THE VISUAL CORTICES OF CONGENITALLY AND NON-CONGENITALLY BLIND INDIVIDUALS BECOME A PART OF COGNITIVE CONTROL NETWORK

A Master's Thesis

by
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Ankara
December 2023

To my wife and my family

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By Hasan Duymuş

I certify that I have read this thesis and have found that it is fully adequate, in scope and in quality, as a thesis for the degree of Master of Psychology.

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ABSTRACT

THE VISUAL CORTICES OF CONGENITALLY AND NON-CONGENITALLY BLIND INDIVIDUALS BECOME A PART OF COGNITIVE CONTROL NETWORK

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Neural plasticity is crucial for understanding the extent to which a biological structure determines its function. As such, the fate of visual and auditory cortices when deprived of their standard inputs has immense significance in neuroscientific research. Empirical findings suggest that the visual cortex of the congenital and early blind activates across a very wide range of tasks in auditory, tactile and olfactory modalities. We hypothesized that these regions may transform into task positive multiple demand (MD) regions. A key feature of these regions is that they activate to all kinds of tasks in all kinds of modalities. In this study, we investigate whether deprived cortices in blind exhibit key characteristic inherent to fronto-parietal MD regions. We had congenitally and non-congenitally blind participants done four fMRI cognitive control tasks in tactile and auditory modalities. The visual cortices of the blind group showed (1) intense activity during more demanding conditions of the four diverse tasks along with the fronto-parietal control regions, (2) the same set of occipital voxels in blind participants activated across diverse modalities under

increased cognitive demands of the four diverse tasks. Our findings suggest that deprived visual cortices of the blind, in fact, become a part of cognitive control network.

Keywords: Neuroplasticity, sensory loss, fMRI, blindness, visual cortex, cognitive control network, multiple demands network.

ÖZET

DOĞUŞTAN VE SONRADAN KÖR OLAN BİREYLERİN GÖRSEL KORTEKSİ BİLİŞSEL KONTROL AĞININ BİR PARÇASI HALİNE GELİYOR

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Nöral plastisite, özellikle duyu kaybı durumlarında, işlevselliğin ne ölçüde biyolojik bir yapı tarafından belirlendiğini anlamak için hayati bir öneme sahiptir. Bu bağlamıda, standart inputlarından yoksun kalan görsel ve işitsel kortekslerin ne ölçüde değişime uğrayacağı, sinirbilimsel araşatırmalar açısından büyük önem taşımaktadır. Deneysel bulgular, doğuştan ve erken dönemde kör olan bireylerin görsel kortekslerinin, işitme, dokunma ve koku modalitelerini kapsayan yapısal açıdan çok çeşitli bilişsel görevlerde aktif olduğunu göstermektedir. Bu bölgelerin içeriği ve modalitesi ne olursa olsun görev yapısına sahip tüm deneylerde aktif olan çoklu talep (MD) bölgelerine dönüşmüş olabileceğini düşündük. Bu çalışmada körlerde yoksun kortekslerin fronto-parietal MD bölgelerine özgü belirli başlı özellikleri sergileyip sergilemediğini araştırdık. Doğuştan ve sonradan kör olan katılımcılara MR'da, dokunsal ve işitsel modalitelerde dört farklı fMRI bilişsel kontrol görevi yaptırdık. (1) Kör katılımcıların görsel korteksleri, bu dört görevin bilişsel kontrol taleplerinin fazla olduğu koşullara fronto-parietal kontrol bölgeleri ile

birlikte yoğun sinirsel aktivite gösterdi. (2) Kör katılımcılarda aynı oksipital voksel grubu farklı modalitelerde dört çeşitli görevin artan bilişsel kontrol taleplerine yoğun aktivasyon gösterdi. Bulgularımız, körlerde yoksun görsel kortekslerinin, aslında bilişsel kontrol ağına dahil olduğunu göstermektedir.

Anahtar Kelimeler: Nöral plastisite, fMRI, duyu kaybı, körlük, görsel korteks, bilişsel kontrol, çoklu talep bölgeleri

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CHAPTER 1

INTRODUCTION

That there are specific brain functions tied to intrinsic biological properties of neural circuits, and these functions have been pre-determined by cytoarchitecture of the brain has been the prevailing idea in neuroscientific research (Passingham et al., 2002). Yet, recent studies increasingly continue to challenge this view. Many brain patients demonstrate full recovery after extensive brain damage. Some patients who had half of their brain removed exhibit no functional impairments in their daily lives and shows no deficiencies on neuropsychological assessments (Eagleman, 2020). Further, there are instances where young patients who undergo left hemidecortictomy demonstrate the ability to recover significant language abilities (Boatman et al., 1999), and there are cases where people lead functional and normal lives despite significant abnormalities and lesions in their brain later discovered in post-mortem examinations(Conway et al., 2020). All of these suggest that functions of brain regions can be dynamic, and a brain region can change its role in cognition and crucially, neuroplasticity persists beyond the critical period of neural development. Indeed, this view has become plausible. Plasticity is now seen as an intrinsic property of the nervous system, and without the concept of plasticity, it is argued, it is not possible to conceive normative psychological function of the brain (Pascual-Leone et al., 2005).

The extent of the change a brain region can undergo in its function, however, still remains an open and intriguing question, particularly because functions of most brain regions remain ambiguous and, adding another layer of complexity to this inquiry.

However, the primary sensory cortices offer a comparatively clearer picture as they are among the better-understood brain regions.

1.1. Primary Sensory Cortices

Sensory cortices are distinct among other brain regions in that they have well-defined functions. Each sensory cortex processes inputs in their own modality. For example, the visual cortex processes visual stimuli, the auditory cortex processes auditory stimuli, and the somatosensory cortex processes stimuli related to touch and somatic sensations. Primary sensory cortices are even more specific in that they selectively respond only to specific aspects of an stimulus. For instance, within the primary visual cortex, a network of neurons responds only to lines and borders of an object oriented in a specific direction (Hubel & Wiesel, 1998). Similarly, certain neurons in the primary auditory cortex demonstrate frequency selectivity, responding only to sounds from a specific tonal range (Purves et al., 2019a). Furthermore, parts of the primary somatosensory cortex receive inputs exclusively from specific body parts(Purves et al., 2019a). Thus, each area within the primary sensory cortices is responsible for processing only a specific aspect of a stimulus, encoding distinct features of a percept within a particular sensory modality.

Evidence suggests that sensory cortices also activate to tasks in other modalities. In situations, where locations of sounds are not predictable, contralateral visual cortices have been seen to activate (Matusz et al., 2016). Unless there is a prior association of sound with visual information, such as a car passing by on the road, the visual cortex does not respond to the sound stimulus alone. Thus, in most cases, sensory cortices respond to stimuli from their own modalities, unless there's a prior cross-modal association.

When brain networks show similar patterns of response to a neuropsychological event, they are said to be functionally connected during a task. When brain networks show (Biswal et al., 1995). That most of the brain networks have functional connectivity during tasks as well as at rest has been evidencedbefore (Smith et al., 2009). Primary visual cortices, as well as primary auditory and somatosensory cortices, have been shown to have robust functional connectivity with other sensory cortices of their respective modalities (De Luca et al., 2006a).

Primary sensory cortices receive projections from distinct sets of thalamic nuclei. These nuclei act as relays, gathering sensory information from sense organs and relaying it to the cortices. The primary sensory cortex receives visual inputs from the lateral geniculate nucleus (LGN)(Purves et al., 2019b). The primary auditory cortex receives inputs from the dorsal and ventral nuclei of the medial geniculate body (MGB) (Mangold & Das, 2020).

Primary sensory regions also receive top-down inputs from multimodal areas as well as receiving bottom-up inputs from thalamic nuclei. Belt and parabelt regions of the auditory cortex receive projections from ventrolateral, orbitofrontal, dorsal areas of the frontal lobe as well as temporoparietal areas and superior temporal areas(Hackett et al., 2001; Kaas & Hackett, 2000). V1 and V2 in the calcarine sulcus get multimodal input coming from parietal and auditory association areas in the macaque monkey (Rockland & Ojima, 2003). Electrical recordings in humans and monkeys have indicated a strong top-down influence from the frontal eye field (FEF) to the V4 area in the visual cortex when attention is directed toward an object. Anatomically, visual and auditory cortices are connected to fronto-parietal cortices via the superior longitudinal fascicle (SLF) (Nakajima et al., 2020). Dorsal SLF is associated with visuospatial attention demands as well as execution of motor tasks while posterior SLFs are involved in language-related networks(Nakajima et al., 2020). The occipitofrontal fasciculus originating from pre-occipital regions and caudal parts of the inferior parietal lobule terminates in the dorsal frontal cortex (Yeterian et al., 2012). In sum, primary cortices receive direct cortico-

cortical connections from fronto-parietal cortices associated with cognitive control and task-demands.

Cortico-cortical connection is not the only source from which sensory cortices receive control-related information such as contexts, task-demands, attention, and salience. A study, found the pulvinar, a thalamic nucleus, regulates and transmits information between visual and frontal cortices in humans and macaques, playing a crucial part in attentional allocation and selection (Saalmann et al., 2012). Thus, it is safe to assume that sensory cortices get task and goal-related information from fronto-parietal cortices. These cortico-cortical and subcortico-cortical connections, thereby, enables task and goal-related information to be conveyed to sensory cortices, amplyfing goal-related sensory information and attenuating the irrelevant ones (Dehaene et al., 2006). In sum, primary sensory cortices receive critical inputs only from sensory organs via thalamus but also top-down inputs coming from supramodal brain regions like control-related fronto-parietal regions.

1.2. Deprived Sensory Cortices

In neuroscientific studies, the functions of primary sensory cortices are well-defined. When they are deprived of their typical inputs, as in congenitally blind or deaf individuals, they don't just cease to function, instead they take up functions different from the non-deprived ones. This present a compelling model for studing neural plasticity and the extent to which a brain can change its function. Thereby, the occipital cortex in blind individuals and auditory cortex in deaf individuals attracted immense scientific interest. While the phemonenon of cortical regions taking up different functions is well-known, the extent and implications of such adaptive processes is of key interest to neuroscience. Elucidating these aspects may offer us insight into the inherent flexibility of brain regions, especially the interplay between structure and function. Furhermore,

such a study would hold potential translational value for developing interventional strategies and advancing principle of neurorehabilitation for deaf and blind people.

1.3. Cross-Modal Accounts for Deprived Sensory Cortices

Visual regions of blind individuals have been seen to activate to various tasks involving auditory, tactile and olfactory modalitities, a phenomenon strikingly absent in sighted participants (Fine & Park, 2018) Intense activation in foci of visual cortices of blind participants has been reported during detection of new complex sounds among the continious ones (Kujala et al., 2005), producing verbs in reaction to nouns presented audibly (Burton, Snyder, Diamond, et al., 2002), verbal memory (Amedi et al., 2003), beat detection (Araneda et al., 2021),and decision if motion sounds are approaching or receding (Bedny et al., 2010). Further, these foci in visual cortices of blind people have also shown increased activation in response to tactile tasks rather than passive tactile stimulation (Sadato et al., 1996), to reading nouns presented through a braille-embossed plexiglass (Burton, Snyder, Conturo, et al., 2002), and to tactile symmetry detection (Bauer et al., 2015). Activity in visual cortices of the blind is not confined to just auditory and visual tasks, they have been seen to activate even in olfactory tasks. In fact, odor detection and recognition tasks have activated visual cortices of the blind (Kupers et al., 2011; Renier et al., 2013). Observations related to the fate of auditory cortices in deaf people have drawn striking parallels. Auditory cortices of the deaf participant exhibit activation during processing of visual stimuli (Finney et al., 2001), visio-spatial working memory task (Ding et al., 2015), detection of visual motion , movement detection and localization (Lomber et al., 2010), lexical processing in proficient deaf readers (Corina et al., 2013), compherending sign language (Nishimura et al., 1999), and discerning temporal sequences and spatial features of visual and tactile stimuli (Dai et al., 2016). A prevaling theory explaining the activation of deprived cortices in both the blind and deaf across diverse tasks involving different modalities is that these regions undergo a functional transfomation. Thus, visual cortices of the blind reconfigure to process information in auditory and somatosensory modalities (Klinge et al., 2010; Uhl et

al., 1991; Vetter et al., 2020; Wittenberg et al., 2004), whereas auditory cortices of the deaf become a different sensory region processing visual or somatosensory inputs (Dai et al., 2016; Kok et al., 2014; Kral, 2007; Lomber et al., 2010).

1.4. Metamodal Accounts for Deprived Sensory Cortices

An alternative perspective posits that brain structures are metamodal in nature working as specialized modules capable of executing a specific tasks irrespective of the sensory modalities of inputs. While such regions might exhibit a preference for a particular sensory input, it does not preclude them from processing inputs of a different modality in so far as it corresponds to the region's inherent functional role (Pascual-Leone & Hamilton, 2001). Thus, middle temporal cortex that activates to motion in visual modality shows selectivity for the auditory perception of motion in congenitially blind participants (Bedny et al., 2010). Similarly, blind participants activates their parahippocampus when they were trained for using tactile information to navigate places, something absent in blindfolded sighted participants (Kupers et al., 2010). Further, visual word form area (VWFA) often associated with visual recognition of written words become active during braille reading in blind (Reich et al., 2011; Sadato et al., 1996), and fusiform gyrus associated with face perception becomes active during voice perception in blind participants (Gougoux et al., 2009).

Metamodal accounts face two main challenges in general. Firstly, researches drawing on metamodal paradigm predominantly focus on the parallels in the brain activities of blind and sighted group, overlooking the differences between them. This focus on similarities might lead to experimental bias. Secondly, demarcating brain regions like hMT+, visual word form are and fusiform face area are quite difficult because their locatio is quite close to each other. Thirdly, comparing the location of BOLD in group level analysis between blind and sighted group might run the risk of inferring misleading overlap of

brain activity. Furthermore, substantial individual variability in brain anatomy is adding another layer complexity to the interpretation of the results (Fine & Park, 2018).

Some proponents of the metamodal accounts offer a refined interpretation on the issue suggesting that cross-modal activation seen in the blind should not be taken as a sign of an adaptive neural processes, instead, they argue, activation in foci of visual cortices in blind simply indicate amplified cross-modal responses something seen even in sighted participants (Merabet et al., 2008a; Ricciardi et al., 2014). For this view, higher sensory regions are primarily about executing certain computations irrespective of sensory mode of input and these regions have no preclivity for any sensory modality. While a number of studies have shown activation in hMT+ of sighted participants in response to auditory and visual motion perception (Battal et al., 2022; Fine & Park, 2023; Poirier et al., 2006a; Ricciardi et al., 2007; Summers et al., 2009) defining criteria in these studies have not been consistent. Most of these studies have relied on anatomical brain mask in region of interest analysis (ROI), or group level averages without localizing hMT+ in individual participants. Researches that utilized individual anatomical localizers did not find activity in hMT+ in response to the perception of auditory motion in blindedfolded sighted and late-blind participants (Alink et al., 2012; Bedny et al., 2010).

Beyond the inconsistent findings of the supramodal resarch, supramodal paradigms face two key challenges. First, when sighted individual engage in cross-modal tasks, e.g. tactile or auditory stimuli evoking visual motion or representational momentum (Senior et al., 2000), perhaps they use their visual imagery and this can explain activation in their visual cortices (Kourtzi & Kanwisher, 2000). Second, if sensory cortices and deprived sensory cortices are supramodal sensory regions, passive sensory stimulation, too, would elicit activity in them (Fine & Park, 2018). However, this is something not seen as they always become active during tasks not during passive stimulation.

1.5. Language Processing in Deprived Sensory Cortices

Crosmodal, metamodal and supramodal theories provide explanations for activations of foci in visual cortices of the blind. Yet, in each of these accounts, common theme was that these deprived cortives remain as sensory regions. However, evidence suggests that deprived sensory cortices in the blind may be involved in functions related to understanding and generating language (Amedi et al., 2004a; Bedny, 2017; Bedny et al., 2011a; Burton, Snyder, Diamond, et al., 2002; Röder et al., 2002; Sadato et al., 1996). In a study conducted by Burton et al. (2002), a blind group was tasked with reading Braille nouns via embossed on plexiglass and generate compatible verbs to them in an MR scanner. The verb generation task led to robust activation in visual cortices along with frontal language areas in the blind group. Notably, contrast between the BOLD actiivity verb generation and mere motor demands of braille reading displayed no sign of adaptive enlargment in the somatosensory cortex suggesting that the language related activity in visual cortices of the blind are not related to the somatosensory demands. Further evidence suggests that precalcarine sulcus of the blind responds more robustly to sentence-level combinations, i.e., meaningful sentences and gibberish sentences composed of non-words that retain gramatical and phonological properties than to non-sentence combinations, i.e., lists of words, non-words and backward speech even if these conditions present greater control and memory demands (Bedny et al., 2011a). Again, in a fMRI study, the visual cortex of the blind showed greater response to syntactical complexity than to a sequential memory task and solving math equations (Lane et al., 2015).

1.6. Cognitive Control and Multiple Demand Regions

Human cognition is characterized by its goal-oriented nature, which underpins human behavior and thoughts. Thought and behavior are composed of complex cognitive

structures. Each complex cognitive structure or episode contains goal-related thoughts or components that can further combine to achieve a more abstract and larger goal (Assem et al., 2020; Badre & Nee, 2018; Luria, 1966). These cognitive structures can be re-constructed and modified upon need and this allows us to flexibly decide , respond or adjust to the contextual demands, even enable us to plan a novel course of action transcending the context in which our behavior and thoughts arise. For all of these, it is presumed that there must a flexible control system necessary for organizing selecting and modifiying our behavior and thought as required (Dehaene et al., 1998; Duncan, 2001; Farooqui et al., 2012; Farooqui & Manly, 2019; Friedman & Robbins, 2022; Panichello & Buschman, 2021).

Through this cognitive control mechanism, we hold goal-related information in our minds, can keep it against distractions, maintaining our focus in the face of intervening habits, and persevere in tasks that are particularly demanding and require effort , and even create new habits. The term cognitive control refers to higher cognitive skills such as attention, short-term memory, task switch, response selection and inhibition. This broad scope of higher cognitive functions are also referred to as “executive functions” and “fluid intelligence”.

Problem- solving and fluid intelligence tests are recognized for predicting success across a diverse range of tasks and cognitive abilities. This observation led Spearman to postulate the existence of a domain- general intelligence in humans (Spearman, 1928) . Studies have associated frontal and parietal lobes with overarching cognitive control functions (Burgess & Shallice, 1996; Duncan et al., 2000; Gray et al., 2003; Luria, 1966; Miller, 2000; Roca et al., 2010). In functional imaging studies, the fronto-parietal cortices are seen activated during a wide variety of cognitive performance tasks involving multiple modalities. These include tasks related to working memory, semantic memory and episodic memory (Nyberg et al., 2003), conflict monitoring (Botvinick et al., 2001), tasks necessiating the assembly and sequencing of behavior (Dumontheil et al., 2011) and tasks involving perceptual challenges and novelty (Duncan, 2006; Duncan & Owen, 2000).

However, the activation of these regions across diverse tasks is not sufficient for assigning a causal role to them in fluid intelligence and cognitive control. Evidence from the patient studies suggests that damage to fronto-parietal regions leads to decreased performance in fluid intelligence tests (Woolgar et al., 2010a, 2018), decreased performance in sentence completion and response inhibition (Burgess & Shallice, 1996), decreased performance in rule switchand social cognition task (Roca et al., 2010). It seems that the extent of the damage not the site of the damage within fronto-parietal cortices is related to loss of fluid intelligence (Woolgar et al., 2010b). Further, lesion mapping studies has identified damages to the fronto-parietal control network, encompassing white matter association tracts within those regions and fronto-polar cortex primarily contribute to declines in fluid intelligence(Gläscher et al., 2010).

In an extensive study conducted by Dosenbach et al. (2006), participants engaged in ten diverse tasks involving visual and auditory modalities. These tasks ranged from letter identification , visual semantics, motor timing to making abstract judgment to auditorily presented tasks. Regardless of the diversity of the demands required by the tasks, medial superior frontal cortex (msFC), dorcal anterior cingulate cortex (dACC), anterior insula (aI) and frontal operculum had increased activation during start cue signal and throughout the task maintainence during all the tasks. One of the defining feature of fronto-parietal cortices is that the same foci of these regions responds to all kinds of demands even in individual level. Fedorenko et al. (2013) had participant done seven diverse tasks including all having hard and easy conditions. The task included a memory task in which participant had to respond to a memory probe appeared in nonwords and sentence condition, verbal and spatial working memory tasks, verbal interference task, stroop task and two math tasks. They used response in hard > easy contrast in one task to localize regions that are most sensitive to cognitive demand of the task individually and measured the responses these individual funcitonal region of interest (fROIs) to the other tasks. They had found that same set of foci within individual subjects in precentral gyrus, inferior frontal gyrus (IFG), middle frontal gyrus, insula, interior and superior banks of parietal cortex respond strongly to the task demands across the seven tasks. Due to its activation across very wide range of tasks in different modalities, these regions have been referred to as multiple-demand (MD) regions (Duncan, 2010).

1.7. Cognitive Control and Deprived Sensory Cortices

Along with the activation of deprived sensory cortice in response to diverse language demands, a number of research studies indicate that the visual cortices of the blind and auditory cortices of the deaf respond to different kinds of cognitive demands. Notaby, right middle occipital sulcus of the blind responds to increasing mathematical complexity in additon to the intraparietal sulcus (IPS), whereas sighted participants deactived their visual cortices in response to increasing math difficulty (Kanjlia et al., 2016). Similarly, right occipital cortex of the blind responded more to a no-go condition than frequent-go condition in addition to their right prefrontal cortex (PFC), suggesting that these visual cortices might be involved in response selection and inhibition (Kanjlia et al., 2021). In this study, the visual cortices of the blind participants, which were more responsive to control demands of no-go condition, showed greater functional connectivity with the frontal cortices associated with control demands than with primary auditory cortices. In a similar vein, there is evidence showing that task perfomance in eposodic retrival, odor detection and working memory, correlates with instensity of cross-modal activation with deprived cortices of the blind and the deaf (Amedi et al., 2003; Ding et al., 2015; Raz et al., 2005; Renier et al., 2013). Apart from episodic retrival, deprived cortices of the blind also respond to working memory tasks. A fMRI study had blind subjects exucute three types of auditory n-back tasks with words, sinusoidal tones and auditory localizations. The study found that in all types of n-back tasks visual cortices of the blind in addition to the fronto-parietal cortices were active whereas the default network regions of the brain were de-active(Park et al., 2011). Not only working memory tasks in auditory modality but also in tactile modality activate the deprived sensory cortices of the blind. Whereas retaining vibrotactile amplitutude and frequency in memory deactivated visual cortices of sighted participants, it activated those of blind participants (Burton et al., 2010). There is at least one fMRI study that indicates deprived cortices of the deaf also activate to control-demands (Ding et al., 2015). In this study, early deaf participants had done visuo-spatial working memory tasks composed of three stages: encoding,maintance and

recognition. Deaf subjects exhibited superior performance in reaction times compared to that of hearing group, and had an increased superior temporal gyrus (STG) activity. The deaf group's task performance, i.e. reaction times and accuracy, positively correlated with the amplitude of STG activity and negatively correlated with earlier and longer usage of hearing aid. All of these findings susggest that the deprived cortices may not be activating to cross-modal tasks sensory discrimination tasks involving intact modalities but activating to more general cognitive control related demands required in each of these tasks.

Studies of functional connectivity on deprived cortices of the blind and deaf provide further evidence that these regions can indeed repurpose to behave more control related fronto-parietal cortices rather assuming a sensory function as proposed by cross-modal and metal modal research.Sensory regions are well known to strong resting state and task-related connectivity among themselves. For example, an auditory region tend to have stronger connectivity with other auditory regions rather than supramodal regions like default network regions or control network regions. The same holds true for visual regions(De Luca et al., 2006b; Lowe et al., 1998) . If the deprived cortices assume an perceptual function, activating to cross-modal sensory tasks, then they should exhibit higher functional and resting state connectivity with auditory or somasensory cortex. However, the connectivity research on deprived cortices shows otherwise. Compared to sighted control participants, the deprived cortices of early blind show even lower connectivity with multimodal visual, auditory and somatomotor regions (Bedny et al., 2011a; Burton et al., 2014; Kanjlia et al., 2016; Liu et al., 2007; Yu et al., 2008). Instead, they shower higher resting state connectivity with fronto-parietal cortices as opposed to sensory cortices of the sighted group who have increased resting state connectivity with other sensory regions and decreased connectivity with fronto-parietal regions (Burton et al., 2014). We should emphasize on the fact that most of the higher tier of visual cortex in sighted participant are multimodal. Indeed, identiying the nature and presence of movement from sounds activated V5 of extra-striate cortex (Poirier et al., 2006b). Identifiying objects compared to textures via touching activated lateral occipital cortex

(LOC) (Amedi et al., 2001). Further, inferring the locations from sound activated cuneus and middle occipital gyrus (Collignon et al., 2006, 2013). Note that all of these findings are from sighted blinded folded participants. Since deprived visual cortices do not show functional connectivity with intact sensory cortices of the blind, the metamodal account may further argue that cross-modal activations in the blind should not necessarily be via cross-regional connections but might be intra-visual cortex connections since these regions are already metamodal However, this also has been ruled out by at least two functional connectivity studies (Burton et al., 2014; Liu et al., 2007). They observed that intra-occipital functional connections in early blind were reduced compared to sighted participants. In sum, the deprived cortices have been seen to activate to all kinds of tasks involving different modalities as mentioned above. Neither cross-modal accounts nor metamodal modal accounts cannot explain these diverse kinds of findings. Further, evidence suggest that deprived cortices activate to task-based paradigms involving sensory tasks but not to gross motor and sensory demands or stimulation (Burton et al., 2010; Burton, Snyder, Conturo, et al., 2002; Gizewski et al., 2003; Sadato et al., 1996). It seems that deprived cortices are activating to higher cognitive issues like language and cognitive control.

The issue still remains as to whether deprived cortices respond to language demands. In fact, the question has been asked by a number of researchers before (Burton et al., 2014; Park et al., 2011). They raised the possibility that the activation of foci in the visual regions of the blind responding to language processing can also be explained by working memory demands and selective attention processes required in those language tasks. These authors are of the opinion that deprived cortices of the blind contribute to working-memory processes , a process normally associated with dorsolateral prefrontal cortex, and this explains superior memory performances in eposodic recall as well as semantic and lexical language tasks (Amedi et al., 2003, 2004b; Burton, Snyder, Diamond, et al., 2002; Raz et al., 2005; Röder et al., 2002) because a better performance in those tasks depends on recognition and remembering. Further, studies suggesting stronger connectivity between the visual cortices and fronto-temporal language areas in the blind

might be biased (Bedny et al., 2011b; Kanjlia et al., 2021; Lane et al., 2015). This is because they often rely on task-based connectivity and Dynamic Casual Modeling (DCM), these techniques focus on response elicited by a specific task or external stimuli, which leads to a directed effect in the brain activation. Morever, DCM examines only limited number of region of interes at a time, failing to look at an overall spatial re-organization of the brain (Burton et al., 2014).

1.8. Hypothesis

Cross-modal and meta-modal understanding on the issue of neural adaptability of deprived sensory cortices have been that they continue to remain a sensory regions e.g. these regions repurpose themselves to become other intact sensory regions (Karns et al., 2012; Kral, 2007; Lomber et al., 2010; Poirier et al., 2006b; Ptito et al., 2008; Uhl et al., 1991; Vetter et al., 2020) or that these regions are already multimodal and have a pre-determined function performing already an abstract processing of an input irrespective of the sensory modality of the input and that via unmasking of neural connections, deprived cortices perform the same function with cross-modal inputs(Cecchetti et al., 2016; Merabet et al., 2008b; Pascual-Leone & Hamilton, 2001; Ricciardi et al., 2014). However, it is becoming increasingly clear that these accounts cannot simply explain a plethora of findings that these regions also respond to language (semantic and syntactic complexity, speech production and comprehension etc.) and cognitive control demands (working-memory demands, response selection and inhibition etc.). Still, an unnoticed observation in all these studies regarding deprived cortices is that they never respond to pure sensory or motor demands. They always respond to diverse kinds of task demands whether the tasks be sensory (tactile, auditory or olfactory), linguistic or an abstract judgment task. In fact, this was the case with blind matematicians whose “visual cortices” activate when judging truthfullness of advanced mathematical propositions (Amalric et al., 2018). A closer look at the issue will reveal that deprived cortices of the blind and fronto-parietal MD regions behave very similarly in so many aspects. First, similar to MD regions, the

deprived cortices do not just respond to tasks in any particular modality, but responds across tasks involving multiple modalities e.g. tasks in tactile, auditory and olfactory modality. Second, similar to MD regions, deprived cortices activate across a very broad range of tasks involving different modalities. This includes and not confined to identication, discrimination and localization of sounds and beat detection, tactile recognition and discrimination, tactile working memory as well as olfactory detection and recognition. These cortices also have been seen to activate to the tasks that requires higher cognitive abilities such as working memory, calculations, abstract mathematical judgements, selective attention, response selection and response inhibition as well as semantic and sentence-level complexity, verb generation and so on. Third, the deprived cortices of the blind shows stronger functional connectivity with fronto-parietal regions both at rest and at task, contrary to what would be expected if they were sensory regions. Note that a sensory region shows stronger functional connectivity among other regions within the sensory regions in sighted participants and fronto-parietal multiple demand regions also shows Further, evidence suggest that similar to MD regions, deprived cortices of the blind respond to all kinds of task demands, that is, when the task requires higher cognitive control and effort, these regions show hightened activity to those demands just as MD regions. Based on all of these reasons, we hypothesized that visual cortices of the blind may become a part of MD network.

The hallmark characteristic of the MD regions is the same set of foci in them consistently respond to diverse cognitive demands even within individual subjects(Fedorenko et al., 2013). In the present study, we tested if deprived cortices of the blind become a part of MD network. To do this, we had blind participants do four diverse tasks in tactile and auditory modalities. All the tasks had an easy and a hard condition. We used response of blind visual cortex to cognitive demand of one task in hard > easy contrast to localize voxels that are most responsive to the task demand and create individual functional region of interest and measured their response to the other three tasks.

CHAPTER 2

THE FATE OF DEPRIVED VISUAL CORTICES IN BLINDNESS

2.1 Funding

This reseach received financial support from the Scientific and Technological Research Council of Turkey TÜBİTAK, grant number: 121K902.

2.2 Design

An increase in regional activity in response to a control demand should not necessarily indicate that such a region becomes cognitive control region. Usually, a sensory region activates to control demands of a task but only when the modality of the task is the same as the modality of the region, i.e. a visual region will correspond control demands of a task on if the task was executed through visual modality. Thus, it won't suffice to show that deprived cortices of blind participant show increased response to a task demand in just one modality e.g. auditory or tactile modality. If we test whether the same foci in visual regions of the blind responds to very different kinds of task demands involving different modalities, it will be a good demonstration that these visual foci in the blind has become a cognitive control region. Hence, we designed four different fMRI tasks involving tactile and auditory modalities. Each of these tasks required participants respond to different kinds of task demands. In a trial of tactile decision making task, participants have to judge which one of the two shapes printed on a plexiglass tablet was larger in size.The other three tasks were of auditory modalities. Participants had to

depend on their hearing to respond to task requirements. These were working memory updating task, sound duration judgement task in which participants had to decide which one of a sound pair they heard sequentally was longer in duration, motor speed task in which participants have to respond to auditory prompts as fast as they can by pressing corresponding button via a button box.

Each task was block-design and had an alternating sequences of easy and hard blocks. These blocks were followed by a rest that jittered between 5-15 seconds for the auditory tasks, and 2-10 seconds for the tactile task. We conducted four fMRI sessions lasting between 12-18 minutes. Participants had the option to complete four tasks in a single session or complete them in two separate sessions.

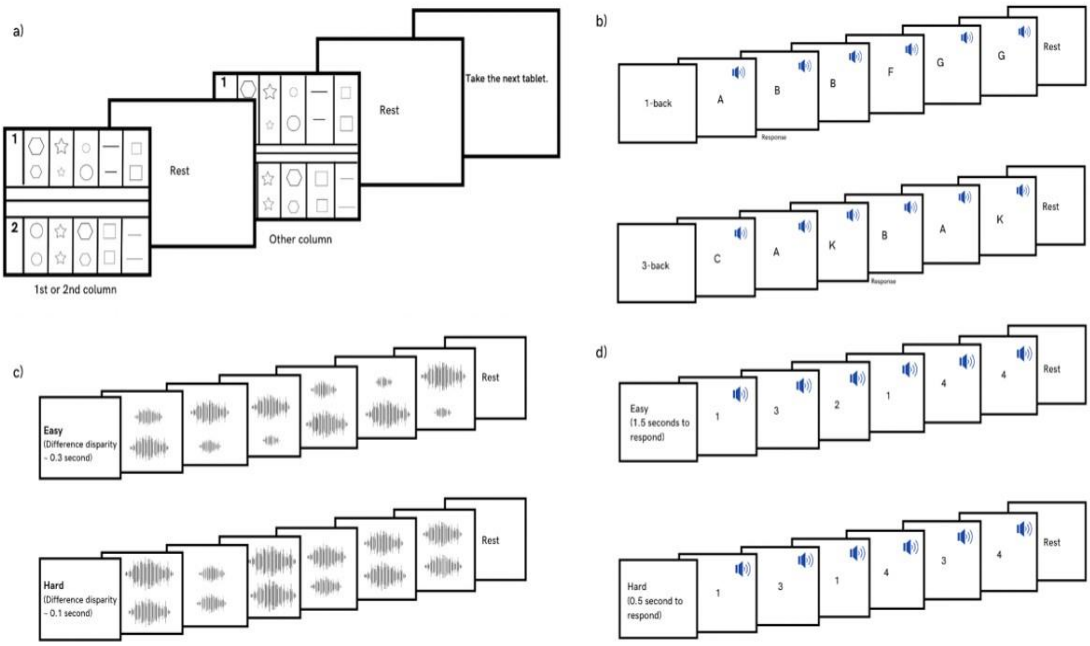

Figure 1. Overview of Four Cognitive Tasks in an fMRI Study: Tactile Decision-Making, Working Memory Updating, Time-Duration Judgment, and Motor Complexity. **a)** In a trial of tactile decision-making task, participants had to decide which one among the vertically aligned pair of shapes was larger in size. The trials were presented on plexiglass tablets on which various shapes differing in size were embossed. Difficulty of the task was manipulated by reducing the raisedness of shapes and size difference

between the two shapes in trials of hard blocks. Task were presented with 10 easy and 10 hard blocks. Each tablet contained one easy and one hard block. The tablets were placed on participants' chest and abdomen in the MR scanner. **b)** In WM updating task, participant listened to a series of Turkish letters and had to determine whether the letter they heard in the current trial mathes the one they heard one or three trials earlier. In a trial of 1- back, they compared the current letter to the one they heard one trial prior and ın a trial of 3- back, they compared to the one they heard three trials prior. Task were presented in blocks of easy and hard.There were 10 easy and 10 hard blocks. Each block contained 10 trials. **c)** In a trial of time-duration judgment task, participants heard a brief sequence of two distinct pure tone and had to decide which one of them was longer in duration. A silent interval in between two pure tones in a sequence was introduced to enable participants to perceive the two tones distinctly rather than as a continious one. Diffuculty in the task was manipulated by reducing the difference in the duration of two tones presented in a trial and the duration of silent interval between them. Task were presented in blocks of hard and easy. There were 10 easy and 10 hard blocks. **d)** In a trial of motor complexity task, participants heard numbers from 1 to 4 and instructed to press the corresponding button as quickly as possible. Note that each number from 1 to 4 were assigned to a specific button in the button box. Difficulty in the task was manipulated by reducing inter-trial interval between trials and response-time window alloted for a button press after presentation of trials in hard trials of the task (from 1.5s to 0.5 s). Task were presented in hard and easy blocks. There were 10 easy and 10 difficult blocks. Each block contained 10 trials.

2.3. Participants

Twenty-three blind subject (10 females) and twenty sighted subjects (12 females,) participated in the research. The average age of blind group was 30.6 years (SD =7.6) and the average age of sighted group was 26.75 (SD = 6.23). Sixteen of the blind group were congenitally blind, possesing minimal or none light perception. The remaing seven reported that they became completely blind between the ages of 7 and 35. Neither blind nor the sighted participants had any hisroty of neurological diseases. The blind participants were recruited from Eğitimde Görme Engelliler Derneği (EGED) in Ankara, as well as via personal contact of the two author in the study. Among the blind group, eighteen were right-handed, three were left-handed and two ambidexterous. Among the sighted group, five reported to be left-handed. Seventeen blind participants undertook working memory (WM) updating task, tactile decision- making task, time duration judgement task and motor complexity task. Two participants did WM updating task,

tactile task, and motor complexity task. One participant did WM updating task, tactile decision-making task and time duration judgement task. Three participant completed only WM updating and tactile decision-making tasks. Note that all blind participants completed WM updating and tactile decision-making tasks. All sighted participants completed only WM updating and tactile decision-making tasks.

2.4. Tasks

Working Memory Updating Task : This was an auditory n-back tasks. In a trial, participant had to decide whether the turkish letter they heard was the same as 3 or 1 they heard prior (3 back or 1 back) via pressing a button in the scanner. Trials were presented in blocks of 10 trials. For 1 back task, participants were instructed to keep the letter in the first trial in mind and pass on the next one by pressing a button. From the second trial onwards, they were to determine if the letter they was the same as the previous one and press a button (index finger: yes, middle finger: no). For 3 back task, the rules were same as in 1 back task except they now have to keep in mind the letters that they heard from the first three trials, and from the fourth trials onward, they had to decide if the letter they heard was the same as the one three prior. In each blocks, as participant pass on the next trial, they had to keep and update their memory about the letters' identity in previous trials until they complete 10 trials. There were ten 3-back and 1 back blocks in total. Each blocks were followed by a rest period jittered between (5-15). Before participants pass on the next block, they were instructed to press a button when they get ready for the next block.

Tactile Decision-Making Task : The tactile task was presented through a plexiglass tablets placed participants chest or abdomen in the scanner. In a trial, participants had to determine which one of a vertical aligned pair of shape was larger in size by touching and respond by pressing a button (index finger : top shape, middle finger : buttom shape) .

Each tablet was bisected horizantally into an easy and hard section by three embossed mid-lines on plexiglasses. This allowed participant to be aware of the boundaries between easy and hard section, take precaution not to execute a trial from the other section while executing a section. Each section was further divided into 5 columns, delineated by 4 vertical lines spaced 2.5-3 cm apart. These lines originated from the bisection line and extended to the outer edges of the plexiglass. Columns represented individual trials. Within each trial or column, there were two shapes vertically aligned, separated by an interspace of 1.5-2 cm. Within each trial or column, there were two shapes vertically aligned, separated by an interspace of 1.5 – 2.cm. Within a single trial, the shapes were identical, but the kind of shapes varied across trials. Participants were tasked with judging which of the shapes was larger in size by a fingertouch. They indicated their decision via a button press. Some participants observed an inverse button press logic, as long as it is applied consistently, we did not intervene. For hard sections, difficulty was manipulated by reducing the size between the two shapes in a trial and by decreasing raisedness of the shapes so that it would harder to discern the shapes via touch. blocks. For the easy trials, the difference in area between the shapes within a trial was kept between 0.8 and 1 cm^2. For the hard trials, this difference was between 0.3 and 0.5 cm^2. The foldedness of shapes on plexiglasses was reduced in hard blocks so that it was more difficult to discern the shapes by touching. For orientation, the terms ‘’ easy’’ and “hard” were embossed on the upper left edge of their respective sections in Braille for blind participants (Below the braille markers, numerical indicators were also embossed for deaf and control participants). This also served as a starting reference point for participant to initiate tactile the sequences of tactile engagement from left to right. In each trial, participants tactually explored and compared the area of two shapes, indicated their decision by a button press. After inter-interval (1.5 seconds for easy and 0.5 seconds for hard trials), they were instructed to proceed with the next trial. Once they completed five trials in a block, a rest period jittered between 2-10 seconds followed. After rest, they continued with the remaining block on the plexiglass.

Auditory instructions were pre-recorded and coded. Participants received these instructions via headphones in the scanner. A collaborater present in the MR room handed the plexiglass tablets to participants and assisted them in positioning it on their chest or abdoments. Participants received auditory prompts indicating which block to begin with (e.g., "Please spot the beginning of the easy block by placing your finger on the corresponding braille marker, then press a button when you are ready to proceed with trial 1). The order of block commencement (easy or hard) after retrieving the plexiglass from the collaborator in the scanner was randomized.

Time Duration Judgment Task : The task was designed with a total of 20 blocks, comprising 10 easy and 10 hard blocks. Blocks were presented in an alternating sequence followed by a rest jittered between 5-15 seconds. Each block contained 10 ten trials. Within a trial, participants were presented with a sequence of two distint pure tone. After the presentation of the first tone, an interval was introduced before the second to ensure that participants perceived two distinct sound rather than a continious one. One of the two tones was always of a longer duration than the other. After listening , participants had to determine which of the two tones had a longer duration. If the first tone they heard was longer in duration, participants were to press the left button on the button box. If the second tone was longer, they pressed the right button. The duration difference between two tones in a trial was reduced and the interval between two tones was shortened to increase the difficulty in hard blocks. Duration difference between tones in easy trials was jittered between 200-350 miliseconds and it was between 60-150 miliseconds in hard trials. The interval between two tones within a trial was set at 0.3 seconds and 0.1 seconds for trials within easy and hard blocks, respectively. Intertrial interval was 1 second.

Motor Speed Task: The task was structured with alternating sequence of 10 easy and 10 hard blocks. Each block is followed by a rest period jittered between 5-15 seconds. Easy blocks contained 8 trials; hard blocks contained 12 trials. On each trial, participants heard

one of four numbers: 1,2, 3 or 4. These mapped to the four buttons of a button-box and the participants pressed the corresponding button as fast as possible. In easy blocks they had 1.5 s to respond to while in hard blocks they had to respond within 0.5 s.

Numbers presented across trials of a block were in a random sequence and had no predictable order. Difficulty was manipulated using two parameters. The first was the response time window. On easy trials, participants had 1.5 seconds to press the corresponding button. On hard trials this window was shortened to 0.5 secs (Failure to respond within the allotted time or pressing an incorrect button result in negative feedback with a brief sound. There was no positive feedback). The second parameter was inter-trial interval (ITI). ITI was reduced from 1.5 seconds to 0.5 seconds on hard trials. This urged participants to be in a state of greater alertness and preparation on hard blocks.

2.5. MRI Acquisition

The MRI scanning was conducted on a 3T Siemens machine with a 12-channel head coil. T2*- weighted echo planar imaging (EPI) with a single shot gradient echo were collected with a top-down sequence with these settings: repetition time of 2000 miliseconds, echo time of 30 miliseconds, 32 oblique slices each have 3 mm thickness and spaced 0.75 mm apart. In plane resolution was 3.0 x 3.0 mm, with a square matrix of 64. Field of view (FOV) was set to 192 mm, with an angle tilted to 78°. Also, T1 weighted magnetization-prepared rapid acqusition gradient echo (M-PRAGE) anatomical images were collected before functional scans. MPRAGE images were acquire with 1 mm slice thickness, with a 1 mm cubic resolution in 176 sagittal slices. The FOV was 256 mm.

2.6. Pre-Processing of Data

We processed the data using fifth version of automatic analysis (aa) workflow and pipeline system (Cusack et al., 2015). Note that this pipeline performs analysis through

Matlab and SPM12. For pre-processing, acquired BOLD images underwent slice-timing adjusment with the middle slice taken as reference. The images were then re-aligned. To do a better anatomical alignment with functional time series in both blind and sighted subjects, images were normalized to the MNI template using DARTEL toolbox and co-registered with structural T1-weighted images. Finally, EPI images were resized to a resolution of 2 x 2 x 2 mm^2 and underwent smoothing with an 8- mm full-width at half-maximum Gausian kernel.

2.7. fMRI Analysis of Tasks

T-maps and beta coeffecients were derived from normalized and smoothened functional data using a general linear model (GLM) . For each task (tactile decision-making, WM updating, time duration judgment and motor complexity), four regressor were employed, one regressor corresponding to these conditions: easy, difficult, rest and press. Each regressor was modelled as an epoch covering the entire length of the respective task blocks. Easy and difficult blocks began when participants heard the auditory task-relevant cue for the first trial and ended when they responded to the last trial with a button press. Press blocks were also modelled as an epoch which began when participants heard the auditory prompts conveying them to press a button when they are ready for the next block and lasted when they press a button to engage with the upcoming block. Six movement parameters were entered into GLM with regressors of no interest. Each of these regressors underwent convolution with a standard hemodynamic response function. Both BOLD time series and the GLM model were underwent temporal filtration, using a Gausian-weighted liner highpass filter with a threshold of 120 s. For second level analysis, four regressors for each task were estimated using these vectors: hard >easy, hard + easy (task) > rest, hard > rest, and press > rest. For the purposes of the present study, only hard > easy comparison was used for the fMRI task analysis. Hard > easy contrasts from each individual task analysis were incorporated into a second-level analysis.

For the combined analysis of the tasks, fixed effect analysis was conducted, averaging activation estimates across runs within each subjects. These average effects for each subject were put into a second-level analysis. Second-level analysis were adjusted for multiple comparison set at a FDR threshold of $p < 0.05$.

2.8. Task-related ROI Analysis

We conducted a region of interest (ROI) analysis focusing on various brain regions in blind and sighted participants. For the blind participants, we examined the visual cortex (V1), fronto-parietal, and auditory regions. In sighted participants, our analysis was centered on the fronto-parietal regions. We included the following fronto-parietal ROIs: anterior prefrontal cortex (APC), pre-supplementary motor area (SMA), inferior frontal sulcus (IFC), intraparietal sulcus (IPS), anterior insula (AI), and extra striate cortex (ESV). The coordinates of these ROIs were taken bilaterally from Dosenbach et al., 2007; Fedorenko et al., 2013. ROIs were deliniated as spheres with a 10 mm diameters centered on their respective cordinates. We took left and right V1 ROI, and auditory cortex ROIs including Te3, Te10, Te11, Te12 from JuBrain Toolbox (Eickhoff et al., 2007).

2.9. Native-Space ROI analysis in the Blind

We created individualized functional region of interest (fROIs) within visual cortex of blind subjects that are responsive control demands of the four tasks. To do this, we used an occipital mask from Jubrain Anatomical mask (https://www.fz-juelich.de/en/inm/inm-7/resources/jubrain-anatomy-toolbox). We unnormalized this mask into the native space of blind subjects' occipital cortex. We then located voxels that are most responsive to control demands across the four tasks using hard > easy contrast at an uncorrected p value of 0.001 within the subjects' unnormalized visual cortex masks. Thus, we created four individualized fROI mask that are most responsive to control demands for each blind

participants. Note that if there were no voxel surviving uncorrected p value of 0.001 in hard > easy contrast in a given task within a subject, we then used a more lenient uncorrected threshold of p = 0.01. Subsequently, we measured responses of individual fROI in one task (e.g. tactile decision-making task) to the other three tasks using MarsBar toolbox (https://marsbar-toolbox.github.io).

2.10. Behavioral Results

2.10.1. Accuracy of Blind and Sighted Group

In the hard conditions, the blin group achieved mean accuracies of 86 %, for tactile decision-making task, 91 % in WM updating task, 90 % temporal judgement task, 95 % for motor complexity task. Sighted control group achieved mean accuracie of 85 % and 93 % for tactile decision-making and WM updating task, respectively. These indicated that participant had sustained attention to the tasks and were able to hear task-related information clearly in the MR scan. A 4x2 repeated measures ANOVA was conducted to evaluate the accuracy of the blind group across four tasks (Tactile Decision, Working Memory Updating, Temporal Judgment, and Motor Complexity) and two levels of difficulty (Easy and Hard). A significant main effect for the task was observed, $F(3,16) = 15.67$, $p < 0.001$, with the Motor Complexity task being the most accurately performed task among the four task. Also, there was a significant main effect for task difficulty, $F(1,16) = 89.13$, $p < 0.001$, indicating a significant performance differences between the easy and hard conditions. Task by difficulty interaction was not significant, $F(3,16) = 1.9$, $p = 0.13$, suggesting that the effect of task difficulty was consistent across the different tasks.

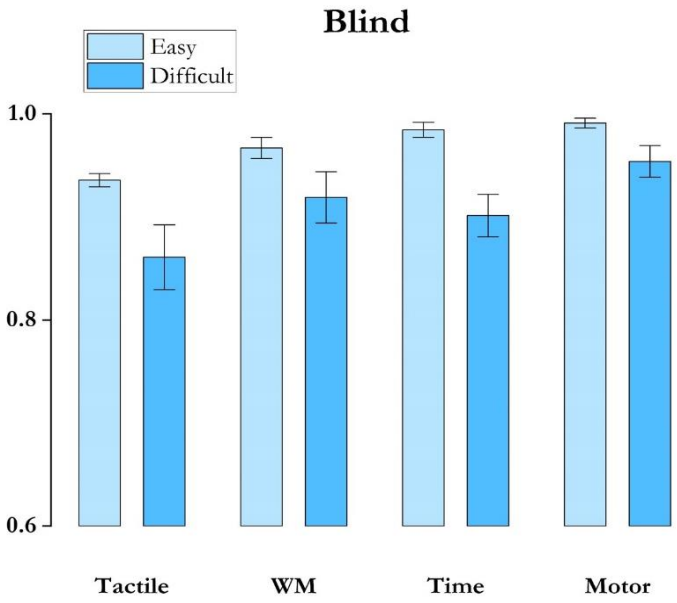

Figure 2. Blind participants' accuracy rates across the four cognitive control related tasks. Error bars indicate 95% confidence interval.

A 2x2 repeated measures ANOVA was conducted to evaluate the accuracy of the control group accoss two tasks(Tactile Decision, WM updating). A significant main effect for the task was obseved $F(1,19) = 42.47$, $p < 0.001$. There was as significant main effect for task difficulty $F(1,19) = 55$, $p<0.001$. Again, task by difficulty interaction was not significant $F(1,19) = 2$, $p = 0.15$.

We conducted a 2 x 2 x 2 repeated measures ANOVA to test the effect of task type (Tactile Decision-Making vs WM updating), task difficulty (easy, hard) and sightedness (blind, sighted) as a between-subject factor on accuracy of both groups. We found significant main effects for task, $F(1, 41) = 55.52$, $p < 0.001$, and for difficulty, $F(1, 41) = 93.03$, $p < 0.001$. However, the interaction effects were not significant: task by difficulty, $F(1, 41) = 3.5$, $p = 0.06$; task by blindness, $F(1, 41) = 2.64$, $p = 0.11$; difficulty by blindness, $F(1, 41) = 0.01$, $p = 0.93$; and the three-way interaction of task, blindness, and difficulty, $F(1, 41) = 0.01$, $p = 0.92$. These results indicate that while task type and task

difficulty significantly impacting accuracy, blindness either in isolation or in interaction with task type and difficulty has no effect on accuracy.

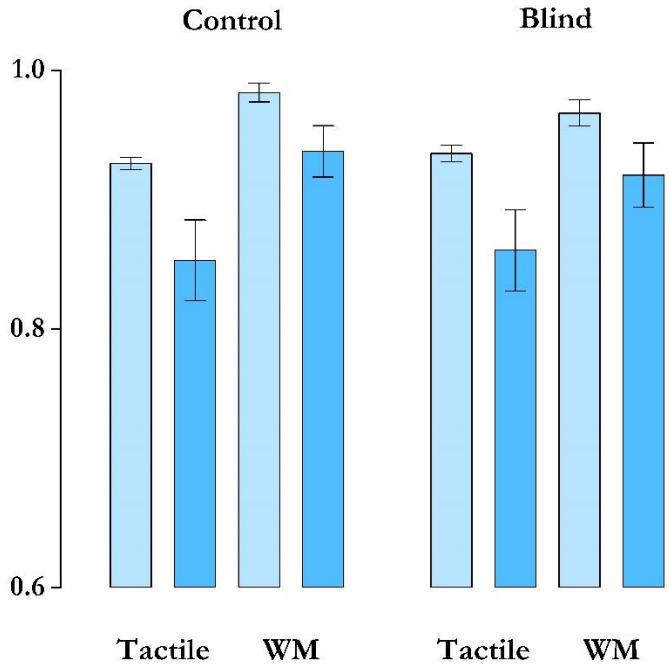

Figure 3. Comparison of blind and sighted participants' accuracy rates on tactile decision-making and WM updating tasks. Dark blue indicates accuracy rates on hard trials, where as light blue on easy trials. Error bars indicate 95% confidence interval.

2.10.2. Reaction Times (RTs) of Blind and Sighted Group

To test the effect of task type and task difficulty on the mean RTs of blind participants across tactile decision-making, WM updating and Time Duration Judgment tasks, we conducted a 3 x 2 repeated measures ANOVA. The results showed a effect of task type on RTs of the blind group, $(2,16) = 450.27$, $p < 0.001$ as well as on task difficulty, $F(1,16) = 290.69$, $p < 0.001$. Furthermore, a significant interaction between task type and

task difficulty on the RT performances of the blind group was found $F(3,16) = 253.74$, $p < 0.001$.

To test the effect of difficulty on reaction times of blind participants, we conducted a paired sample T test. The result revealed a significant difference between the two conditions, with participants demonstrating lower RTs in the hard block, t (18) =5.91, $p < 0.001$. Please note that given the distinct pattern of the motor complexity task relative to the remaining ones, we' ve decided to present RTs of motor complexity task separately to avoid potential misunderstanding or confusion. The hard block of this task required participants to respond faster than in the easy block. It is important for readers to understand that the lower in the hard blocks of motor complexity task caused by design, and not indicative of decreased effort or alertness.

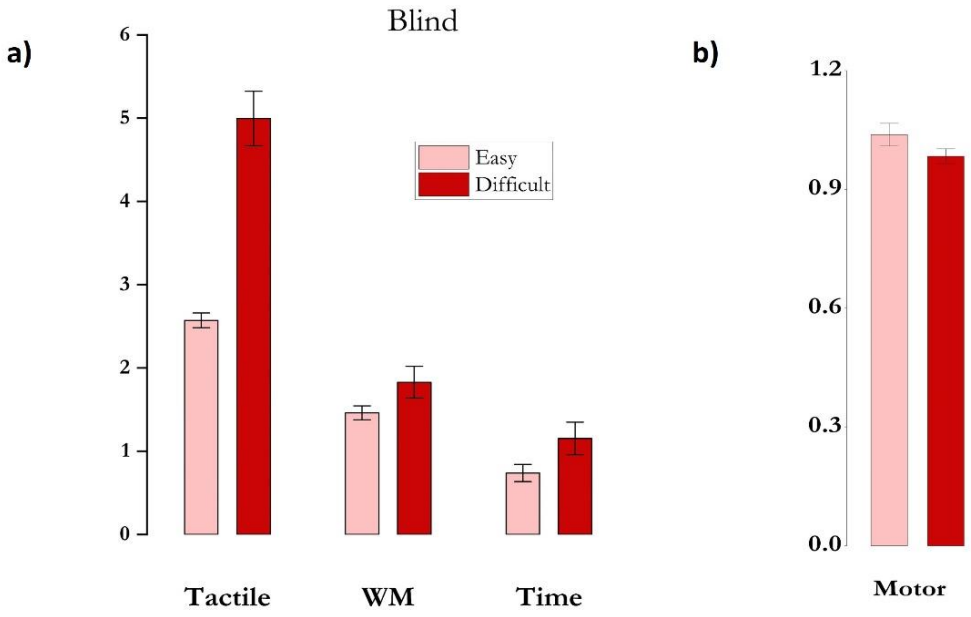

Figure 4. Reaction times of blind participants across hard and easy conditions of the four tasks. Note that motor complexity task was distinct from the other three tasks in that partipants had to respond to trials in hard blocks faster than to trials in easy blocks. Error bars indicate 95% confidence interval.

We conducted a 2x2x2 repeated measures ANOVA to test the effects of task type (tactile decision , WM updating), difficulty level (easy, difficult), and blindness (blind, sighted) on RTs of the blind and sighted group , with sightedness as a between-subjects factor. We found a significant main effects for task type, $F(1, 41) = 1442.60$, $p < 0.001$, and for difficulty, $F(1, 41) = 890$ $p < 0.001$, and also there was an effect of blindness on RTs, $F(1,41) = 74$ Sighted control group was slower than blind participants on tactile decision-making task [$t(1,41) = -13$, $p < 0.001$], but not on WM updating task [$t(1,41)= -0.048$, $p = 0.962$].

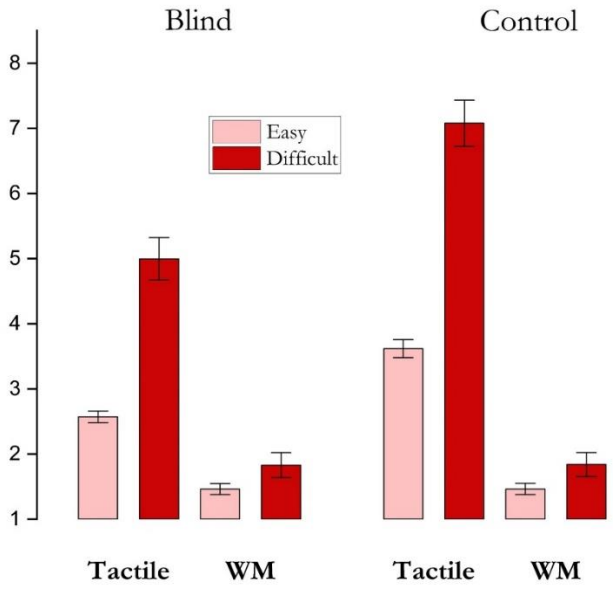

Figure 5. Comparison of RTs of blind and control participants across tactile decision-making and WM updating tasks. Error bars indicate 95% confidence interval.

2.11. Whole Brain fMRI Analysis of Blind Group

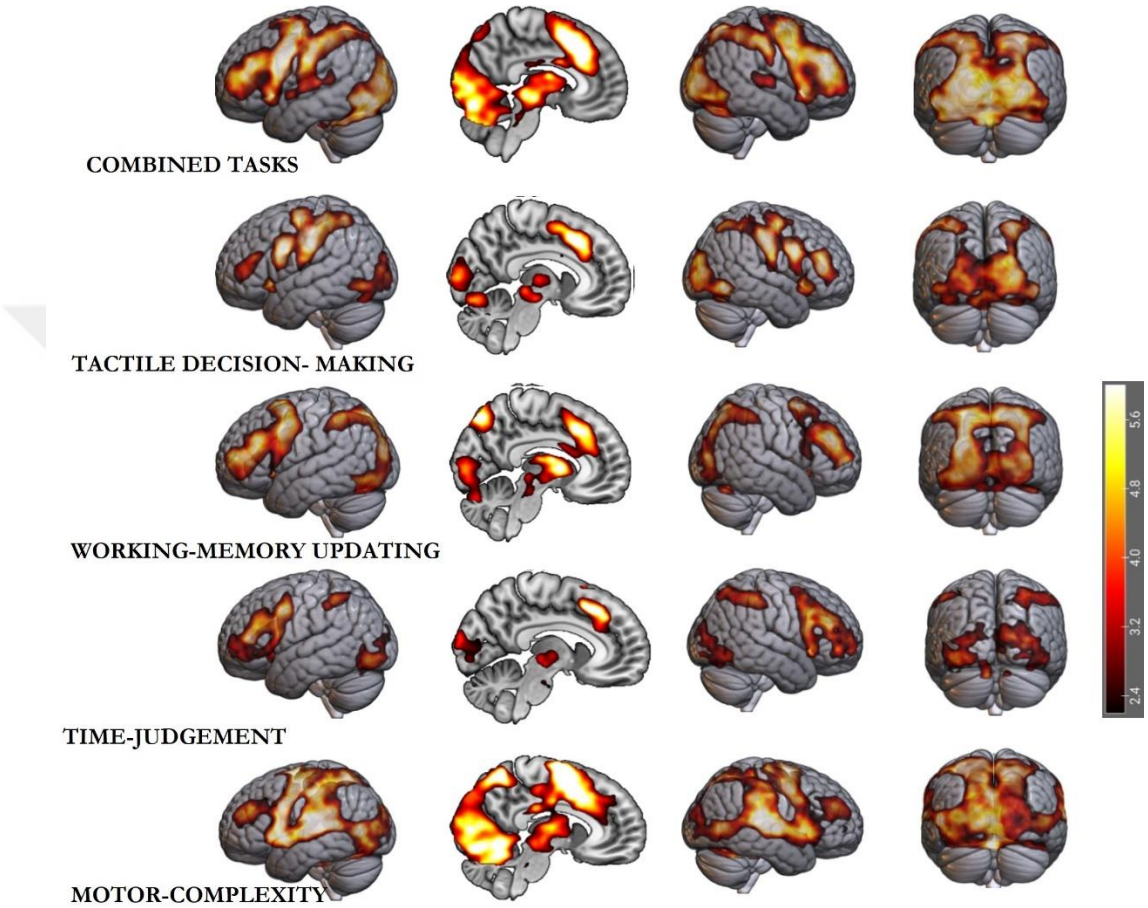

Figure 6. Whole-brain activations of blind participants across the four diverse control demands and their averaged activitity across the four tasks (Combined Tasks) at a FDR correction of $p < 0.05$.

In response to the four diverse control demands (hard > easy) involving auditory and tactile modalities, blind participants activated almost all of their visual cortices.These included occitipal fusiform gyrus in conjuction with temporal occipital fusiform cortex, lateral occipital cortex (both inferior and superior parts), lingual gyrus, cuneus, upper and lower banks of calcarine cortex. Note that all of these activation was bilateral. A visual inspection revealed that these activation of middle and lateral parts of visual cortex in the blind extended forward into posterior parts of the parietal cortex (See, Figure 6).

Conjuction analysis of the four task ($p<0.05$) revealed that a large cluster in lateral occipital cortex responds consistently across the four diverse demands.

In addition to the widespread activation in visual cortex, blind participants also activated their canonical multiple demand regions. These included bilateral activation of IFS, IPS, AI, SMA and APFC. Middle frontal gyrus was most active region across the four task demands in the blind group. Also, upper regions of cerebellum (cerebellum VI bilaterally) did respond robustly to the task demands (See, Figure 6).

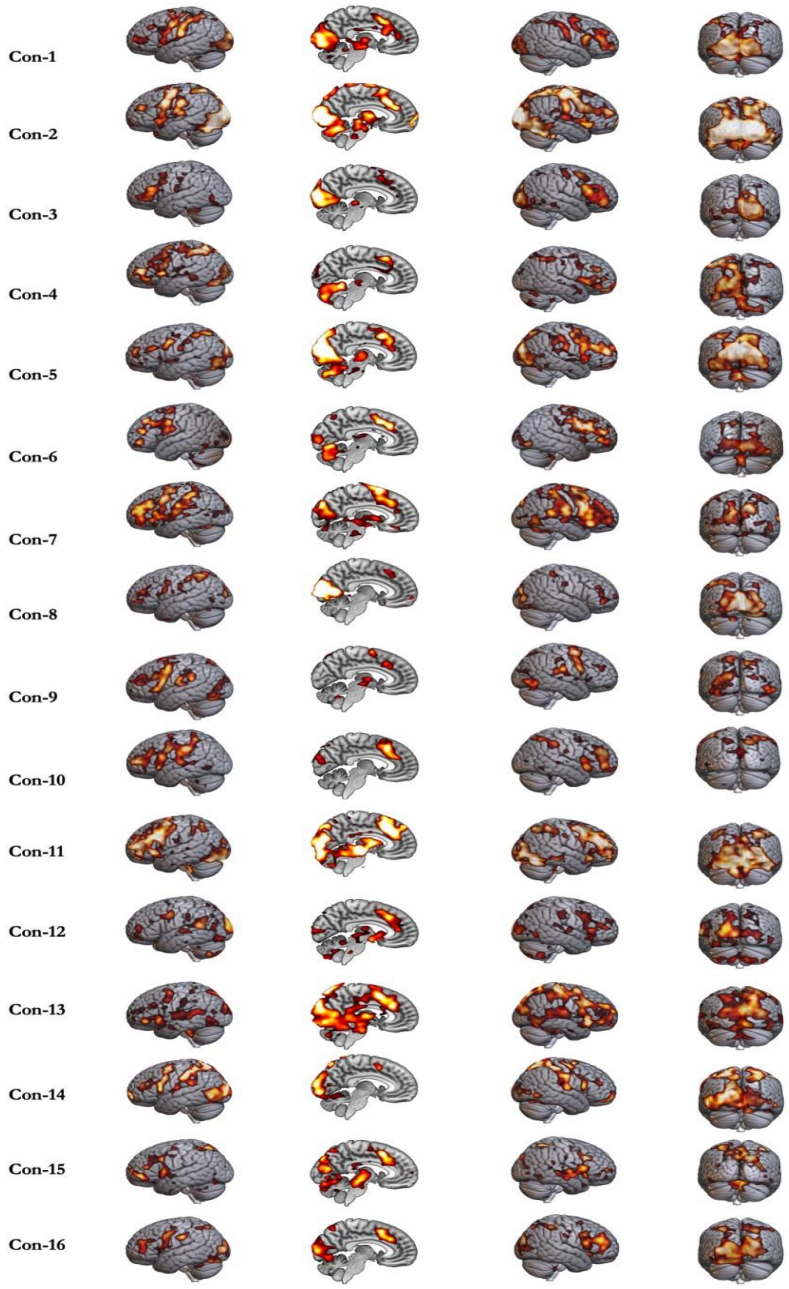

Figure 7. Whole brain-results of individual congenitallly blind participants averaged across the tasks all of the tasks they completed. Note that almost all of them activated their extra-striate cortex and early visual regions to increased control demands. The voxel cluster that was most active in their brains during control demands was predominantly in the visual cortex. The results are displayed at a FDR correction of $p < 0.05$.

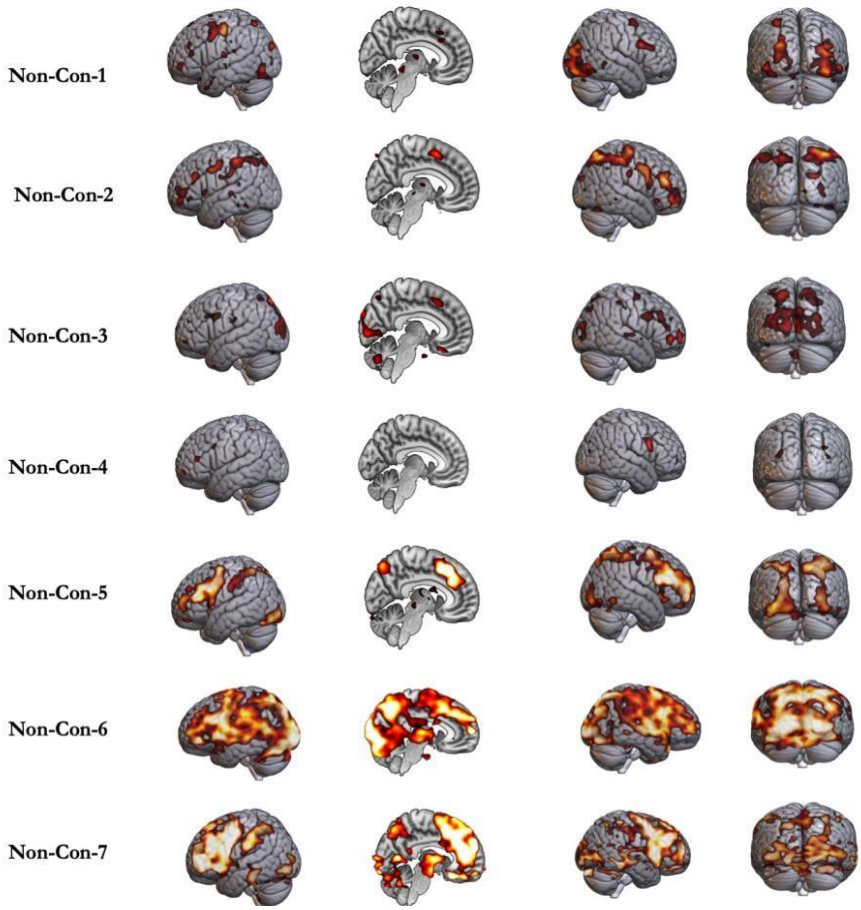

Figure 8. Whole brain results of non-congentially blind participants averaged across the task demands. Note that most of them activated their extra-striate cortex but not their early visual cortex to increased control demands. The results are displayed at a FDR correction of $p < 0.05$.

Individual whole-brain analyses showed that for the majority of congenitally blind participants, the foci that respond most robustly to diverse task demands were in their visual cortex (See, Figure 7). In contrast, participants who became blind later in their life exhibited a different pattern from that of congenitally blind. While a few of these individuals did respond strongly to the control demands of the tasks, most of them did not activated their visual cortices consistenly to the control demands of the tasks they completed (See, Figure 8). Notably there was one participant whose visual cortex was only active during time-duration judgement task that required to judge the duration of a sound pair, but not during the other three demands. Interestingly, non-congenitally blind participants activated only their higher visual regions that are associated with multi-

modal functions rather than early visual cortices. In contrast, congenitally blind participants activated both their early and higher cortices.

2.12 Comparison of Blind and Sighted Group

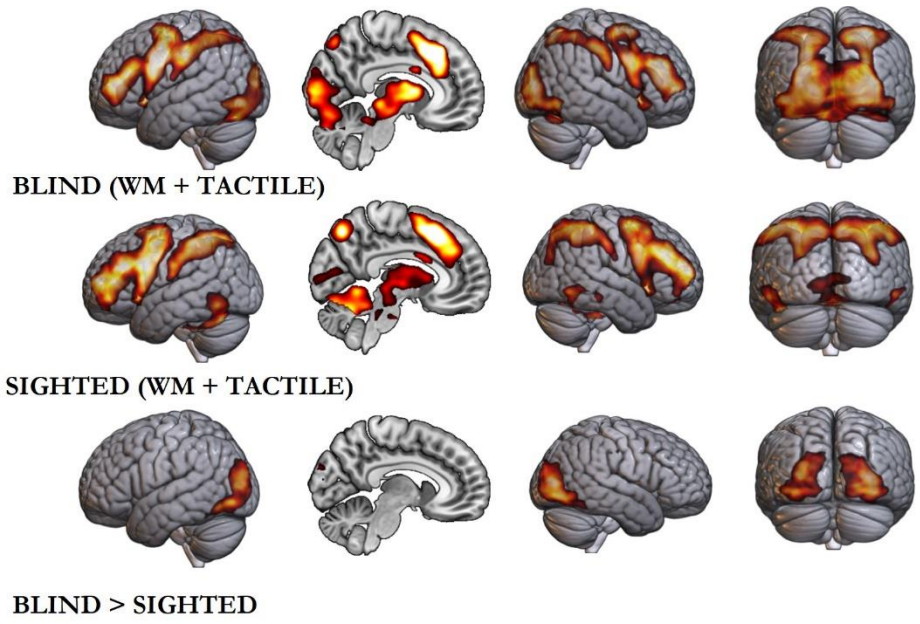

Figure 9. Comparitive whole brain activation in blind vs. sighted participants averaged across tactile decision making and WM updating tasks. MD regions of the both group showed robust response to the control demands. The only region that was more active in blind participants than sighted participants was visual cortex in group-level comparison. The results are displayed at a FDR correction of $p < 0.05$.

Tactile and working memory updating tasks activated the canonical MD regions in both blind and sighted participants. In addition, these task also activated visual cortices of the blind group, whereas this effect was absent in visual cortices of blindfolded sighted participants (See, Figure 9). Group-level analysis showed activation in their primary visual cortices of the sighted participants in response to the task demands. However, this activation was weak compared to much stronger activity observed in the visual cortices of the blind participants. We found that when compared to sighted participants only visual cortices in blind participants was more active during task demands while everything else remains identical (See, Figure 9).

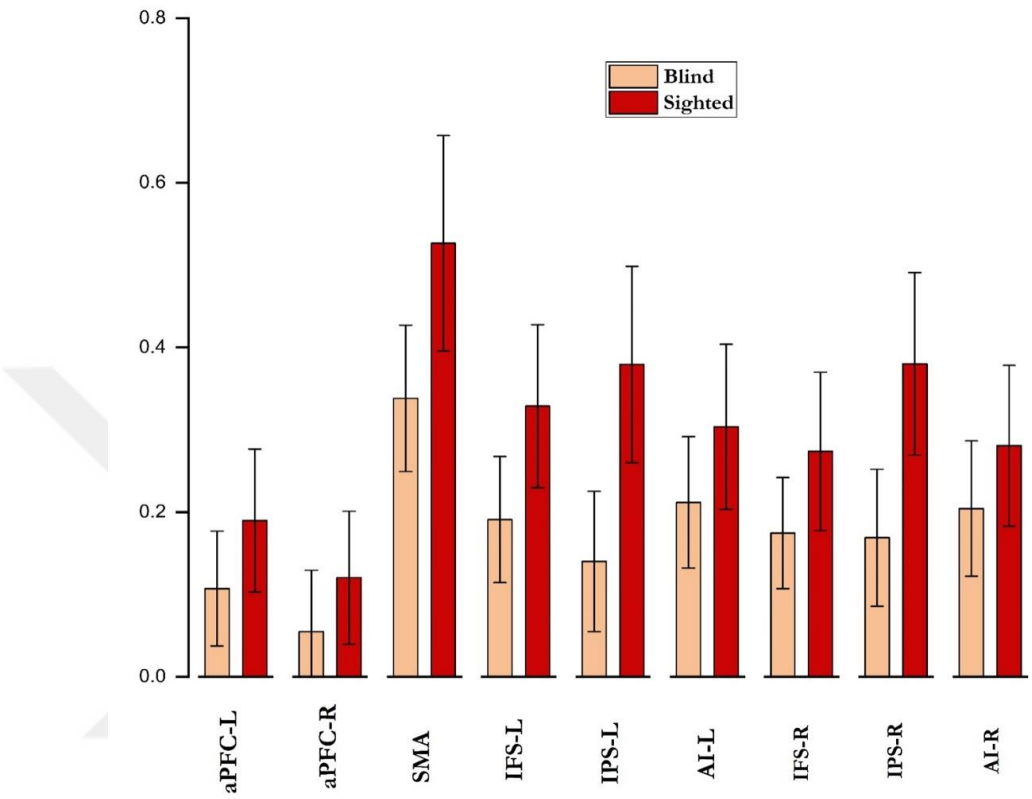

Figure 10. Blind participants showed less activity in their MD regions than sighted participants during tactile-decision making and WM updating tasks.Bars represent the difference of mean activity between hard and easy conditions of the tasks. aPFC stands for anterior prefrontal cortex, SMA for supplemantary motor cortex, IFS for inferior frontal sulcus, AI for anterior insula, IPS for intra-parietal sulcus. Error bars indicate 95% confidence interval.

Compared to the blind group, we observed significantly greater level of activity within the canonical MD regions of sighted participants (See, Figure 10). Bayesian repeated measures ANOVA with MD regions taken as a within-subject factor and with sightedness (blind, sighted) taken as a between subject factor revealed that sighted participants activated their canonical MD regions significantly more than blind participants in response to the control demands of tactile decision-making and WM updating tasks ($F_{1,41}$ = 8.2, p = 0.007, η^2_p = 0.32; BF_{10} = 11.2). This difference might be attributed to the fact

that the visual cortices in blind participants works as an additonal MD regions, so that they don't need to activate their canonical MD regions as much as sighted participants need. Alternatively, it could be that sigted participants activates their MD regions more in response to the diverse task demands because they are relatively younger than blind participants. Nevertheless, this latter suggestion seems not plausible as the reduced activation of MD regions in the blind group is more marked in left IPS (BF_{10} = 26.15, t(41) = 3.5), rather being equally reduced in all across MD regions. This specific effect seems not to be a result of age-related factor instead it is perhaps more- related to blind participants' brain spatial re-organization or modification.

2.13 Native Space Analysis of Blind Group

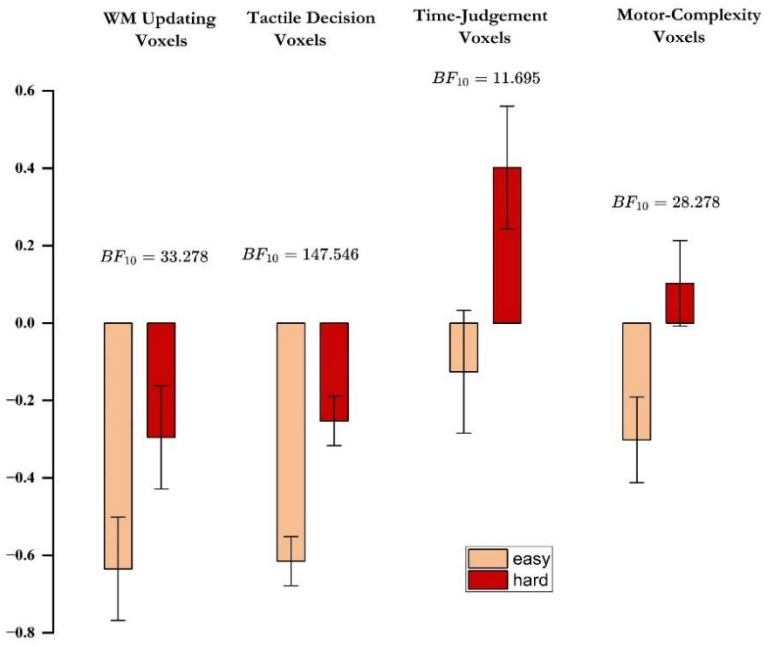

Figure 11. Occipital fROI Responses to Various Control Demands: Differential Activation in Hard vs. Easy Conditions Across Tasks (Bayes Factor and 95% Confidence Intervals). Averaged response of four occipital fROIs, each defined by its peak response to one specific control demand, to the remaining three control demands. E.g. The initial bar pair on left shows mean response of occipital voxels that were most

sensitive to the control demands of WM updating task on the easy and hard conditions of the remaining three control demands (tactile-decision making, time-duration judgment and motor complexity. The Bayes Factor (BF_{10}) are presented above each bar pairs, indicating the evidence for differential activation of these fROIs across the hard and easy conditions of the three tasks in favor of hard conditions. Error bars indicates 95% confidence interval.

One of the key characteristics of fronto-parietal regions is that their activation across diverse control demands even if the modality of the tasks are different (Dosenbach et al., 2007b; Fedorenko et al., 2013). We tested if the same set of foci in the visual cortex of blind participants respond to the four diverse task demands. To do this, we identified a set of voxel that showed the strongest response to a one specific task demand (e.g., tactile decision making) at hard > easy contrast at an uncorrected p value of 0.001 using unnormalized visual cortex mask in blind participants' native space. Subsequently, we measured the activation of these voxel across the three control demands (e.g. WM updating, time-duration judgment, motor-complexity). We applied this procedure iteratively for each blind participants. As shown in Figure 11, Bayesian repeated measures ANOVA with the four different fROIs and task difficulty as factor confirmed that each of the fROIs responded robustly to incresed difficulty in the other three tasks. BF_{10} for difficulty level of WM updating, tactile decision-making, time-duration judgement, and motor complexity tasks to the task demands combined across the three tasks were 33, 147, 11 and 28 respectively. Further, Bayesian t-sample test showed that each fROI in visual cortex responds robustly to the remaining three control demands individually as well (See Figure 12; Table 1).

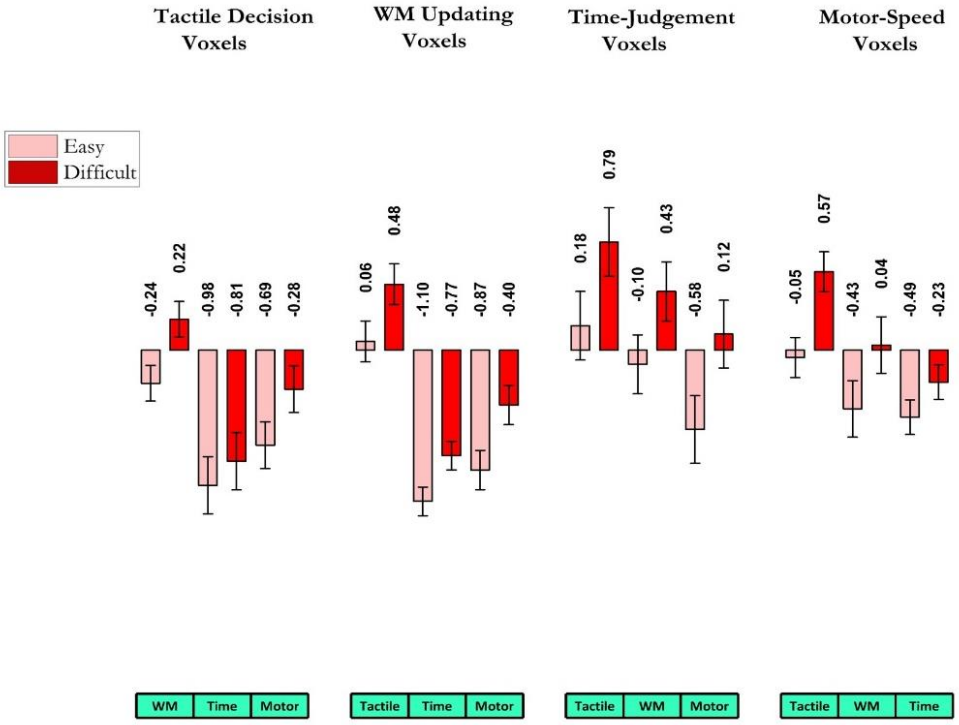

Figure 12. Response Patterns of Occipital fROIs Across Four Tasks: Specific Responses in Easy and Hard Conditions of Each Task . Detailed response patterns of four occipital fROIs, each defined by its peak response to the control demands of a specific task (tactile decision, WM updating, time-duration judgement and motor complexity,) across the easy and hard conditions of the remaining three tasks individually. The numbers above the bars indicate the mean. Error bars indicates 95% confidence intervals.

Table 1. Statistical analysis of the four task-based individual fROIs in the visual cortex of blind participants to the control demands of the remaining three tasks individually. BF_{10} represent the likelihood of activating these fROIs to the hard conditions more than the easy conditions of the tasks.

	Easy vs Hard	BF_{10}	t	df	p
Tactile Decision-Making Voxels	WM updating	7.151	2.7	21	0.01
	Time Duration Judgement	17.549	3.2	16	0.006
	Motor-Complexity	48.558	3.8	16	0.002
WM Updating Voxels	Tactile Decision-Making	433.111	4.7	21	<0.001
	WM updating	11.011	3	16	0.01
	Motor-Complexity	10.145	2.9	16	0.01
Time-Duration Judgement Voxels	WM updating	7.109	2.7	17	0.02
	Tactile Decision-Making	6.911	2.7	17	0.02
	Motor-Complexity	9.958	2.9	15	0.01
Motor-Complexity Voxels	WM updating	5.561	2.5	15	0.02
	Tactile Decision-Making	173.723	4.5	15	<0.001
	Time Duration Judgement	2.043	1.9	15	0.07

2.14. Comparison of the behavior of visual and auditory cortices to the control demands in the blind group

Under the conditions where tasks require more demanding processing within a particular modality, corresponding sensory regions can activate more compared to baseline conditions of the tasks. This increased activity of sensory regions to control demands in their own modalities is usually attributed to control-related top-down inputs coming from higher- order control regions in response to the increased attentional demands necessiated

by the tasks (Dehaene et al., 1998). For instance, higher somatosensory regions activated more to tactile demands in the tactile decision-making tasks in our study. It may be that increased activation to the increased task demands of the visual cortex in the blind group can be attributed to the fact that they become auditory regions or somasensory regions processing more demanding inputs in auditory or tactile modality. However, it is certanly not the case. We have shown that same set of voxels the visual cortex of the blind group respond to control demands across both auditory and tactile modality. Further, Bayesian analyses have shown that primary (Te11, Te12, Te13) and secondary auditory regions (Te3) do not respond to the three auditory control demands of WM-updating, time-duration judgment and motor complexity task whereas early (V1) and higher visual regions (ESV) have shown robust response (See Figure 14; Table 2).

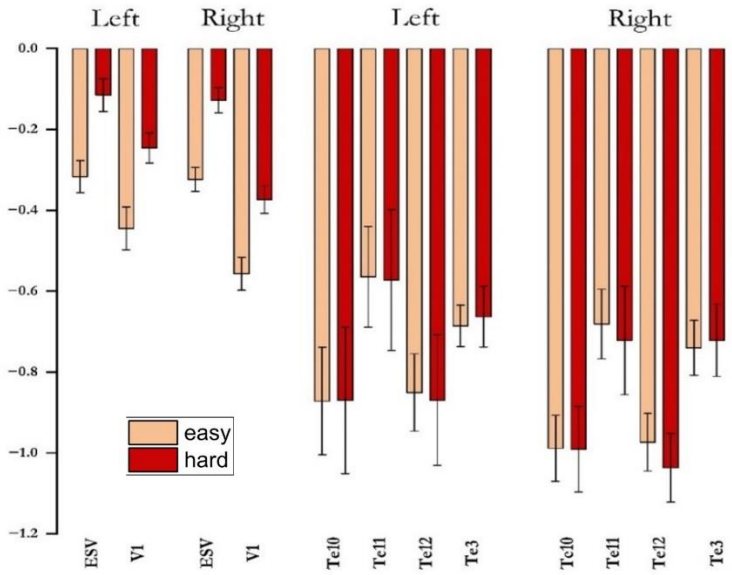

Figure 13. Averaged activity of visual and auditory regions of blind participant across the three tasks whose execution depended on audition (WM updating, time-duration judgement and motor complexity). While ESV and V1 bilaterally activated more to the hard conditions of the tasks, primary (Te10, Te11, T12) and secondary auditory regions (Te3) bilaterally remained unresponsive to the difficulty across the tasks. Error bars indicate 95% confidence intervals.

Table 2. Averaged activations of the visual (ESV and V1) and auditory (Te10, Te11, Te12, Te3) cortex of the blind participants across the control demands of the three auditory presented task. BF_{10} represents the likelyhood of these regions activating more to hard conditions rather than the easy conditions of the tasks. BF_{01} represents the vice versa.

Region	Laterality	Sub-region	BF10	BF01
Auditory Cortex	Left	TE_10	0.219	4.569
		TE_11	0.221	4.515
		TE_12	0.226	4.416
		TE_3	0.263	3.804
	Right	TE_10	0.219	4.568
		TE_11	0.317	3.159
		TE_12	0.332	3.011
		TE_3	0.241	4.146
Visual Cortex	Left	ESV	$1.253\times10^{+6}$	7.979×10^{-7}
		V1	400.343	0.002
	Right	ESV	45.554.544	2.195×10^{-5}
		V1	1.028.130	9.726×10^{-4}

CHAPTER 3

DISCUSSION

We have shown that the occipital cortex of blind participants exhibited a strong response to the four diverse control demands involving tactile and auditory modalities. Almost the entire visual cortex, except some parts of the occipital pole, was more active during the hard conditions of the four tasks in addition to the canonical MD regions. In contrast, some parts of the visual cortex in blindfolded sighted participants remained unresponsive and the remaining parts of it deactivated to the control demands. Canonical MD regions of sighted participants exhibited strong response to these control demands even at a higher rate than blind participants' MD regions. Stronger activity of MD regions of sighted participants more than blind participants' MD regions is perhaps due to blind participants' occipital cortex becoming a part of cognitive control network. Critically, the same voxels in the occipital cortex of the blind participants have shown robust response to four diverse demands, which is a key sign of MD regions. The same voxels in MD regions also show increased activation to a wide array of task demands (Fedorenko et al., 2013). Unlike the sensory regions that show activity to control demands only if the demands are within their respective modalitities (e.g. somatosensory regions showing increased activity only if the task involves difficuty related to haptic perception), occipital cortex of the blind participants showed increased activation not just for one kind of sensory demand, but across the four different task demands, irrespective of tasks' sensory modalities. All of these certainly show at least one part of visual cortex of the blind becomes MD regions.

A metamodal argument (Merabet et al., 2008b; Pascual-Leone & Hamilton, 2001) with regard to the interpretation of the present study's results may be that that these regions in the occipital cortex of the blind are already related to computations of abstract inputs and that insofar as the same voxel are engaged in the processing of the same abstract input, it should not matter whether the modality of the tasks involve different modalities. Yet, claming that tactile-decision making and motor complexity task, which are inherently different in their sensory and cognitive demands, are processed by the same abstract module in the deprived cortices of the blind seems far- fetched. We have noted that the the location of foci that are most active during the four tasks in the visual cortex of blind participants shows substantial variation from one subject to another. Such findings contradict the metamodal argument that spefic brain regions are dedicated to specific functions. For these reasons, a possible metamodal interpretation of our findings is not only difficult to sustain, but also almost seem impossible to reconcile with our observation that the same set of visual voxels in the blind activates to diverse control demands, and the most active cluster of these visual voxels to each four task demands also varies while they remain responsive to the other three tasks. Contrasting with the increasingly untenable metamodal perspective, the observation that deprived visual cortices work as multimodal-task positive regions coherently and parsimoniosly accounts for the extensive evidence of these regions activating to any-task relevant event regardless of the task's sensory modality rather than to pure sensory stimulation.

That these deprived cortices in the blind turns into another sensory region (e.g., auditory) is equally implausible. We have found that while the visual regions in the blind activates to the three diverse tasks whose medium was auditory, the auditory regions remain unresponsive,if not deactivated, to any event related sound stimuli in these three auditorily presented tasks.

The question remains as to whether cognitive control-related activation in visual cortex of the blind can be explained by top-down feedback from control related MD regions. In

fact, researches has raised this issue before (Burton et al., 2010, 2014; Park et al., 2011). There are two main reasons to why it is hard to explain it by top-down feedback control mechanism. First, if these visual regions of blind groups get inputs from control-related regions through execution of the auditorily presented tasks (WM updating , time-duration judgement and motor complexity tasks) these regions should have activated along with primary or secondary auditory cortices. However, it was not the case. There was a moderate evidence that Te10, Te11, Te12 in primary auditory cortex and Te3 in secondary auditory cortices remained unresponsive to control demands of the auditory presented tasks . In contrast, V1 and ESV bilaterally activated to the auditorily presented task demands (See, Figure 14; Table 2). Second, for the same voxels to be activated by feedback during tasks involving different modalities, there would have to be neurons related to these auditory and tactile modalities in those voxels. However, this is unlikely because neurons that are engaged in specific types of processing are usually cluster together in specific regions of the brain, that is, voxels containing neurons are unlikely to be related to different types of processing involving different modalities. Indeed, studies have shown that top-down feedbacks are related to specific processing in a dominant modality (Bassett & Bullmore, 2017; Latinus et al., 2010).

V1 of sighted participants activated across tactile decision-making and WM updating tasks, which are distinct in terms of the kinds of control demands they have (See, Figure 9). We observed that in some sighted participants tactile decision-makind and WM updating tasks led to robust activity in V1. While it may be true that execution of tactile decision-making task can be evoke visual imagery in sighted participants, it is difficult to explain V1 activity in WM updating task. This task required participants uphold information about the Turkish letters they heard from previous trials and matched with the current one. It is counterintutive to think that participants used imagery to execute this task. The common denominator in the two tasks is thay they both depended on working memory performance for succesful completion. It may be V1 in those sighted individuals also exhibits characteristics of MD regions like occipital regions of blind participants. Thus, one can further argue that default developmental trajectory of the visual cortex is to

become domain-general cognitive control regions and this path might be altered by visual experiences as one grows. However the visual cortex keeps to this developmental trajectory in some individuals.

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