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Research report

Working memory training in congenitally blind individuals results in an integration of occipital cortex in functional networks

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ABSTRACT

The functional relevance of crossmodal activation (e.g. auditory activation of occipital brain regions) in congenitally blind individuals is still not fully understood. The present study tested whether the occipital cortex of blind individuals is integrated into a challenged functional network. A working memory (WM) training over four sessions was implemented. Congenitally blind and matched sighted participants were adaptively trained with an *n*-back task employing either voices (*auditory training*) or tactile stimuli (*tactile training*). In addition, a minimally demanding *1*-back task served as an active control condition. Power and functional connectivity of EEG activity evolving during the maintenance period of an *auditory 2*-back task were analyzed, run prior to and after the WM training. Modality-specific (following *auditory* training) and modality-independent WM training effects (following both *auditory* and *tactile* training) were assessed. Improvements in auditory WM were observed in all groups, and blind and sighted individuals did not differ in training gains. Auditory and tactile training of sighted participants led, relative to the active control group, to an increase in fronto-parietal theta-band power, suggesting a training-induced strengthening of the existing modality-independent WM network. No power effects were observed in the blind. Rather, after auditory training the blind showed a decrease in theta-band connectivity between central, parietal, and occipital electrodes compared to the blind tactile training and active control groups. Furthermore, in the blind auditory training increased beta-band connectivity between fronto-parietal, central and occipital electrodes. In the congenitally blind, these findings suggest a stronger integration of occipital areas into the auditory WM network.

1. Introduction

The brain is able to flexibly adapt to new requirements due to neuroplasticity, which enables both structural and functional changes [1–3]. In deaf or blind humans, a large number of neurophysiological and brain imaging studies have reported an activation of visual and auditory brain regions by non-visual and non-auditory stimuli, respectively. This phenomenon is referred to as crossmodal plasticity and has been observed during basic perceptual tasks as well as during higher cognitive tasks, such as language and memory processing, including working memory [4,5]. However, the functional relevance of such a crossmodal reorganization after sensory deprivation is still a matter of debate [5–7].

Recently, research in deaf cats has provided evidence for a functionally specific and task-relevant reorganization of the auditory cortex [8]. A deactivation of sub-regions of the auditory cortex in congenitally deaf cats resulted in a functionally selective performance decrement in visual tasks, in which these cats had outperformed control cats before deactivation. Recent results in blind humans have been interpreted as evidence for similar functionally specific reorganizations of the deprived occipital cortex. The dorsal occipital areas have been found to be more activated during auditory spatial [10–12] and motion tasks [13], while the ventral occipital areas seemed to be more activated during auditory object recognition [14], including voice identity processing [15]. Thus, it was postulated that the crossmodal reorganization of occipital areas in the blind brain follows the functional organization of occipital areas in the sighted brain [4,12,16–18]. Studies comparing the network structure of the brain revealed differences

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in connectivity patterns between blind and sighted participants, during both rest [19–21] and tasks [22,23], suggesting that crossmodal plasticity comprises an alteration of functional brain connectivity as well. Further experimental support for this assumption comes from a magnetoencephalographic (MEG) study by Schepers et al. [24]. In this study, a correlation between oscillatory activity in the gamma-frequency band arising from the auditory and visual cortex was observed in congenitally blind, but not in sighted individuals [24]. The authors speculated that these results might reflect an integration of the deprived occipital cortex into processing networks and that such an integration might constitute a mechanism of crossmodal plasticity. The present study explicitly tested this hypothesis. Importantly, extending the study by Schepers et al. [24], here we not merely measured differences in processing networks between blind and sighted individuals. Rather, we were interested in whether in the blind the occipital cortex can get integrated into existing networks when acquiring new skills. The advantage of this approach is that pre-existing differences between the congenitally blind and the sighted are controlled for. Furthermore, we addressed neuronal network plasticity more directly by measuring oscillatory phase coupling, instead of power correlations. We hypothesized that, in the congenitally blind, WM training would result in an integration of occipital areas in neural networks associated with WM, while in sighted controls strengthening of the WM network as previously observed in functional magnetic resonance imaging (fMRI) studies [25,26] would emerge. The WM is a capacity-limited system for maintaining and manipulating information [27–29]. WM is known to show a high susceptibility to practice [30–32]. A large body of neurophysiological studies has analyzed oscillatory activity during the maintenance phase of WM tasks, that is, during the delay period between stimulus presentation and a subject's response, representing the phase during which information has to be maintained in WM. This epoch is not confounded by stimulus encoding or response related processes. Typically, sustained power increases, mainly in the theta- and gamma-frequency bands, have been reported and were interpreted as indicating an active maintenance of sensory information in WM [for reviews see 33–35]. Brain imaging studies have identified a domain-general fronto-parietal network involved in WM [for reviews see 36,37]. This WM network has also been identified in source analyses of both electroencephalographic (EEG) and MEG recordings [for a review see e.g. 34]. Accordingly, fronto-parietal theta- and gamma-band power during the delay period have been repeatedly shown to positively correlate with WM performance [38–40].

Furthermore, WM maintenance has been linked to enhanced functional connectivity between frontal and parietal regions, in the theta-, gamma- and, particularly, beta-frequency band [41–44]. While oscillatory activity is thought to reflect local processing [45,46], functional connectivity, as for instance assessed via phase-coherence, is assumed to reflect the degree of the temporal alignment of brain activity in distributed networks [46,47]. Temporal coherence of neural oscillatory activity has been suggested to be associated with the communication between brain sites [48,49] and the integration of (distant) neural assemblies into processing networks [50,51].

In the present study, WM of congenitally blind and sighted adults was trained either with auditory or tactile stimuli or was not adaptively trained at all (active control group). Prior to and after training, participants were tested in an auditory WM task, while the EEG was recorded. With respect to the auditory WM task, changes following the auditory training indicate modality-specific effects, while changes following both the auditory and tactile training indicate modality-independent effects. Pre-post training changes in WM performance, oscillatory power and connectivity (imaginary coherency) were compared between groups and between blind and sighted participants. We predicted a training-induced coupling of the occipital cortex activity with activity in the auditory WM network in the congenitally blind, but not in sighted controls.

We analyzed theta-, beta- and gamma-band oscillatory activity since these frequency bands have been associated with WM. Although alpha-band activity has previously been related to WM as well [e.g. 34,52], the alpha band was not analyzed since this activity is well known to be largely reduced in congenitally blind humans [53–56].

2. Material and methods

2.1. Participants

Twenty-seven congenitally blind adults were recruited from all over Germany to participate in the study. Additionally, 27 sighted participants were locally recruited e.g. through newsletters or advertisement at adult education institutions. The sighted were matched to the blind with respect to gender and age. Data of two sighted participants were discarded from the analyses, due to a decrease in post-training performance relative to their pre-training performance (deviating by more than −2 SD from the mean pre-post difference for the sighted). We considered the training loss as a lack of motivation or failure to follow task instructions. To maintain matching between the blind and the sighted, the two corresponding blind participants were excluded from all analyses as well. Thus, the data reported here are based on the remaining 25 blind participants (12 females; mean age: 37 years; SD: 11 years; age range, 21–55 years; education, 21 participants with > 10 years of schooling) and the 25 sighted (12 females; mean age: 38 years; SD: 10 years; age range, 22–55 years; education, 18 participants with > 10 years of schooling; Table 1).

All sighted participants had normal or corrected-to-normal vision. In the blind, the loss of vision resulted from pre- or perinatal anomalies in peripheral eye structures resulting in a total congenital blindness ($n = 8$) or no more than residual light perception ($n = 17$; causes of blindness are summarized in Table 2). One blind participant was left-handed; all other participants were right-handed. All participants had normal hearing according to self-report. None of the participants had a history of neurological or psychiatric disorders (self-report). Participants gave written informed consent prior to the experiments. They received monetary compensation for participation. The study was approved by the German Psychological Association.

Variables such as the perceived current stress level [57], wellbeing [58], and intelligence have been shown to affect WM capacity [59]. Therefore, we assessed all participants with the German version of the PSQ-20 [Perceived Stress Questionnaire: 60, German modified version: 61], and the HSWBS [German Habituelle Subjektive WohlBefindens Skala: 62], a scale for wellbeing. An estimate of the verbal intelligence score was obtained with the MWT-B [German Mehrfachwahl-Wortschatz-Test: 63]. To keep the assessment situation identical for blind and sighted participants, all questionnaires were orally administered, including the MWT-B. The blind and sighted groups did not differ in any of these tests (PSQ-R20: mean(congenitally blind) = 1.38 (SD = 0.40); mean(sighted) = 1.33, (SD = 0.53); $t(48) = 0.40$, $p = .694$; HSWBS: mean(congenitally blind) = 4.69 (SD = 0.59); mean

Table 1
Description of participants.

	N		Gender (females)		Mean age in years (range)		Education (> 10 years schooling)	
	SC	CB	SC	CB	SC	CB	SC	CB
AG	9	9	4	4	39 (27–55)	41 (26–53)	7	6
TG	8	8	4	4	32 (21–48)	33 (25–50)	6	6
CG	8	8	4	4	39 (24–55)	40 (22–55)	8	6

SC, sighted controls; CB, congenitally blind; AG, auditory training group; TG, tactile training group; CG, active control group.