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Trained to silence: Progressive signal inhibition during short visuo-motor training

Meir Meshulam, Rafael Malach *

Department of Neurobiology, Weizmann Institute of Science, Rehovot 76100, Israel

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ABSTRACT

Short training is often sufficient for human individuals to become adept at performing a complex new task. However, the precise nature of the changes in cortical activity during short-term training of under an hour is still not fully understood. In this study, we have examined the effects of such short training in a visual recognition task on cortical activity using functional imaging (BOLD fMRI). Participants performed a gender/age discrimination task on face images for 28 min, preceded and followed by resting state scans. Our results reveal a consistent and progressive signal reduction during stimuli presentation compared to a fixation baseline, which was reflected in participant's subjective experience as evaluated by post-scan questionnaires. The BOLD reduction surprisingly included both task-positive and task-negative regions. While higher order face-selective regions showed a reduced positive peak response, negatively-responding areas – including the peripheral visual representations as well as the Default Mode Network – showed deeper negative BOLD responses during the visual stimulation periods. Interestingly, these training effects have left significant traces in the spontaneous resting-state fluctuations following the training period in areas that partially correspond to those that showed response changes during task performance. The results reveal the widespread cortical changes underlying short-term training.

1. Introduction

Humans possess a remarkable ability to rapidly improve in performing complex tasks. This ability is mediated by changes in cortical networks, which are modified by training. Training-induced changes in cortical activity, presumed to underlie skill and learning effects, have been studied extensively using functional brain imaging. The specific set of regions that increase their activity following training is task-dependent; and activations that diminish with training have been suggested to reflect "scaffolding" built to cope with demands posed by the new task (Petersen et al., 1998). In tasks requiring externally-focused attention, training has been shown to *reduce* positive activation in executive and attention networks. These reductions are believed to reflect increased automaticity and reduced attention (Floyer-Lea and Matthews, 2004; Jansma et al., 2001; Kelly and Garavan, 2005; Patel et al., 2013). In contrast, long term training produced *increases* in brain activity in task-negative brain regions defined by the decrease in their activity during task performance (Patel et al., 2013). Since signal inhibition during externally oriented tasks is a hallmark of the "Default Mode Network" (DMN), which has been linked to self-related thoughts and processes (Buckner et al., 2008; Golland et al., 2007; Preminger et al., 2011; Raichle, 2015; Raichle and Snyder, 2007), activity increases in these areas have been interpreted as a marker that task-irrelevant activity is less suppressed with training (Kelly and Garavan, 2005; Patel et al., 2013).

However, changes that take place over extended periods of days and weeks have, to date, received the most attention in the literature (Buschkuehl et al., 2012; Kelly and Garavan, 2005). Therefore, it is unclear whether shorter training has similar effects on task-related activity. Notably, rapid and prolonged training may have markedly different effects on cortical activity. For example, Karni et al. (1995), (1998) reported decreased fMRI BOLD response in motor cortex during the performance of a new motor sequence but enhanced response later in training. In the case of task-negative areas, it is unknown how such effects develop in time, though higher activations have been linked with increased mind-wandering on a per-trial basis (Christoff et al., 2009; Mittner et al., 2014). We set out to study this question directly by using fMRI to scan participants while they performed a short (~30 min), complex yet relatively easy face categorization task in which performance rapidly reached ceiling and reported automaticity was high. Our hypothesis was that short training would elicit rapid behavioral and cortical effects that are qualitatively different from those previously reported for long-term training.

* Corresponding author.
E-mail address: rafi.malach@gmail.com (R. Malach).

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2. Materials and methods

2.1. Participants

Twenty right handed participants took part in the study. The data from two participants were omitted due to excess movement during task scans, with the final sample consisting of 18 participants (9 female, mean age ± SD, 26.95 ± 2.46, range 22–31). All participants had normal or corrected-to-normal vision. Participants gave written informed consent for their participation. All procedures were approved by the local ethics committee.

2.2. Tasks and stimuli

Stimuli were 1008 color images of faces, with an equal number of male, female and children faces (250 × 250 pixels, 4° × 4° visual angle). For each participant, images from each category were randomly assigned to each task run (189 in each, no repetitions) and the rest used in a subsequent memory test. Images were taken from the LFW database (Huang et al., 2007) and supplemented by images from various internet sites using a Google search. Images of persons highly familiar to the participant population (local celebrities and persons with over a million Google search results) were not included in the study. Stimuli were delivered using Presentation (Neuro Behavioral Systems, CA).

Participants performed an age/gender categorization task during four consecutive 7-min runs inside the MRI scanner. Task runs were comprised of 21 blocks; each block consisted of a 6 s "fixation" period followed by a 12 s "faces" period, consisting of nine face stimuli presented for 300 ms each and followed by a fixation point presented for 1300 ms (Fig. 1). Participants were asked to respond via right hand button press as quickly as possible and categorize each face as that of an adult male, an adult female or a child. Button order (fingers 2–4) was counterbalanced across participants. Resting-state scans were performed before and after task runs. In these scans, participants were asked to lie down in the scanner with their eyes closed for 8 min and refrain from sleeping.

Following their exit from the scanner, participants were administered a memory test and completed a questionnaire about their behavior and thoughts during task and rest times using a 7-point Likert scale in an adjacent testing room. The memory test consisted of 504 images in total: one half new to the participant (see above), and the other half shown during the task (a random sample of 1/3 of the images shown in each run, by category). Images were shown for 300 ms with a 1000 ms fixation point interval between them. Participants were instructed to press one keyboard button for seen images and another for unseen images, as quickly as possible.

2.3. MRI acquisition

Imaging data were acquired on a 3T Siemens Trio MRI scanner with a 12-channel head coil at the Weizmann Institute of Science, Rehovot, Israel. Three-dimensional T1-weighted anatomical images were acquired in high-resolution (3D MP-RAGE sequence; TR, 2300 ms; TE, 2.98 ms; 1 × 1 × 1 mm voxels). Functional data were acquired using a T2*-weighted echo planar imaging sequence. For task scans: TR, 3000 ms; TE, 30 ms; flip angle, 90°; FOV, 240 mm; matrix size, 80 × 80; scanned volume, 46 axial slices of 3 mm thickness, 3 × 3 × 3 mm voxels. For resting state scans: TR, 2000 ms; TE, 30 ms; flip angle, 75°; FOV, 240 mm; matrix size, 80 × 80; scanned volume, 31 axial slices of 4 mm thickness, 3 × 3 × 4 mm voxels.

2.4. fMRI data analysis

MRI data were processed using FSL 5.0.2.1 (http://www.fmrib.ox.ac.uk/fsl/) and in-house Matlab code (MathWorks, Natick, MA, USA). Cortical surface maps were constructed using Caret v5.65 (http://brainvis.wustl.edu/wiki/index.php/Caret:About). Functional data were analyzed using FMRIB's expert analysis tool (FEAT, version 6). The following preprocessing was applied to the data of each individual participant: motion correction using MCFLIRT (Jenkinson et al., 2002), slice timing correction, brain extraction using BET (Smith, 2002) and high-pass temporal filtering with a cut-off period of 60 s. Participants whose head motion exceeded 1.5 mm were omitted from the study. Functional images were aligned with high-resolution anatomical volumes initially using linear registration (FLIRT), then optimized using boundary-based registration (Greve and Fischl, 2009). Structural images were transformed to standard MNI space using a nonlinear registration tool (FNIRT), and the resulting warp fields were applied to the functional images for across-subjects analyses. Normalized files were manually inspected to verify that the transformation was successful.

2.5. GLM analysis

For task runs, we used a general linear model (GLM) that included regressors for task blocks ("Faces") and fixation periods ("Fixation"), as well as the six MCFLIRT motion regressors. At the first level of analysis, head movements that might affect the BOLD signal were identified via the calculation of RMS intensity difference from one volume to the next (DVARS) (Power et al., 2012) and were modeled out by adding a single time point regressor for each 'to be scrubbed' volume (Siegel et al., 2014). Faces and Fixation regressors were convolved with a canonical double-gamma

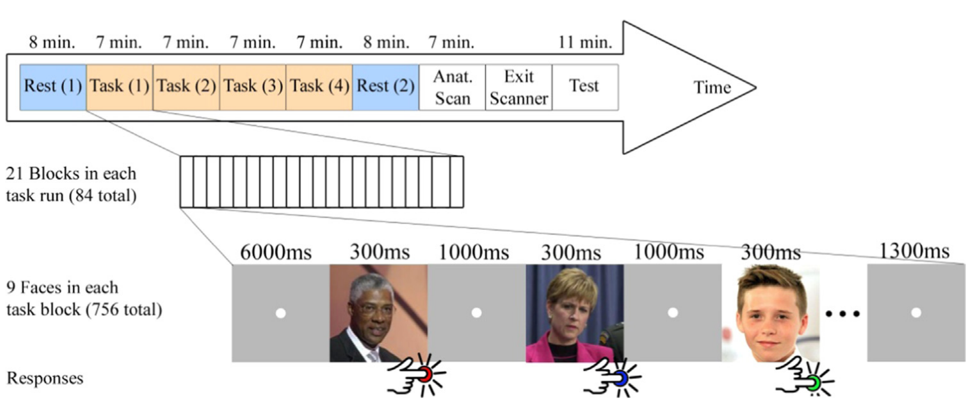

Fig. 1. Experimental paradigm. Top, participants performed four training task runs (orange), preceded and followed by resting-state scans (blue). Participants were asked to categorize each image as depicting an adult male, adult female or a child by pressing different buttons (bottom). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)