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Memory-guided drawing training increases Granger causal influences from the perirhinal cortex to V1 in the blind

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Highlights

- The proposal that the perirhinal cortex (PRC) modulates V1 in the blind was tested.
- FMRI scans were conducted before and after Cognitive-Kinesthetic drawing training.
- The training led to enhanced top-down Granger causal influences from the PRC to V1.
- Results suggest that the PRC is a potential source of V1 reorganization in the blind.

Abstract

The perirhinal cortex (PRC) is a medial temporal lobe structure that has been implicated in not only visual memory in the sighted, but also tactile memory in the blind (Cacciamani & Likova, 2016). It has been proposed that, in the blind, the PRC may contribute to modulation of tactile memory responses that emerge in low-level "visual" area V1 as a result of training-induced cortical reorganization (Likova, 2012, 2015). While some studies in the sighted have indicated that the PRC is indeed structurally and functionally connected to the visual cortex (Clavagnier, Falchier, & Kennedy, 2004; Peterson, Cacciamani, Barense, & Scalf, 2012), the PRC's direct modulation of V1 is unknown—

particularly in those who lack the visual input that typically stimulates this region. In the present study, we tested Likova's PRC modulation hypothesis; specifically, we used fMRI to assess the PRC's Granger causal influence on V1 activation in the blind during a tactile memory task. To do so, we trained congenital and acquired blind participants on a unique memory-guided drawing technique previously shown to result in V1 reorganization towards tactile memory representations (Likova, 2012). The tasks (20 s each) included: tactile exploration of raised line drawings of faces and objects, tactile memory retrieval via drawing, and a scribble motor/memory control. FMRI before and after a week of the Cognitive-Kinesthetic training on these tasks revealed a significant increase in PRC-to-V1 Granger causality from pre- to post-training during the memory drawing task, but not during the motor/memory control. This increase in causal connectivity indicates that the training strengthened the top-down modulation of visual cortex from the PRC. This is the first study to demonstrate enhanced directed functional connectivity from the PRC to the visual cortex in the blind, implicating the PRC as a potential source of the reorganization towards tactile representations that occurs in V1 in the blind brain (Likova, 2012).

Introduction

Acquiring and accessing previously formed memories of objects that we encounter is crucial to interacting with our surroundings. In sighted adults, this process of memory encoding and retrieval is seamless and automatic; we can quickly visually assess all aspects of an object in parallel. In those who are blind, however, forming and accessing memory representations must be accomplished through other sensory modalities, such as the tactile modality, which makes this seemingly simple act much more difficult. A key structure that has been shown to be involved in object memory is the perirhinal cortex (PRC) of the medial temporal lobe (MTL). The majority of research on the PRC has demonstrated its role in visual object recognition (Brown and Aggleton, 2001, Suzuki et al., 1993, Mumby and Pinel, 1994), although it has also been implicated in perceptual processes (Baxter, 2009, Bussey et al., 2002, Murray and Bussey, 1999, Murray et al., 2007, Peterson et al., 2012).

Importantly, recent research has shown that the PRC is also involved in tactile object memory in those who are blind (Cacciamani & Likova, 2016). In this previous study, as well as in the current study, the experimental paradigm was a replication of that in Likova (2012). Blind participants underwent a unique tactile memory training, known as Likova's Cognitive-Kinesthetic method (Likova, 2010, Likova, 2012, Likova, 2013), wherein over the course of 5 days, they learned how to draw guided solely by memory. The experiment consisted of 3 tasks (see Fig. 1a). Participants first perceptually explored and memorized raised line drawing stimuli with their left hand (Perceptual Exploration, or PE, condition). They then were taught how to use that memory representation to draw the stimulus from memory with their right hand (Memory Drawing, or MD, condition). The last task was a motor and memory control task, where participants drew random scribbles with their right hand (Scribble, or S, condition). Importantly, using different hands for exploring and drawing required participants to rely on their memory representation rather than motor movements. Over 5 days, participants were trained on these tasks, such that by the end of training, they were successfully able to draw each stimulus. Before and after training, functional magnetic resonance imaging (fMRI) scans were conducted in order to assess the effect of training on representations in the PRC. Cacciamani and Likova's (2016) results showed that the PRC signaled the object memories of each stimulus created during the training, thereby indicating that the PRC represents tactile memory in the blind as it does visual memory in the sighted.

In addition to the PRC, dramatic neural changes have also been observed in primary visual area V1 as a result of the Cognitive-Kinesthetic training. Specifically, Likova, 2012, Likova, 2013, Likova, 2014 found that blood oxygen level dependent (BOLD) waveforms in V1 went from being erratic, immature, and weak before training to well fit to the BOLD predictor for the MD task after training. This prominent shift indicates that, after only 5 days of this well-targeted training, "visual" areas of the brain as low as V1 can reorganize to represent tactile memory information in those who are blind. Based on these important findings, Likova, 2012, Likova, 2013 implicated V1 as a site suitable for the neural implementation of the theoretical working memory “visuo-spatial sketchpad” and allowed for its re-conceptualization into a “supramodal spatial sketchpad”.

The training-induced cortical reorganization observed in both the PRC and V1 separately is suggestive of a possible interaction between these two seemingly disparate brain areas. Indeed, Likova, 2012, Likova, 2015 proposed that the PRC may be a source of the reorganization that has been observed in visual area V1 during a memory task. The present experiment tests Likova’s proposal.

This PRC-to-V1 feedback hypothesis is also consistent with previous research in the sighted that has shown that the PRC is both structurally and functionally connected to the visual cortex. In rats, visual area 17—the equivalent to human V1—has been shown to receive direct structural projections from the PRC (Miller & Vogt, 1984). Clavagnier, Falchier, and Kennedy (2004) also found direct connections from the PRC to V1 using a retrograde tracer injection technique in sighted monkeys. Uncovering the existence of these structural connections laid the foundation for further research on the functional influences that the PRC can exert on the visual cortex. Given the PRC’s well-known role in primarily declarative memory processes, its ability to modulate activation at low-level “visual” areas is a new concept that has recently challenged the traditional “memory-only” view. The first evidence of the PRC’s ability to modulate visual cortex activation was observed by Peterson et al. (2012; based on proposal by Barense, Ngo, Hung, and Peterson (2012)). In Peterson et al.’s study, sighted participants made familiar/novel judgments to silhouettes presented in the periphery while activation in both the PRC and the visual cortex was assessed via fMRI. Their results demonstrated that the PRC signaled the familiarity of both the whole object depicted by the silhouette and the familiarity of the object’s individual parts—a finding that extended previous work showing that the PRC only responds to whole object familiarity (e.g., Barense, Henson, & Graham, 2011). Of even greater interest to the present study, Peterson et al. also found that the visual cortex mimicked the PRC’s pattern of activation and signaled the familiarity of not only the parts, but also the whole object. Given that receptive field sizes of V1–V2 neurons (1–2° of visual angle) are not large enough to encompass the whole silhouetted object (4°), this object-level response in low-level visual cortex must have originated from a higher level such as the PRC (Peterson et al., 2012). This prior study therefore suggested that the PRC modulates functional responses at low-level visual regions (Barense et al., 2012, Peterson and Cacciamani, 2013)—a finding consistent with a feedforward-feedback view of PRC-to-V1 connectivity. These studies, however, did not examine any causal influences and were restricted to the sighted population.

In the present study, we searched for direct evidence of modulation of area V1 specifically by the PRC during a tactile memory task in the blind. To do so, we used Likova’s Cognitive-Kinesthetic Drawing Training method in order to generate training-induced changes in PRC-to-V1 causal connectivity during memory-guided drawing. As in previous studies using Likova’s experimental paradigm (e.g., Likova, 2012, Likova, 2012, Likova, 2013, Cacciamani and Likova, 2016), fMRI was conducted before and after 5 days of training. To interrogate causal relationships between the PRC and V1, a Granger causality analysis was employed on the pre- and post-training BOLD data and compared between them. Granger causality (Granger, 1969) is a method of assessing directed functional connectivity based on the principle of temporal precedence and predictability. Specifically, it can be conceptualized as follows: activity in brain area X (the “seed” region) is said to “Granger cause” (or G-cause) activity in brain area Y if the past activation in X is a better predictor of future activation in Y than the past Y activation alone. This analysis technique has been applied to both bivariate and multivariate BOLD data (Deshpande et al., 2008, Roebroeck et al., 2005, Seth, 2010) and has been shown to be robust to changes in hemodynamic properties (Seth, Chorley, & Barnett, 2013). We employed this analysis in order to go above and beyond any implied or correlative interactions between the PRC and the visual cortex that have been previously found in the sighted (Peterson et al., 2012) or suggested in the blind (Likova, 2012) and search for a more direct top-down relationship—specifically in a blind population where connections between and reorganization of these “visual” areas is pertinent. Doing so can provide insight into the mechanisms of cortical plasticity and top-down interactions in the blind brain, thereby answering previously posed questions as to the origin of V1 reorganization (Likova, 2012, Likova, 2015) and laying the foundation necessary for future rehabilitative initiatives.

If the PRC indeed modulates tactile memory-related activation in V1 in the blind, then we expected to observe a significant increase in the top-down PRC-to-V1 Granger causal influence from before to after training. We specifically expected to see this effect during memory-guided drawing (the MD task) when cortical reorganization in both the PRC and V1 has been observed previously (Likova, 2012, Likova, 2013, Likova, 2014, Likova, 2015, Cacciamani and Likova, 2016). We also investigated the bottom-up Granger causality from V1 to PRC, although our previous findings did not lead us to expect any training effects in this direction.

Section snippets

Participants

The participants were 8 congenital and acquired blind volunteers (4 females, 4 males; ages 31–76) whose demographics are summarized in Table 1. The experimental protocol was approved by the Smith-Kettlewell Institutional Review Board; prior to participating, all volunteers provided their informed consent. Participants were compensated for their time and were right-handed.

Our participants did vary somewhat with respect to their age of blindness onset and their degree of remaining vision. The…

Results

The results of the PRC-to-V1 (and vice versa) Granger causality analysis are depicted in Fig. 2. In short, we did observe strong training-induced increases in top-down Granger causality across all 8 blind participants. Specifically, our averaged data show that with the left PRC as the seed ROI, a significant pre- to post-training increase in Granger causal influence from the PRC was evident in the left V1 during the memory-guided drawing task [$t(7)=2.24$, $p=0.038$; see Fig.2a]. Likewise, with…

Discussion

This study is the first to provide evidence that within only 5 days, directed top-down functional connectivity from the PRC (a “memory” area) to the visual cortex (a “visual” area) in those who are blind can be enhanced. Specifically, an increase in PRC-to-V1 Granger causality after the Cognitive-Kinesthetic training was observed during a tactile memory task that involved retrieving stored object representations and drawing them from memory. Previous research has found that V1 and the PRC…

Authors contributions

LC and LTL both contributed to the idea, subject recruitment, data analysis, and writing of the manuscript. LTL had developed the experimental design and the Cognitive-Kinesthetic Drawing Training and conducted the drawing training of each blind participant.…

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