusion effect only during perceptual estimation, while autistic individuals were affected during estimation and grasping. In Experiment 2, we presented a standard stimulus (40mm) in two blocks of stimuli: a “wide” range (20-60mm) and a “narrow” range (35-45mm). Again, non-autistic participants showed a strong effect of context on their sensitivity, but only for the estimation task, exhibiting higher thresholds in the “wide” block. Autistic participants showed consistent effects of the experimental context for both tasks. Together, these results provide novel evidence for a reduced functional dissociation between

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[1] In acknowledgment of the ongoing discourse regarding terminology about individuals diagnosed with autism, we use "autistic individuals" and “non-autistic individuals” in line with recent conventions.

perception and action in autistic people, supporting the reduced specialization account as a possible underlying mechanism mediating perceptual alterations in autism.

4.2 Introduction

Autism spectrum disorder (ASD) is an early-onset neurodevelopmental condition characterized by difficulties in social interaction, communication, and repetitive or restricted interests and behaviors (*Diagnostic and Statistical Manual of Mental Disorders*, 2013). Changes in sensory perception is a fundamental characteristic and a consistent phenotypic marker of the condition (Robertson & Baron-Cohen, 2017). However, studies testing sensory and perceptual functions have yielded mixed findings. Some basic perceptual functions, such as visual acuity (Kéïta et al., 2010; Tavassoli et al., 2011) and contrast discrimination (de Jonge et al., 2007; Koh et al., 2010) are intact, while other fundamental abilities such as adherence to Weber's Law (Hadad & Schwartz, 2019), contour integration (Frith, 2003; Happé & Frith, 2006) and stereopsis and depth perception (Kaplan, 2005; Scharre & Creedon, 1992), are altered. Modulations have also been reported for high-level perceptual processes such as face recognition (Dawson et al., 2002; Hartston et al., 2023; Hadad et al., 2019), gender discrimination (Njiokiktjien et al., 2001), and facial emotional expressions (Teunisse & de Gelder, 2001; Twito et al., 2024).

The Bayesian inference and predictive coding, two related theoretical frameworks, have recently suggested an underlying mechanistic account for these various perceptual alterations, involving canonical processes of perceptual inference (Brown et al., 2013). In both frameworks, perception is the outcome of inference processes that combine noisy external (sensory) information with internal models of the world. Bayesian inference is a computational framework in which sensory uncertainty (likelihood) and internal models (priors) are combined according to Bayes' rule (Knill & Richards, 1996; Mamassian et al., 2002). According to these theoretical frameworks, altered perception in autism arises from reduced use of prior beliefs.

The Bayesian account postulates that difficulties in learning and forming perceptual priors (Pellicano & Burr, 2012) or enhanced sensory evidence (Brock, 2012; Karvelis et al., 2018; Lawson et al., 2014) could lead to an underuse of prior information in autism. The predictive coding view assumes an inability to adjust prediction errors when sensory input deviates from expectations (Sapey-Triomphe et al., 2021; Van Boxtel & Lu, 2013; Van De Cruys et al., 2014).

Despite these strong claims, evidence remains inconclusive and often depends on post hoc interpretations of results. Recent studies directly manipulating prior information show a typical use of perceptual priors (Binur et al., 2022), as well as an integration of priors and sensory uncertainty (Allenmark et al., 2021; Fazioli et al., 2024; Skewes et al., 2015). However, modulations are shown specifically in the flexibility with which priors are updated (e.g., Arthur et al., 2021, 2023; Binur et al., 2022, Twito et al., 2024). These findings point to more general aspects such as learning and flexibility, rather than the mere use of priors, as the underlying cause of these perceptual modulations.

Emerging evidence for more broadly tuned perceptual representations in autism (Bedford et al., 2016; Hadad & Yashar, 2022) led to a different hypothesis suggesting that the atypical perceptual processing is a result of reduced perceptual specialization (Hadad & Yashar, 2022). Contrary to the specialization of perceptual functions to environmental regularities typically seen over the course of development (Pascalis et al., 2014), autistic people show reduced tunning of perceptual representations to exposure. For instance, face processing undergoes a long period of refinement that improves face perception abilities (Morton & Johnson, 1991; Simion & Giorgio, 2015), but typically accompanied by narrowing effect, such that non-autistic observers show an advantage in discriminating own-race faces compared to other-race faces (Meissner & Brigham, 2001; Walker & Tanaka, 2003). Autistic individuals demonstrate a substantial reduction of the other race effect arising specifically from reduced proficiency in recognizing the predominant, own-race faces (Hadad et al., 2019). This broader tuning may disrupt the fine-tuning necessary for typical perceptual processing and impact various aspects of sensory experience.

One of the most prominent examples of functional specializations in the human brain is the division of labour between visual computations for action and for perception. According to the Two Visual Pathway Hypothesis, perception and action are subserved by two distinct cortical pathways. Originally, it was suggested that the two pathways represent differential visual qualities (Mishkin & Ungerleider, 1982). However, Goodale and Milner (1992) revised this framework and redefined the functions of the two pathways by their output requirements. According to this influential view, computations carried out by the ventral pathway support perceptual processes (i.e., “what”), while computations carried out by the dorsal pathway promote visually guided actions (i.e., “how”). While the original findings for this functional dissociation were from investigations of non-human primates (Mishkin & Ungerleider, 1982) and neuropsychological cases (Goodale & Milner, 1992), later studies demonstrated the dissociation in neurotypical individuals using different psychophysical approaches.

Specifically, it has been shown that perception and action are differently affected by context induced by spatial and temporal aspects of the stimuli. Unlike their robust effect on perception, spatial size context, such as the one induced by visual illusions, or context over time of stimulus presentation has little effect on grasping (Ganel, Tanzer, et al., 2008; Namdar et al., 2018; Whitwell et al., 2016). For spatial context, studies testing size perception within the

Ponzo illusory settings, demonstrated this dissociation as early as 5 years of age (Ahmad et al., 2023; Freud et al., 2021). This illusion occurs when two identical lines appear different in length because they are placed over converging lines, creating a sense of depth (Figure 1). Typically, the brain interprets the line closer to the narrow end of the converging lines as farther away, making it perceived longer than it actually is.

Notably, size perception is also sensitive to the context over time. Namdar et al. (2018) found that perceptual resolutions of a target stimulus depends on the context within it is presented: perceptual sensitivity to a stimulus is heightened when the contextual stimuli tested are of similar magnitudes, compared to when they are spread over a broader range of magnitudes (Hellström, 2000; Namdar et al., 2016). However, as in the case of the Ponzo illusion, temporal effects of context are not found for visually guided actions such as in grasping (Namdar et al., 2018).

We used these dissociative effects of context on perceptual estimations and action to examine the specialization of the visual system in autism. Specifically, we examined the effect of spatial context (Experiment 1) and the stimulus context over time (Experiment 2) on perceptual and visuomotor behaviors in both autistic and non-autistic participants. This is a unique opportunity to test two significant competing hypotheses of perceptual alterations in autism: if Bayesian accounts of attenuated priors hold true, there should be minimal influence of spatial context or context over time on autistic individuals on both the grasping and in perceptual estimation tasks. Conversely, if the hypothesis of reduced functional specialization is correct, we would expect these effects of prior information to be consistently observed across both grasping and perception tasks (Figure 1A). A persistent pattern of broad contextual effects across both spatial context (Experiment 1) and context over time (Experiment 2) would indicate a generalized reliance on prior information that is not confined to the typical division of labor between perception and action. This would suggest a less specialized visual system in autism.

4.3. Experiment 1 – Spatial Context

4.3.1 Methods

The research protocol for both experiments was approved by the Institutional Review Board of York University and by the Institutional Review Board (IRB) of the University of Haifa. Written informed consent was obtained from all participants before testing and after an explanation of the nature and possible consequences of the study. Participants received monetary compensation or course credits for their participation. The current procedures were based on methodologies outlined in previous works (Ahmad et al., 2023; Freud et al., 2021).

4.3.1.1 Participants

We recruited a group of 26 adults with high functioning ASD (7 females; mean age = 26.1 ±4.5 years) and 25 non-autistic adults (10 females, mean age 26.3 ± 2.5 years) for the spatial context study (Table 1). Both groups reported normal or corrected to normal vision. The groups were matched based on their intelligence — as measured by the Test of Nonverbal Intelligence (TONI4 test, Brown et al., 2010). The TONI allows testing of intelligence without the confounding effects of linguistic skills (Table 1). Participants were recruited via the local community and the “Beit Ekstein Center” for adults with communication difficulties. Four non-autistic participants were tested at the University of Haifa. The remaining (21) non-autistic participants were tested using the same experimental setup (see Apparatus and Stimuli for details) at York University, Toronto. Some participants with ASD completed both Experiment 1 and 2, with a gap of at least 12 months between the two experiments.

Table 1. Participants' Details, IQ Scores and AQ Scores for the Two Groups

	Experiment 1				Experiment 2			
	N (female)	Age (SD)	IQ (SD)	AQ (SD)	*N* (female)	Age (SD)	IQ (SD)	AQ (SD)
Autistic	26 (7)	26.1 (4.5)	99.9 (11.9)	27.24 (7.5)	31 (6)	27.3 (5.1)	99.5 (11.9)	27.1 (7.3)
Non-Autistic	25 (10)	26.3 (2.5)	*	19.96 (2.8)	28 (17)	28.8 (7.6)	101.9 (12.9)	19.8 (7.4)

* TONI IQ scores were not collected for the non-autistic cohort in this experiment

4.3.1.2 Apparatus and Stimuli

Participants sat in front of a small table on which the illusory context and the two objects were presented (Figure 1B). The two target objects were rectangular 3D plastic blocks matched in width (10 mm), depth (10 mm), and color (black) but differed in length by 2 mm (small: 40 mm & large: 42 mm) (Figure 1B). The illusory background (a version of the Ponzo Illusion) was flipped every 15 trials to counterbalance right, and left movements directed to the larger and smaller objects.

Grasping movements and manual estimations were recorded using an Optitrack system (Natural Point DBA OptiTrack, USA). The system included six Prime 13W cameras and three passive reflective markers attached to the participant's hand in such a way that permitted complete freedom of movement of the hand and fingers (Figure 1C). The system tracked the 3D trajectory of the participants' index, thumb, and wrist movement using a 100 Hz sampling rate and the resultant data permits the calculation of the aperture between the fingers at any given time point.

4.3.1.3 Procedure

The experiment consisted of two separate tasks, a grasping task, and a manual estimation task. These tasks were completed in two different experimental blocks. The order of the tasks was counterbalanced across participants with half of the participants completed the grasping task first followed by the manual estimation task, and half run on the opposite order. In the grasping task, participants were instructed to reach for the target object with the thumb and index finger across its length and to lift it off the table (approximately 15 cm) before setting it down in the same spot 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 to estimate the corresponding width. They were instructed to hold the finger posture for two seconds before returning to the "home" position

In each of the trials, one of the two target objects was placed on the illusory setting on either the "close" or "far" side of the display in front of the participant within arm's reach (approximately 40 cm). In each block, each of the two target objects was presented 30 times in a randomized order, resulting in a total of 60 trials per block.

4.3.1.4 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 by a conjunction of three conditions; 1) the Z (superior-inferior) location of the fingers was at its local minimum value, which indicated that the fingers were positioned along the same plane as the target object, 2) the Y (right-left) location of the fingers was at its maximum, which indicated that the fingers were furthest away from the “home” position, and 3) the delivery velocity (the speed of the overall hand movements) reached the minimum speed, indicating that the grasping movement had come to end as the hand had made contact with 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. The MGA is known to be well correlated with the size of the goal object (Jakobson et al., 1991).

For the estimation task, the aperture between the thumb and index finger that was held constant over 10 consecutive frames was determined to reflect the perceived width of the object (Freud et al., 2016). All trials (grasping and manual estimation) 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.

To assess the illusion magnitude for the grasping task, we first calculated the average MGA of the small object under both the far and close conditions and repeated the procedure for the large object. We then subtracted the average MGA for grasping movements directed to the far surface (for both large and small objects) from the average MGA for grasping movements directed to the close surface. Values that are greater than 0 (mm) reflect an effect of the Ponzo illusion. We employed similar calculations on the aperture values at the estimation point to assess average effect of the illusion for the perceptual task.

4.3.2. Results

To examine whether the experimental spatial context modulated the precision of grasping and estimation movements differently in the two groups, we conducted a three-way mixed ANOVA with task (grasping or estimation) and perceived distance (close or far) as within-subject factors, and group (autistic and non-autistic) a between-subject factor. A three-way interaction between these variables was found significant [$F_{(1, 49)} = 7.073$, $p < .05$, $\eta_p^2 = 0.126$]. Additional analyses were subsequently performed separately for each group to further explore this effect.

As shown in Figure 1D, non-autistic individuals showed sensitivity to the experimental spatial context under the manual estimation, but not under grasping, as indicated by the significant interaction between distance and task [$F_{(1, 24)} = 16.778$, $p < .001$, $\eta_p^2 = 0.411$]. The spatial context affected only the manual estimations [$F_{(1, 24)} = 15.775$, $p < .001$, $\eta_p^2 = 0.387$], such that participants' MGAs were greater when the target object was presented on the "far" side of the illusion (62.8 mm) and smaller MGAs when the same object was placed on the "close" side (61.5 mm). In contrast, under the grasping task, we did not observe a modulation of the MGAs as function of the illusion [$F<1$], (80.9 & 81.0 mm, for "far" and the "close" conditions (Figure 1D), displaying a clear dissociation between perception and action for non-autistic participants.

The autistic participants demonstrated a different pattern of results showing the effects of spatial context under both their manual estimations and grasping (Figure 1E). Under the "far" condition higher MGAs were observed for both the grasping and manual estimation. A mixed ANOVA with distance (close or far) and the task (grasping or estimation) as within-subjects variables revealed significant main effects for both the distance [$F_{(1, 25)} = 6.675$, $p < .05$,

$\eta_p^2 = 0.211$] and the task [$F_{(1, 30)} = 23.244$, $p < .001$, $\eta_p^2 = 0.482$], indicating that each independently affected performance. Critically, there was no interaction between the two factors [$F < 1$], suggesting that the influence of distance on performance is consistent across both grasping and estimation tasks for the ASD group (Figure 1E).

To further explore the differences between the groups, we plotted every individual's effect of perception versus grasping, with the x-axis corresponding to relative perception scores and the y-axis to grasping scores (Figure 1F&G). The dashed diagonal line ($y = x$) signifies a hypothetical equivalent effect of context on both perception and action. For the non-autistic participants, it is observed that most of the data points are shifted to the right of the dashed diagonal line, indicating that spatial context had a more pronounced effect on perception than on action in this group. This suggests that non-autistic individuals are more sensitive to changes in spatial context when they complete a perceptual task compared to when they engage with a visuomotor task. Unlike the non-autistic group, the data points for the autistic participants (Figure 1G) are clustered around the diagonal line, indicating a similar influence of spatial context on both perception and action. For autistic participants, the effect of spatial context is evenly distributed across both perception and action, indicating a consistent effect of spatial context in both domains. These observations were further supported by a statistical analysis that shows that for the non-autistic group, the average distance of each dot from the diagonal line ($y = x$) was -1.132mm, while the autistic group's average distance was -0.317mm [$F_{(1, 51)} = 5.72$, $p < .05$, $\eta_p^2 = 0.101$].

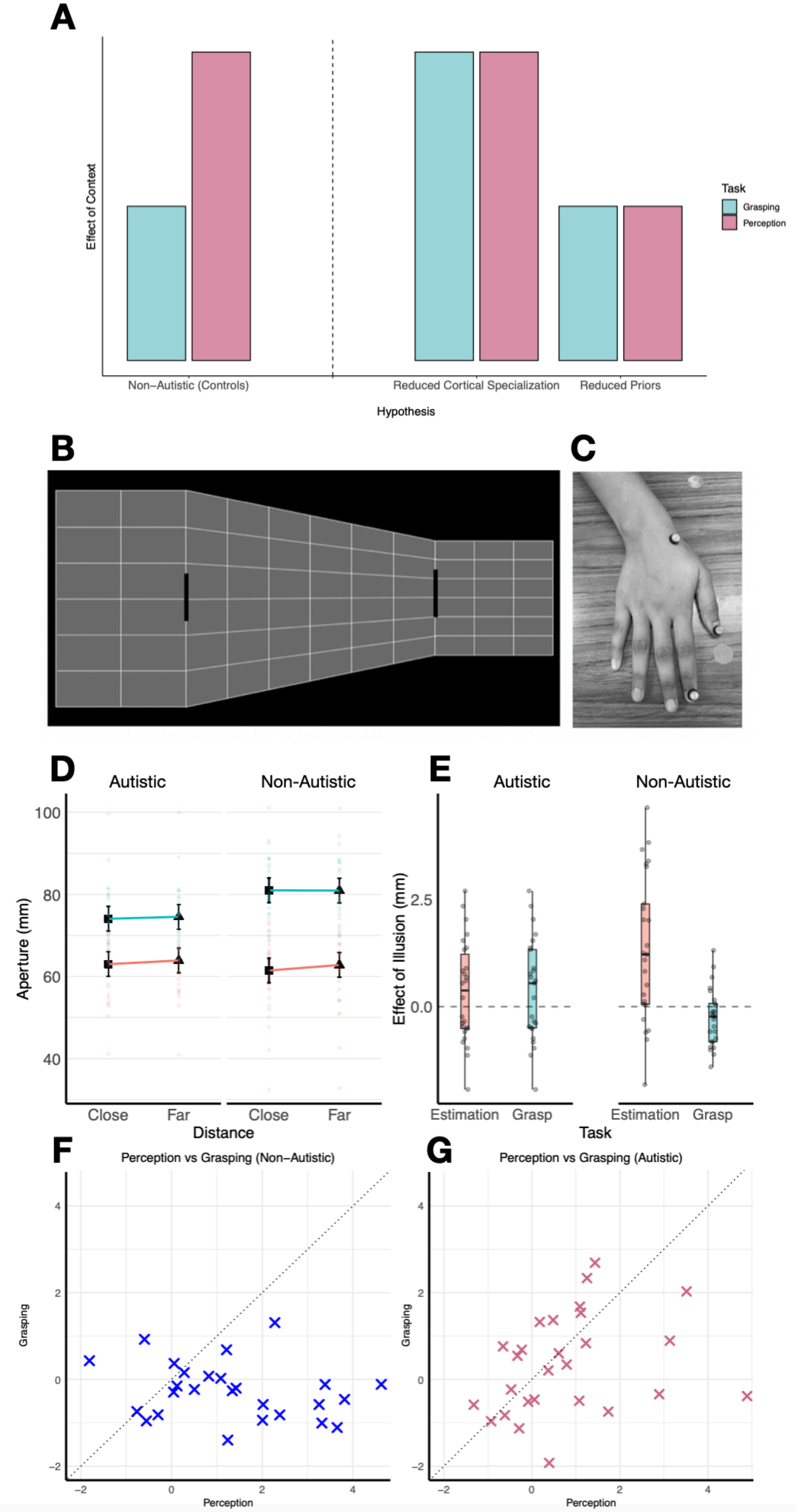
A
Effect of Context
Task
Grasping
Perception
Non–Autistic (Controls)
Reduced Cortical Specialization
Reduced Priors
Hypothesis
B
C
D
Autistic
Non-Autistic
100
80
60
40
Aperture (mm)
Close
Far
Close
Far
Distance
E
Autistic
Non-Autistic
2.5
0.0
Effect of Illusion (mm)
Estimation
Grasp
Estimation
Grasp
Task
F
Perception vs Grasping (Non–Autistic)
4
2
0
−2
Grasping
−2
0
2
4
Perception
G
Perception vs Grasping (Autistic)
4
2
0
−2
Grasping
−2
0
2
4
Perception

Figure 1 (**A**) **Expected Effects of Context on Grasping and Estimation Tasks:** The bar graph depicts the anticipated impact of temporal and spatial context on grasping (pink) and estimation (blue) tasks for autistic participants based on the two differing accounts. Based on previous studies, for non-autistic individuals, effect of context is expected mostly for the perceptual task. If the Bayesian decision theory holds true, it is anticipated to observe attenuated influence of spatial or temporal context on both the grasping and estimation tasks for the autistic participants. Conversely, if the hypothesis of reduced functional specialization is accurate, it is expected that contextual information would modulate both grasping and perception behaviors.

Experimental Design for Spatial Manipulation (B): The figure displays the illusionary background (Ponzo Illusion) that the stimuli were placed on. **Optitrack System Setup (C)**: Distance between the fingers was measured with an Optitrack system, which tracked the 3-D position of light-reflecting diodes attached separately to each participant's index finger, thumb, and wrist.

Spatial Experiment Results. **(D)** The average MGAs and apertures in manual estimations as a function of group and conditions. Error bars reflect the standard error. The result of every individual is plotted as a singular data point for both groups. The red line indicates the perceptual estimation task results, and the blue indicates the grasping results. Autistics participants (left) had higher average MGAs for the “far” surface compared to the MGAs observed for the objects placed on the close surface across the tasks. The non-autistic had higher average MGAs for the “far” surface and smaller MGAs on the “close” surface in the perceptual task only. The non-autistic (right) had similar MGAs for the stimuli across the “far” and “close” surface for the grasping task. The results seen in panel B are computed from the aperture results found in panel A. **(E)** The result of every individual is plotted as a singular data point for both groups. The red box plot indicates the perceptual task results, and the blue indicates the grasping results. Group means are indicated by the bold black line. The lower and upper limits of the box plots correspond to the first and third quartiles (the 25th and 75th percentiles). Individual points above and below these limits signify outliers. The dotted grey line indicates the results if there was to be no effect of the illusion (0mm). The non-autistic (right) did not exhibit susceptibility to the illusory size of the objects in the grasping whereas the autistic participants (left) did. Both groups displayed an effect of the illusion in the perceptual task.

Effect of Spatial Context on Perception and Grasping (F). The scatter plot illustrates the impact of spatial context on perception and action, with each blue data point representing an individual non-autistic participant. The x-axis indicates the effect of the illusion on perception, while the y-axis indicates the effect of the illusion of grasping movements. The dashed diagonal line signifies a hypothetical equivalent effect of context on both perception and action. For the non-autistic participants, there is a general shift to right of the diagonal line suggesting greater effect of context on perception vs. action. **(G)** The plot illustrates the impact of spatial context on perception and action, with each red data point representing an individual autistic participant. The clustering of data points around the diagonal line indicates a similar contextual effect on both perception and action in autistic individuals.

4.3.3 Interim Discussion

In Experiment 1, we manipulated the spatial context using the Ponzo illusion. We replicated previous findings showing that non-autistic individuals displayed a clear dissociation between perception and action (Ahmad et al., 2023; Ganel, Tanzer, et al., 2008; Ganel & Goodale, 2003). Specifically, the illusion significantly affected their performance on the estimation task but had no effect on their grasping task. In contrast, autistic participants showed a consistent influence of the illusion across both the perceptual and the visuomotor task, suggesting a reduced functional dissociation between perception and action.

One interpretation of these findings is that visual representations promoting perception and visuomotor control are less specialized in autism such that perceptual representations intrude visuomotor representations. This enhanced crosstalk between the systems supports the notion of a reduced functional specialization of the visual system. It is consistent with previous work that has found the broader tuning of perceptual processes (Hadad et al., 2017, 2019), and more flexible visual computations in autism (Bedford et al., 2016).

At the same time, the results provide evidence against the Bayesian account of perceptual alterations in autism. Reduced susceptibility to perceptual illusions was extensively used to support Bayesian accounts for autistic perception. However, contrary to these claims, and consistent with recent empirical evidence (Avraam et al., 2019; Binur et al., 2022; Manning et al., 2017), we show here intact susceptibility to perceptual illusions in autism. No evidence for reduced magnitude of the illusion was found. In fact, atypical effects of perceptual priors in autism were demonstrated only in an elaborated manner of their use; even within a visuomotor task where visual computations are typically shown to be immune to stimulus context.

While this first experiment provides evidence for reduced functional specialization in autism using spatial context, one might suggest that the Ponzo illusion represents a specific type of context manipulation (i.e., spatial). Moreover, some earlier research has criticized the use of visual illusions to investigate the perception-action dissociation (e.g., Franz et al., 2000, 2001). A more detailed understanding of this phenomenon requires testing whether such atypicalities extend beyond spatial framing to other forms of contextual structure. Specifically, one key dimension of context that shapes perceptual and motor processing is the distribution of stimulus magnitudes over time, what we refer to here as size context over time. In typical observers, judgments of a given stimulus are modulated by the range of surrounding stimuli encountered within a block, reflecting adaptive tuning of internal representations based on stimulus history (Namdar et al., 2018). This form of contextual sensitivity is well-documented in perception but, crucially, tends to spare visuomotor behavior.

By investigating whether this pattern holds in autism, Experiment 2 enables us to test whether the reduced dissociation observed in Experiment 1 is a feature of generalized contextual integration across domains, rather than a spatially specific phenomenon. Moreover, unlike illusions, which rely on cue conflicts and perceptual reinterpretations, range-based manipulations offer a cleaner test of representational flexibility and contextual weighting. If autistic individuals show similar range effects in both perceptual and grasping tasks, this could provide converging evidence for broader, stimulus-driven crosstalk between the systems that are typically functionally segregated. In this way, Experiment 2 critically complements the spatial paradigm, advancing our understanding of how context influences the dissociation between perception and action in atypical development.

4.4. Experiment 2 – Context over time

4.4.1 Methods

4.4.1.1 Participants

We recruited a group of 31 adults with high functioning ASD (six females; mean age = 27.3 ±5.1 years) and 28 non-autistic adults (17 females; mean age = 28.8 ±7.6 years) for the context over time study (Table 1). Seven non-autistic participants were tested at the University of Haifa. The remaining (21) non-autistic participants were tested using the same experimental setup (see Apparatus and Stimuli for details) at York University, Toronto.

4.4.1.2 Apparatus and Stimuli

Participants sat in front of a small table on which the stimuli were presented. The stimuli were five objects of a constant width and height of 5 mm. The values of length were 20, 35, 40, 45, and 60 mm (Figure 2A&B). Each object was placed 30 cm from the participant, in the center of the table, along the midline of the participant. Objects were placed on the table perpendicularly to the participant's viewing plane. The parameters of the motion tracking system were similar to those described in Experiment 1.

4.4.1.3 Procedure

Similar to Experiment 1, the main experiment consisted of two separate tasks, a grasping task and a manual estimation task. Each task included two experimental blocks, the wide and the narrow range conditions resulting in a total of four experimental blocks. The wide range condition consisted of stimuli of 20 mm, 40 mm and 60 mm in length, whereas the narrow range condition consisted of stimuli of 35 mm, 40 mm, and 45 mm in length (Namdar et al., 2018). Both experimental blocks included the common target stimulus of 40 mm. The blocks differed only by the flanking stimuli, defining the range. In both range conditions (in each task), each of the three stimuli was presented 20 times, resulting in a total of 60 trials per block and 240 trials across the entire experiment.

In each trial, participants were introduced with one object and were asked to grasp or manually estimate the size of it. The order of the tasks was randomized for each participant, such that half of the participants completed the grasping task first followed by the manual estimation task and vice versa.

4.4.1.4 Data analysis

See section 4.3.1.4.

4.4.1.5 Statistical analysis

Statistical analyses were conducted using JASP (JASP Team, 2024). We employed mixed analysis of variance (ANOVA) on the grasping and estimation data. To calculate the JND for the grasping condition, we initially computed the MGA from the grasping movement trajectory trials under both narrow and wide conditions, using the common 40mm sized block. Subsequently, we determined the JND as the respective standard deviations of all those trials (Foster & Franz, 2013; Ganel et al., 2012; Ganel & Goodale, 2014). To assess the effect of the context over time, we subtracted the JND obtained under the wide condition from that obtained under the narrow condition. In the manual estimation (perception) task we used similar calculations on the aperture values, at the estimation point, to determine the JNDs.

4.4.2 Results

We examined whether the experimental context over time modulated the precision of grasping and estimation movements in a group of autistic and non-autistic individuals (Figure 2C.i-iv). As shown in Figure 2D, for non-autistic participants, we observed a clear dissociation between perception and action. The experimental context modulated the estimation apertures with greater JNDs for the 40mm object when it was presented in the “wide” context, while no effect of context was found for the grasping aperture. In contrast, for autistic individuals the effect of the experimental context was evident for both tasks (Figure 2D). This pattern was supported by a three-way interaction between task (grasping or estimation), temporal context (wide or narrow), and group (autistic or non-autistic) [$F_{(1, 58)} = 4.276$, $p < .05$, $\eta_p^2 = 0.070$] (Figure 2E). Additional analyses were subsequently performed for each group, to further explore this interaction.

As shown in Figure 2D, non-autistic individuals showed sensitivity to the experimental temporal context only under the perceptual task. This is shown in the significant interaction of task (estimation, grasping) and range (narrow, wide) [$F_{(1, 27)} = 12.668$, $p < .005$, $\eta_p^2 = 0.319$] (see Figure 2E). The range of the stimulus affected only the manual estimations [$F_{(1, 27)} = 19.085$, $p < .005$, $\eta_p^2 = 0.414$]. JNDs were greater when the target object (40mm) was presented along with flankers that were considerably different in size (20mm, 60mm), compared to when flankers were close in size to the target object (35mm, 45mm). In contrast, under the grasping task, we did not observe substantial modulation of the JNDs as function of the flanker’s size [$F < 1$].

The autistic participants demonstrated a different pattern of results. As in the spatial context, the experimental temporal context affected their precision under both the manual estimation and grasping tasks. Under the wide flanker condition, higher JNDs were observed for both the grasping and manual estimation task. A mixed ANOVA with range of stimuli presented (narrow or wide) and the task (grasping or estimation) as the independent variables revealed significant main effects for both the range of stimulus [$F_{(1, 30)} = 7.128$, $p < .05$, $\eta_p^2 = 0.193$] and the task type [$F_{(1, 30)} = 9.257$, $p < .005$, $\eta_p^2 = 0.236$], indicating that each factor independently affected performance. The autistic individuals had higher variability (larger JNDs) in both tasks when the stimulus range was wide compared to when it was narrow, (estimation: [$F_{(1, 30)}$ = 4.495, p < .05], grasping: [$F_{(1, 30)}$ = 4.051, p = .05]), demonstrating a consistent effect of temporal context across tasks. Importantly, there was no significant interaction between task and range [F < 1], suggesting that the influence of stimulus range on performance was consistent across both grasping and estimation tasks for the ASD group (Figure 2E).

To further visualize the observed group differences, we plotted the individual effects of perception versus grasping, with the x-axis representing the effect of context of perception and the y-axis representing the effect of context on grasping (Figure 2F&G). For non-autistic participants (Figure 2F), most data points shifted to the right of the dashed diagonal line, indicating a more substantial influence of context over time on perception than on action. In contrast, for the autistic group (Figure 2G), the individual data points are clustered closely around the diagonal line, indicating a similar influence of context over time on both tasks. This clustering suggests that for autistic individuals, the effect of context over time is evenly distributed across perception and action. The difference between groups was confirmed by ANOVA that showed that the non-autistic group's average distance of each dot from the line (y = x) was -1.132mm, while the autistic group's average distance was -0.558 mm [$F_{(1, 57)}$ = 3.98, p = .050, η_p^2 = 0.065].

To conclude, our analysis reveals a striking disparity in performance between the two groups, indicated by a significant three-way interaction. Non-autistic participants showed a clear dissociation between tasks, with grasping unaffected by context over time, while estimation was significantly impacted. In contrast, autistic participants exhibited context-driven effects in both tasks. This pattern of results converges and extends the results found in Experiment 1, but now for temporal, rather than spatial context.

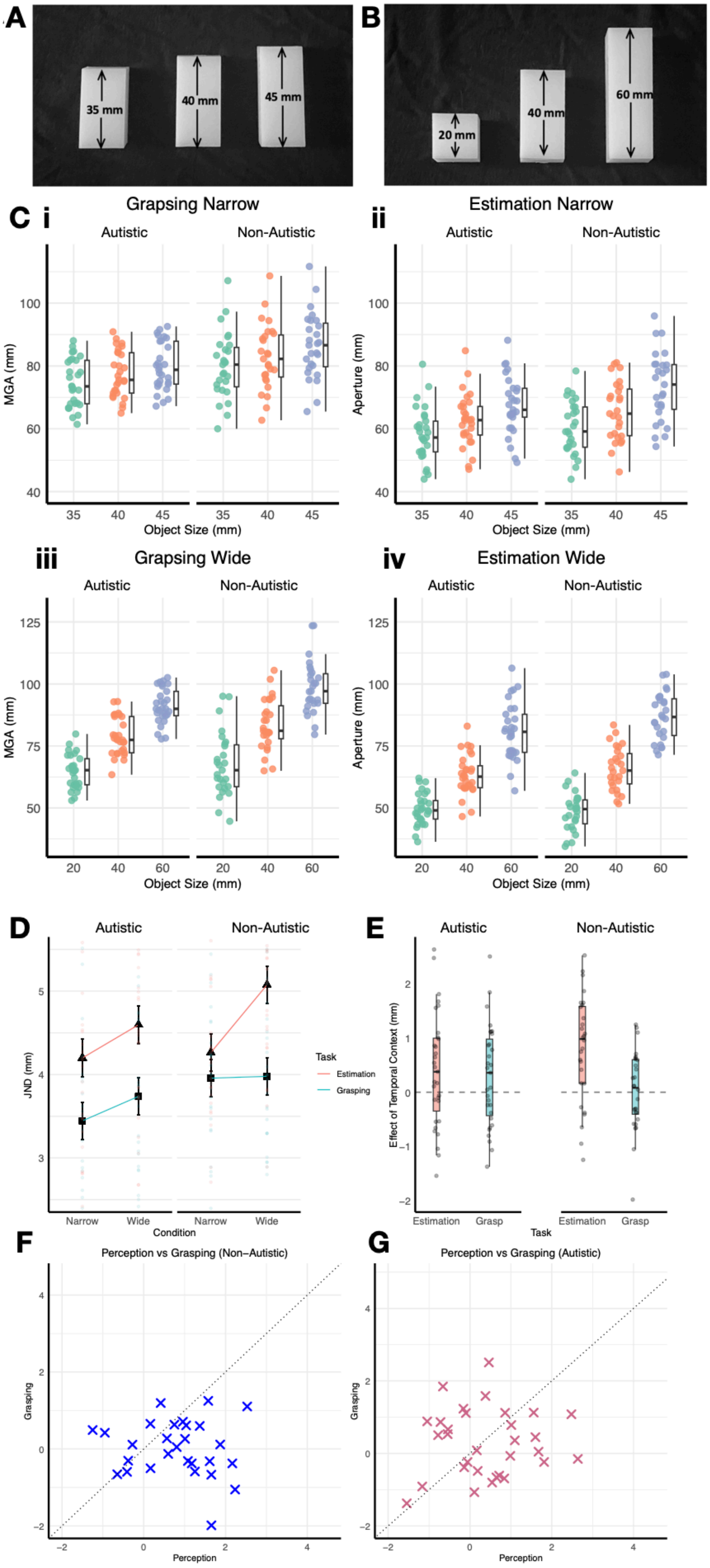
A
35 mm
40 mm
45 mm
B
20 mm
40 mm
60 mm
C i
Grapsing Narrow
Autistic
Non-Autistic
MGA (mm)
Object Size (mm)
ii
Estimation Narrow
Autistic
Non-Autistic
Aperture (mm)
Object Size (mm)
iii
Grapsing Wide
Autistic
Non-Autistic
MGA (mm)
Object Size (mm)
iv
Estimation Wide
Autistic
Non-Autistic
Aperture (mm)
Object Size (mm)
D
Autistic
Non-Autistic
JND (mm)
Narrow
Wide
Condition
Task
Estimation
Grasping
E
Autistic
Non-Autistic
Effect of Temporal Context (mm)
Estimation
Grasp
Task
F
Perception vs Grasping (Non–Autistic)
Grasping
Perception
G
Perception vs Grasping (Autistic)
Grasping
Perception

Figure 2. **(A&B) Experimental Design for Temporal context**: The figure displays the three stimuli used in the “narrow” and “wide” conditions for the size context over time. **(A) Narrow Condition.** The narrow range condition consisted of stimuli of 35 mm, 40 mm, and 45 mm in length. **(B) Wide Condition**. The wide range condition consisted of stimuli of 20 mm, 40 mm, and 60 mm in length. Both experimental blocks included the common target stimulus of 40 mm.

Raw MGA and Endpoint Aperture Result. **(C)** The average MGAs and endpoint apertures as a function of group and condition, displayed across four panels (i-iv). Each individual’s data is represented by a single point, with separate points plotted for each group and object size. The box plots to the right of the data points represent the group averages, with the boxes extending from the first quartile (25th percentile) to the third quartile (75th percentile). Points lying outside the box plot's whiskers indicate outliers, which are data points that fall outside the range of typical values.

Context Over Time Experiment Results. **(D)** The average JNDs as a function of group and conditions are plotted. Error bars reflect the standard error. The result of every individual is plotted as a singular data point for both groups. The red line indicates the perceptual task results, and the blue indicates the grasping results. The ASD group (left) had higher average JNDs for the “wide” condition across the tasks and likewise smaller JNDs when the same block was placed in the “narrow” condition. The non-autistic group had higher JNDS for the “wide” condition and smaller JNDs in the “narrow” condition in the perceptual task only. The non-autistic group (right) had similar JNDs for the stimuli across the “wide” and “narrow” condition for the grasping task. The results seen in panel E are computed from the JND results found in panel D (i.e. for each task, the JND for the narrow condition is subtracted from the wide condition). **(E)** The result of every individual is plotted as a singular data point for both groups. The red box plot indicates the perceptual task results, and the blue indicates the grasping results. Group means are indicated by the bold black line. The lower and upper limits of the box plots correspond to the first and third quartiles (the 25th and 75th percentiles). Individual points above and below these limits signify outliers. The dotted grey line indicates the results if there was to be no effect of the temporal context (0mm). The non-autistic group (right) did not exhibit susceptibility to the temporal context of the stimuli in the grasping whereas the ASD group (left) did. Both groups display an effect of the temporal context in the perceptual task.

Effect of Context Over Time on Perception and Grasping (F). The plot illustrates the impact of context over time on perception and action, with each blue data point representing an individual non-autistic participant. The x-axis denotes the effect of context on perception , while the y-axis indicates the effect of context on grasping. The dashed diagonal line signifies a hypothetical equivalent effect of context on both perception and action. For the non-autistic participants there is a general shift to right of the diagonal line suggesting greater effect of context on perception compared to action. **(G)** The plot illustrates the impact of context over time on perception and action, with each red data point representing an individual autistic participant. The clustering of data points around the diagonal line indicates a similar contextual effect on both perception and action in individuals with autism.

4.5 Discussion

We tested the effects of spatial context and context of stimulus history over time on perceptual estimates and grasping. The two experiments were designed to compete different hypotheses arising from two different accounts for perceptual alterations in autism. The Bayesian accounts predict an overall attenuated use of priors in perception, while the reduced functional specialization account predicts broad contextual effects that carry over visual computations that subserve perceptual and visuomotor behaviors. The observed results provide novel support for the functional specialization account such that autistic individuals showed a consistent susceptibility for irrelevant contextual effect under both perceptual and visuomotor tasks.

In Experiment 1, we utilized the Ponzo illusion to manipulate the spatial context of stimulus presentation. Non-autistic individuals demonstrated a clear dissociation between perception and action. In contrast, autistic individuals showed a consistent influence of the spatial context across both tasks, suggesting a reduced functional dissociation between perception and action.

In Experiment 2, we manipulated the context-over-time of stimulus presentations. As found by previous studies for non-autistic individuals (Namdar et al., 2016, 2018), perceptual sensitivity to the common stimulus was heightened when the other stimuli in the range were of similar magnitudes (narrow condition), compared to when they were spread over a broader range of magnitudes (wide condition). However, this was the case only for the perceptual task. In the grasping task, the non-autistic group displayed comparable sensitivity levels across the range of magnitudes. Autistic individuals exhibited a consistent contextual effect in both the grasping and estimation tasks, with larger JNDs for the standard stimulus presented during the wide block. This consistent influence of the temporal context across both tasks in the ASD group highlights the reduced dissociation between perception and action, consistent with the findings from the spatial context manipulation (Experiment 1). These results suggest that reduced functional specialization in ASD extends beyond spatial manipulations (such as the Ponzo illusion) to include other contexts (such as context over time) as well.

4.5.1 Reduced Functional Specialization in ASD

The results of the two experiments provide novel evidence for a reduced functional dissociation between perception and action in autism. We suggest that these findings reflect a broader phenomenon of changes in the degree of specialization in the autistic brain. There is now a growing body of research that has found reduced specialization in various modalities in individuals with ASD.

For instance, a study on face recognition (Hadad et al., 2019) shows that individuals with ASD have a substantially reduced processing advantage for own-race faces compared to non-autistic individuals, indicating a lack of specialization in the perceptual system for the own-race faces. Reduced experience-based learning of regularities in the environment has also been demonstrated in autism for basic features. Autistic individuals are shown to process dimensions that are typically perceived as integral (e.g., color) and separable (e.g., size and brightness) in a less pronounced distinction (Hadad et al., 2017). For non-autistic individuals, integral dimensions like hue and brightness are processed holistically, whereas separable dimensions like value and size are processed more analytically. These different dimensions are less distinguished in individuals with autism, indicating a more generalized and less specialized approach to processing sensory information.

The reduced specialization account in autism is also supported by studies that examined multisensory integration. In one study, autistic children experienced the flash-beep illusion over an extended range of stimulus onset asynchronies relative to children with typical development (Foss-Feig et al., 2010). This indicates that children with autism have altered multisensory temporal function, characterized by a broader and less specialized temporal binding of auditory and visual stimuli. In a separate study, Nakano et al., (2012) found that individuals with autism exhibited superior performance in haptic-to-visual shape-matching tasks. This suggests that if the perceptual systems in autism are less specialized, there may have increased cross-modal interactions. Consequently, this increased cross-talk could result in better performance in certain tasks where integration across sensory modalities is advantageous. Together, these findings highlight the pervasive nature of reduced specialization across different sensory modalities in ASD.

Neuroimaging studies have provided evidence for the neural mechanisms that might give rise to the atypical specialization in ASD. It has been reported that individuals with autism exhibit less specialized areas of face perception perhaps due to a failure of the amygdala in supporting cortical face specialization (Grelotti, Gauthier, & Schultz, 2002). Along similar lines, developmental work has shown that infants at risk for autism often show atypical hemispherical specialization for faces (Keehn et al., 2015). Together, these findings point to atypical cortical specialization tendencies which presumably may be the cause of the altered functional specialization observed in autism.

Atypical perception and action in autism due to a failure of functional specialization somewhat challenges the prevailing theory of Bayesian statistics that suggests that attenuated priors or enhanced likelihood results in atypical perception (Brock, 2012; Lawson et al., 2014; Pellicano & Burr, 2012). Such theories, for example Pellicano and Burr's (2012) attenuated-prior account, suggests that perceptual differences in ASD result from atypicalities in either the construction of prior expectations about sensory input or in the combining of priors with new sensory information. In essence, priors in autistic individuals are seen as overly flat or weak, thereby exerting an attenuated impact on sensory processing.

Nonetheless, the current work is not the first to suggest that the theories of attenuated priors based on Bayesian statistics may not adequately explain all the perceptual alterations often observed in ASD. Recent studies, such as Arthur et al. (Arthur et al., 2021, 2023), have reported findings that contradict this account in both motor and perceptual tasks. Consequently, there is growing evidence that the diminished use of priors is not a satisfactory explanation for the entirety of autistic perceptual and motor behaviors, suggesting the need for other models to better capture the complexity of these processes in ASD. In particular, Arthur et al. (2023) explored predictive coding theories of ASD through computational modeling of motor behaviors and suggested that predictive sensorimotor control in ASD is not characterized by a chronic underweighting of prior information. Instead, their study indicated that individuals with ASD had difficulties in flexibly adapting their learning rates in response to changes in the environment, a concept referred to as volatility. Similarly, results from an immersive virtual reality study (Arthur et al., 2021) suggest that sensorimotor difficulties in ASD may stem from context-sensitive mechanisms related to precision modulation rather than generalized underweighting of priors. These findings along with our current ones highlight the importance of considering context-specific processing mechanisms in understanding perception and motor control in ASD.

4.5.2 Long-term and short-term contextual information

In the current study, we manipulated contextual information in two distinct ways. In Experiment 1, we varied the immediate spatial information, while in Experiment 2, we altered the range of stimuli within an experimental block to change the context over time. Notably, these two manipulations also differ in the timescales at which the context was created.

Experiment 1 used the Ponzo illusion, which can be considered a long-term prior, as it depends on interpreting relative size based on depth cues in 3D space. Research suggests that susceptibility to this illusion may be almost innate. For example, Gandhi et al. (Gandhi et al., 2015) found that newly sighted children, who gained vision after extended early-onset blindness, were immediately prone to the Ponzo illusion. This supports the idea that the Ponzo illusion is linked to long-term or even innate perceptual priors. It is also worth noting that while some studies suggest that autistic individuals may not be affected by visual illusions—implying reduced reliance on priors—our findings indicate a consistent effect of the Ponzo illusion in autistic individuals (see Hadad & Yashar, 2022 for a comprehensive review on this topic).

On the other hand, the priors in Experiment 2 were set within a limited short-term time frame, such that in each experimental block, priors could have been generated based on the accumulated stimulus history. Previous research indicates that autistic individuals may have weaker learned priors (as compared to innate priors), allowing for more flexibility in how they adapt to changing contexts. Rather than simply having reduced priors, autistic individuals may have a more dynamic, less rigid application of priors, allowing them to adjust more fluidly to new or changing information (Van de Cruys et al., 2014). Notwithstanding, our findings suggest that autistic individuals generated those learned, short-term, priors, but in contrast to non-autistic individuals, generalize those priors across both perceptual and visuomotor tasks.

4.5.3 Dorsal Pathway Vulnerability

Alterations in visuomotor skills and other visual behaviors associated with computations carried out by the dorsal pathway, have been observed not only in autistic individuals but also in various other neurodevelopmental conditions, such as developmental dyslexia (Conlon et al., 2009), amblyopia (Ahmad et al., 2023; Atkinson, 2017), cortical resections (Ahmad et al., 2022; Ayzenberg et al., 2023), Williams syndrome (Dilks et al., 2008) and others (for review see Atkinson & Braddick, 2011). Interestingly, it appears that the impact on behaviors associated with the dorsal pathway is often disproportionately greater compared to abilities associated with the ventral pathway in several neurodevelopmental disorders. Hence, this phenomenon has been termed "dorsal pathway vulnerability" (Atkinson & Braddick, 2011; Braddick et al., 2003).

While the current study did not directly examine visuomotor deficits, but rather focused on reduced specialization between perception and action, previous research has shown that autistic individuals also exhibit motor performance deficits. Glazebrook et al. (2006) observed atypical reaching and grasping behaviors in autistic children, pointing to deficits in the dorsal pathway’s ability to guide motor actions based on visual input. This suggests less efficient integration of visual information with motor commands in ASD.

Additionally, the development of the dorsal pathway and its associated functions appears to follow an atypical developmental trajectory in autism. Kaiser et al. (2009) reported delayed or altered maturation of dorsal pathway functions, such as motion processing, which may contribute to the persistent motor deficits observed in individuals with ASD. These findings underscore the significant impact of atypical dorsal pathway functioning on the visual and motor abilities of autistic individuals.

Based on the current results, we suggest that the atypical functional specialization between action and perception in autism likely stems from abnormal cortical development of both the ventral and dorsal pathways. This atypical development leads to more diffuse representations of visual information which in turn impacts normal visuomotor behaviors. It is essential to recognize that normal visuomotor control involves some crosstalk between the ventral and dorsal pathways, emphasizing the complexity of the neural mechanisms that integrate perceptual and motor processes. This reduced specialization of the pathways might enhance an increased crosstalk between perceptual and visuomotor systems, such that perceptual representations intrude into visuomotor representations. By incorporating neuroimaging techniques, future studies could further supplement behavioral studies like ours by providing more direct evidence of the neural mechanisms involved in the perceptual and visuomotor differences observed in individuals with ASD. Addressing these factors in future research could provide a more comprehensive understanding of the mechanisms underlying reduced functional specialization in ASD.

4.5.4 Measuring Grasping Sensitivity Using JND

The term Just Noticeable Difference (JND) originates from classical psychophysics, where it is defined as the smallest detectable difference between two stimulus magnitudes under conditions of uncertainty. According to foundational treatments of this concept (Baird & Noma, 1978; Marks & Algom, 1998), the JND reflects the threshold at which a physical difference in stimulus becomes perceptually discriminable to an observer 50% of the time. Traditionally, it is derived from psychometric functions based on forced-choice paradigms and has served as a cornerstone in quantifying perceptual resolution and scaling laws such as Weber’s Law.

In contemporary visuomotor research, however, the term JND has been adapted for slightly different purposes. Specifically, in the context of grasping studies, JNDs have been operationalized as the standard deviation of maximum grip apertures across repeated trials of a single object size (e.g., Ganel et al., 2008). This approach treats motor variability as an analogue to perceptual uncertainty and has been instrumental in demonstrating differential sensitivity to contextual manipulations across perception and action. For instance, in studies where the adherence to Weber’s law is assessed, perceptual JNDs typically scale with stimulus magnitude, whereas grasping JNDs remain relatively constant, reflecting a decoupling of visuomotor outputs from perceptual priors (Namdar et al., 2018).

Given this established precedent, our use of JND, defined as the within-condition standard deviation of the maximum grip aperture responses, reflects a widely accepted approach to measuring resolution across modalities in visuomotor research. Importantly, this usage enables direct comparison between perceptual and motor domains using the same computational framework. While we acknowledge that this deviates from the classical threshold-based definition, it is consistent with prior work and appropriate for capturing the sensitivity of action-related representations (Ahmad et al., 2022; Freud et al., 2016; Namdar et al., 2018)

4.6. Conclusion

In conclusion, our study provides novel and consistent evidence for reduced functional dissociation between perception and action in autistic individuals. By examining the effects of spatial context over time, we demonstrated that visual representations in autism are less specialized, influencing both perception and action. These findings highlight the critical role of functional specialization in typical development and its disruption in autism.

CHAPTER 5: GENERAL DISCUSSION

4. General Discussion

The dissociation between visuoperceptual and visuomotor behaviors has long been recognized as a fundamental principle of visual processing, rooted in the Two Visual Pathway Hypothesis proposed by Goodale and Milner (1992) and Ungerleider and Mishkin (1982). However, the developmental emergence of this functional dissociation between action and perception remains an open question. By examining visuomotor and visuoperceptual behaviors in three distinct populations of individuals with atypical development and cortical lesions, the current work explores the interplay between these behaviours in neurodevelopmental conditions, as well as alterations in visuomotor behaviors. The findings consistently highlight (1) altered visuomotor behaviors and (2) a reduced perception-action dissociation.

In the studies presented in this dissertation, I harnessed motion-tracking technology to assess visuomotor and visuoperceptual behaviours in patients with neurodevelopmental conditions. The results of this dissertation clearly demonstrate a heightened sensitivity of visuomotor behaviours in atypical development. This was evident in Chapter 2, where the left hemisphere-lesioned (including both the dorsal and ventral pathways) individual TC, performed significantly worse than matched controls on an motor task using Efron blocks, despite intact perception of the same objects (Ahmad et al., 2022). This investigation revealed preserved visuoperceptual functions despite significant visuomotor deficits, highlighting the resilience of the ventral pathway associated behaviours and the relative vulnerability of the dorsal pathway associated behaviours to structural damage sustained early in life. Unlike the other chapters, this study involved a single case study, offering rare insights into recovery profiles and plasticity following cortical injury.

In Chapter 3, perception and action in children with amblyopia were examined using visual illusions. Unlike the individualized focus of the earlier chapter, this study investigated a group of children, revealing a consistent reduced dissociation between perception and action. These findings stressed the importance of early visual input in shaping the emergence of the functional dissociation (Ahmad et al., 2023).

Lastly, Chapter 4 investigated adults with autism spectrum disorder (ASD), a population marked by widespread sensory and motor deficits. This chapter, focusing on a relatively large young adult cohort, where perceptual and motor systems had presumably fully matured, allowed for an evaluation of long-term alterations in visuomotor and visuoperceptual behaviors. The results revealed persistent reductions in perception-action dissociation in two different contextual experiments. These findings suggest that the observed deficits in ASD are not developmental delays but rather alterations in the overall functional specialization of the cortical system in the autistic brain (Ahmad et al., under review).

Together, these studies highlight that while the etiology of each condition may differ, they converge on a common theme: reduced dissociation between perception and action, emphasizing the robustness of this phenomenon across different neurodevelopmental profiles. Importantly, the results reveal two key insights: first, visuomotor behaviors are more sensitive to neurodevelopmental atypicalities relative to perceptual behaviors, as demonstrated in the study on TC. Second, the dissociation between perception and action itself is sensitive to atypical development, as observed in Chapter 3 (amblyopia) and Chapter 4 (ASD). The current work provides a more detailed perspective on how developmental conditions influence visuomotor and visuoperceptual behaviors and how the dissociation emerges across different populations.

4.1 Integration within Theoretical Frameworks

Two Visual Pathway Hypothesis

As discussed in the introduction, the Two Visual Pathways Hypothesis postulates distinct behaviours mediated by the ventral and dorsal pathways in visual processing. This framework has been foundational in shaping our understanding of perception and action as two distinct behaviours mediated by specialized cortical pathways. Although the framework of perception and action as distinct processes is well established, much of the existing research has examined the dissociation in in healthy adults, with relatively little attention given to the developmental trajectory of this functional dissociation. Notably, Freud et al. (2021) and Hadad et al. (2012) conducted grasping studies that specifically examined the development of this dissociation in children aged 5 – 8 years. however, such studies have primarily concentrated on healthy participants.

The findings in this dissertation extend these foundational insights by specifically demonstrating that the dissociation between perception and action is highly sensitive to atypical development. In Chapters 3 and 4, neurodevelopmental conditions were found to consistently disrupt the emergence of this dissociation, highlighting the interdependence of normal visuoperceptual and visuomotor behaviors, which, although are functionally distinct, rely on a delicate balance for typical development. Importantly, these results challenge the traditional approach of testing of visuoperceptual and visuomotor abilities as independent processes. Instead, they reveal that the dissociation itself is highly susceptible to neurodevelopmental changes. This finding emphasizes the importance of examining not just the independent roles of each behaviour but also their interactions and how the functional dissociation emerges under atypical conditions.

Evidence for a Third Visual Pathway and Dorsal Pathway Segregation

Often the dissociation between perception and action is framed within the dominant dual-pathway model of visual processing (Goodale & Milner, 1992; Mishkin & Ungerleider, 1982), in which the ventral pathway supports object perception, and the dorsal pathway subserves visually guided action. However, emerging evidence suggests that this dichotomy may be overly simplistic, and recent proposals suggest functional organisation of the human visual system involves not two but three cortical pathways.

One prominent revision is the identification of a third visual pathway, a lateral pathway running from early visual areas through motion-sensitive regions in the superior temporal sulcus (STS) toward the anterior temporal lobe (Haak & Beckmann, 2018; Pitcher & Ungerleider, 2021). This pathway is thought to specialize in the visual analysis of dynamic social information, such as body movements and facial expressions, and is functionally distinct from both the ventral and dorsal pathway. While the present experiments do not explicitly investigate this third pathway, its proposed role in processing socially relevant stimuli suggests it may be particularly relevant in neurodevelopmental conditions like autism, where the perception of social cues is often altered (Blakemore & Choudhury, 2006).

Furthermore, it has been largely reported that dorsal pathway itself is not monolithic. Rizzolatti and Matelli (2003) proposed a division of the dorsal pathway into two functionally distinct substreams: a dorso-dorsal stream (formed by area V6 and areas V6A and MIP of the superior parietal lobule) for online sensorimotor control, and a ventro-dorsal stream (formed by area MT and by the visual areas of the inferior parietal lobule) implicated in action understanding and tool use. This subdivision may help explain the differential vulnerabilities of dorsal functions across developmental conditions (Atkinson, 2017) and is especially relevant for interpreting the types of grasping or context sensitivity observed in Chapters 2 and 4. For example, variability in grasping JNDs across participants may reflect differential reliance on fast, online control (dorso-dorsal) versus more integrative context-sensitive mechanisms (ventro-dorsal).

Incorporating these alternative revised models does not undermine the utility of the perception-action dissociation but rather reinforces the idea that functional specialization within the visual system is distributed and graded. The current findings, particularly those showing reduced dissociation in individuals with neurodevelopmental disorders, may be best understood considering this broader architecture, where multiple partially overlapping visual pathways interact to support both perceptual and motor behaviors.

Visuomotor Deficits & Reduced Dissociation

The findings of this dissertation highlight two core results observed across the experiments: first, visuomotor deficits, and second, a reduced perception-action dissociation. Visuomotor deficits were explicitly observed in Chapter 2, which focused on TC, a pediatric patient with cortical resection, but were also evident implicitly in Chapter 3 (amblyopia) and Chapter 4 (ASD). Meanwhile, reduced perception-action dissociation was a key finding in Chapters 3 and 4, where atypical development prominently affected the dissociation between these behaviors.

As previously mentioned in the introduction, the dorsal vulnerability account suggests that the dorsal pathway, which supports visuomotor behaviors, is particularly sensitive to developmental disruptions. Studies have demonstrated that dorsal pathway functions, such as motion processing and visuomotor control, are more likely to be affected by neurodevelopmental disorders (e.g., developmental dyslexia, Williams Syndrome) (Atkinson et al., 1997; Atkinson & Braddick, 2005; Atkinson, 2017, Dilks et al., 2008). Under this account, behaviors mediated by the ventral pathway are often more resilient and preserved even in conditions of atypical development.

The findings presented in the current studies affirm the dorsal vulnerability account (specifically in patient TC in Chapter 2), as visuomotor deficits were disproportionately greater than any visuoperceptual impairments across all three studies. Importantly, the current studies also include an important distinction compared to other work that reports dorsal pathway vulnerability. Specifically, Chapters 3 and 4 of the current work showed that the perception-action dissociation is also vulnerable in cases of atypical development, suggesting that this dissociation itself may also be particularly sensitive to neurodevelopmental perturbations.

What leads to the reduction of the perception-action dissociation in children with neurodevelopmental conditions? While the answer to this question is not clear, one plausible mechanism involves intrusions of perceptual representations computed by the ventral pathway into computations carried out by the dorsal pathway which usually mediate visuomotor behaviors. In particular, neurodevelopmental conditions such as amblyopia or ASD, may impair the typical development of the dorsal pathway, leading to visuomotor deficits as often observed and suggested by the dorsal vulnerability hypothesis (Atkinson, 2017; Hay et al., 2020, Ahmad et al. under review). In response, the visual system leverages the available perceptual representations from the ventral pathway to compensate for the compromised dorsal pathway representations. This adaptive compensation process may result in the current observed reduction in dissociation between perception and action. This proposed mechanism (Figure 1) stresses the interdependence of these pathways and highlights the need to consider both the independent and interactive roles of perception and action in understanding neurodevelopmental conditions.

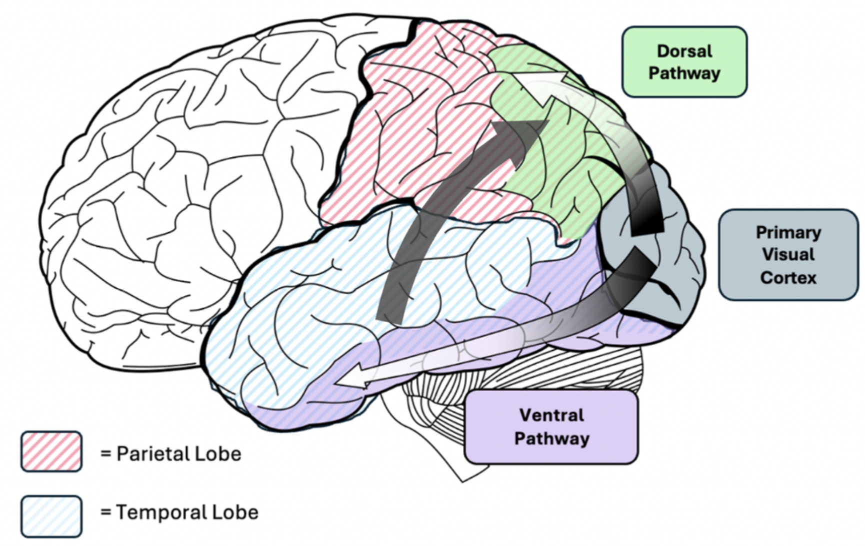

Figure 1: Proposed Mechanism of Perceptual Intrusions. Dorsal (green) and ventral (pathway) pathways extending from V1 into parietal and temporal lobes. The figure suggests compensatory perceptual intrusions (dark grey arrow) from the ventral pathway into the dorsal pathway's functions. This perceptual bias reflects an uneven interaction, with the ventral pathway providing compensatory input to mitigate compromised dorsal functions, ultimately contributing to the observed reduction in dissociation between perception and action. Figure adapted from: psynso.com/two-streams-hypothesis/

Role of Experience in Shaping the Perception-Action Dissociation

The results from this dissertation consistently reveal a cross-syndrome vulnerability in the dissociation between action and perception. Previous research (e.g., Freud et al., 2016; Held & Hein, 1963) has shown that normal visual experience can influence these behaviours and that the typical development of one modality is shaped by the other. We propose that abnormal visual experiences, as observed in the conditions examined in this dissertation, disrupt the typical developmental trajectory of the dissociation between action and perception, resulting in reduced dissociation between the two behaviours.

Early work by Held and Hein (1963) highlighted the importance of active visual experience in shaping the relationship between perception and action. In these studies, kittens that were allowed to move freely and interact with their environment developed normal visuomotor coordination and depth perception. In contrast, kittens whose movement was restricted or passively guided failed to develop these critical skills. This seminal work demonstrated that typical active interaction with the environment is necessary for the normal development of visual perception. The findings specifically highlight that normal visuomotor experience (in this case self-directed, active engagement) with the environment is has a clear link in driving the emergence of proper perceptual and visuomotor behaviors.

In a similar way, there are a number of studies that show that the development of perceptually related behaviours also relies on typical visual experience. For instance, Arcaro et al. (2017) found that monkeys raised without exposure to faces did not develop face-selective cortical domains, despite showing normal retinotopic organization and developing domains for other object categories. This highly selective deficit suggests that early visual experience is essential for the formation or maintenance of specialized face processing areas. Along similar lines, the lack of normal binocular vision and stereopsis can be observed in studies involving children with amblyopia or cataracts (Birch, 2013; de Heering & Maurer, 2014; Ming et al., 2024; Shandiz et al., 2011) where impairments in various perceptual functions have been consistently revealed. In another study, Freud et al. (2016) investigated the visuomotor performance in a developmental visual object agnosia patient (LG). While the visual control of action based on the MGA alone seemed normal, a more holistic analysis of the movement trajectory revealed deficits in visuomotor functions, demonstrating that disruptions in one domain (i.e., perception) can influence the development of the other domain (i.e., action). Importantly, this study also highlighted how early impairments in perceptual abilities can lead to compensatory changes in visuomotor behaviors over time. Collectively, these findings demonstrate that both visuoperceptual and visuomotor systems are highly sensitive to experiential visual input during critical developmental periods.

In this dissertation, the impact of suboptimal visual experiences is mainly explored in Chapter 3, focusing on children with amblyopia. Amblyopia is characterized by deficits such as poor visual acuity, impaired binocular vision, and reduced stereopsis (Birch, 2013; Birch & Kelly, 2023; Grant et al., 2014), all of which represent atypical visual input during development. The findings demonstrate a reduced dissociation between perception and action in children with amblyopia suggesting that the atypical visual input associated with amblyopia disrupts the typical development of the perception-action dissociation as well as leading to disproportionate effects on visuomotor behaviors compared to visual perceptual abilities. These results highlight the significant influence of early-life compromised visual input on the development of the dissociation between action and perception.

Evidence for the impact of poor visual experience has been observed in autistic individuals as well. Altered eye movement patterns, such as reduced fixation on socially relevant stimuli (e.g., faces) and atypical scanning of scenes, suggest that these individuals engage in atypical visual exploration compared to typical development (Jones et al., 2008; Keles et al., 2022). In Chapter 4, we observed reduced dissociation between action and perception in autistic individuals under two different experimental conditions, indicating that this phenomenon is robust and not context-dependent. This work might provide evidence that differences in visual exploration during development could contribute to the observed reduced dissociation between perceptual and action systems. According to these results, sub-optimal visual experiences during critical developmental periods appear to influence both the degree and the nature of the dissociation between action and perception.

Taken together, these studies emphasize the critical role of experience in modulating the dissociation between perception and action. They show that this dissociation is not an inherent or fixed property of the visual system but rather one that develops and is highly sensitive to individual visual experiences. Notably, this dissociation appears particularly vulnerable to suboptimal visual experiences. Future research should further explore how variations in visual input across different developmental windows shape the organization and integration of these systems.

Operational Definition of JND in Visuomotor Contexts

It is important to note that while the term Just Noticeable Difference (JND) traditionally refers to a perceptual threshold derived from psychometric functions (Marks & Algom, 1978), we adopt a widely used operational definition in visuomotor research whereby JNDs are computed as the standard deviation of grip aperture or perceptual estimates (e.g., Ganel et al., 2008; Freud et al., 2016). As outlined in Chapter 2, this approach allows for a common metric of resolution across both perceptual and action-based tasks. In Chapter 4, we applied this method to gauge the sensitivity in grasping and estimation under different contextual conditions, enabling direct comparisons between task modalities. While this usage departs from classical definitions, it reflects current conventions in grasping literature and facilitates meaningful interpretation of precision for both perception and action tasks.

4.3 Limitations

Despite the novel insights provided by the current investigation, several limitations must be acknowledged to guide future research.

First, methodological constraints in the current set of experiments limit the scope of interpretation. Most studies, with the exception of Study 1, relied heavily on kinematic metrics, such as maximum grip aperture (MGA), to infer visuomotor computations. While MGA offers valuable insights into grasping behavior, it neglects other critical aspects of visuomotor processing, such as movement trajectories, grip force, and coordination patterns. Expanding kinematic analyses beyond traditional measures like MGA is essential for capturing the broader scope of visuomotor deficits and potential compensatory mechanisms. Moreover, the data collected in these projects can be leveraged for future secondary analyses to further explore fundamental group differences. For example, in a recent study we utilized data from Chapter 4 to show that kinematic data can be used to train machine learning algorithms to successfully classify autism (Freud et al., revised and resubmitted). Future studies should adopt additional metrics to create a more comprehensive understanding of visuomotor behavior and the nuanced interplay between perceptual and motor systems under varying conditions.

Second, the absence of neuroimaging data across the three studies represents a notable limitation. Behavioral findings, while meaningful, do not directly reveal the neural computations underpinning perception, action and the dissociation between these functions. Incorporating neuroimaging techniques, such as functional MRI, would allow researchers to uncover neural computations and connectivity differences across populations. It is important to note, however, that collecting neuroimaging data from children and patients with neurodevelopmental conditions presents significant challenges. Despite these hurdles, overcoming these challenges would provide a more direct connection between structural deficits and functional outcomes, thereby enhancing our understanding of the underlying neural processes.

Third, participant demographics presented challenges that limited the scope of this research. The ASD cohort included only adults, preventing the examination of developmental changes in perception-action dissociation in children with ASD. Conversely, the amblyopia cohort focused exclusively on children, precluding comparisons with adults to determine whether the observed deficits persist or resolve with age. Understanding whether the reduced dissociation observed in children with amblyopia persists into adulthood or resolves over time represents a critical avenue for further exploration. Longitudinal studies that track changes in perception-action dissociation across neurodevelopmental populations, including children with

ASD and those with unilateral cortical resection, could identify critical developmental windows and provide insights into the dynamic nature of this dissociation. Such studies would offer valuable information on the long-term developmental trajectories of visuomotor and visuoperceptual dissociation, enabling the development of targeted interventions.

By addressing these limitations and pursuing these future directions, this work can significantly enhance our understanding of the complex interplay between perception and action, while offering new avenues for therapeutic strategies and a more comprehensive view of neurodevelopmental pathways.

Conclusion

This dissertation highlights the critical role of perception-action dissociation in typical development and elucidates its disruption across a range of neurodevelopmental conditions. The findings consistently demonstrate that atypical developmental trajectories are associated with a reduced dissociation between perceptual and motor systems, thereby offering valuable insights into the dynamic interplay between these modalities. In addition, the research confirms that visuomotor behaviors are particularly sensitive to developmental disturbances.

These results have significant implications for the fields of cognitive neuroscience, developmental psychology, and clinical practice. By advancing our understanding of the mechanisms underlying the perception-action dissociation, this work not only reinforces the validity of the two-visual pathway hypothesis but also paves the way for the development of targeted interventions aimed at mitigating the effects of neurodevelopmental impairments. The integration of cognitive neuroscience methodologies with clinical observations in this dissertation provides a robust framework for future translational research. Ultimately, these findings advocate for a more nuanced examination of the developmental processes governing perceptual and motor systems, with the potential to inform both theoretical models and practical approaches to assessing and treating developmental disorders.

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