

COGNITIVE NEUROSCIENCE

Learning to filter out visual distractors

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Abstract

When learning to master a visual task in a cluttered natural environment, it is important to optimize the processing of task-relevant information and to efficiently filter out distractors. However, the mechanisms that suppress task-irrelevant information are not well understood. Here we show that training leads to a selective increase in motion coherence detection thresholds for task-irrelevant motion directions that interfered with the processing of task-relevant directions during training. Furthermore, using functional magnetic resonance imaging we found that training attenuated neural responses associated with the task-irrelevant direction compared with the task-relevant direction in the visual cortical areas involved in processing of visual motion. The strongest suppression of functional magnetic resonance imaging responses to task-irrelevant motion information was observed in human area MT+. These findings reveal that perceptual learning leads to the suppression and efficient filtering of task-irrelevant visual information.

Introduction

Developing perceptual expertise is essential in many situations, from an air traffic controller monitoring complex video displays to a radiologist searching for a tumor on an X-ray. With practice, these complex tasks become much easier, a phenomenon referred to as perceptual learning. Previous functional neuroimaging research in humans has focused on the role of training in increasing neural sensitivity for task-relevant visual information; such plasticity in early sensory cortices is thought to support improved perceptual abilities (Dolan *et al.*, 1997; Vaina *et al.*, 1998; Gauthier *et al.*, 1999; Schiltz *et al.*, 1999; Schwartz *et al.*, 2002; Furmanski *et al.*, 2004; Kourtzi *et al.*, 2005; Sigman *et al.*, 2005; Op de Beeck *et al.*, 2006; Mukai *et al.*, 2007). However, in most complex natural scenes, an ideal observer should also attenuate task-irrelevant sensory information that interferes with the processing of task-relevant information (Ghose, 2004; Vidnyánszky & Sohn, 2005). The implementation of this optimal strategy is supported by the observation that training leads to much stronger learning effects when the task-relevant information is displayed in a noisy, distractor-rich environment compared with when no distractors are present (Doshier & Lu, 1998, 1999; Gold *et al.*, 1999; Li *et al.*, 2004; Lu & Doshier, 2004; for a review see Fine & Jacobs, 2002). However, previous studies have not examined how training influences the neural representation of task-irrelevant information to facilitate learning.

Previous behavioral research addressing the effect of perceptual learning on the processing of task-irrelevant information showed that pairing a very weak task-irrelevant motion stimulus with a task-relevant stimulus during training actually increased perceptual sensitivity for the task-irrelevant stimulus (Watanabe *et al.*, 2001, 2002; Seitz & Watanabe, 2003). Based on this result, the authors proposed that perceptual learning involves a diffuse reinforcement signal that improves information processing for all stimuli presented concurrently with the task-relevant information during training, even if the stimulus is a task-irrelevant distractor (Seitz & Watanabe, 2003, 2005). However, in contrast to the weak task-irrelevant stimuli used by Watanabe and co-workers, real world perception more often involves suppressing highly salient and spatially intermingled distractors. Accordingly, recent psychophysical studies suggest that salient stimulus features are suppressed when they are present as task-irrelevant distractors during the training phase of a perceptual learning task (Vidnyánszky & Sohn, 2005; Paffen *et al.*, 2008). These findings are also in line with the results of a previous neurophysiological study showing that neural responses to irrelevant masking patterns are suppressed in the monkey inferior temporal cortex as a result of training to recognize backward-masked objects (Op de Beeck *et al.*, 2007).

In the present study we use psychophysics and functional magnetic resonance imaging (fMRI) to directly test the hypothesis that perceptual learning involves learning to suppress distracting task-irrelevant stimuli. We find that learning decreases perceptual sensitivity for the specific motion direction that was continuously present as a task-irrelevant distractor during training. Furthermore, we also show

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that, after training, distractor stimuli evoke weaker fMRI responses in the early visual cortical areas compared with target stimuli.

Materials and methods

Subjects

Fourteen subjects (six females; age range 22–25 years) participated in the main experiment and four additional subjects (one female, age range 23–27 years) participated in the control experiment. All had normal or corrected-to-normal visual acuity and reported no history of neurological problems. Informed consent was obtained from all subjects according to the Declaration of Helsinki and the study was approved by the local ethics committee of Semmelweis University. fMRI data of four observers were excluded due to excessive head movement in the scanner.

Stimuli and apparatus

Stimuli were programmed in MATLAB 7.1 (The MathWorks, Inc., Natick, MA, USA) using the Cogent 2000 Software Toolbox (Cogent, <http://www.vislab.ucl.ac.uk/Cogent.php>) and were presented on generic PCs. All visual stimuli were rendered in white on a black background. The luminance of the background and moving dots was < 2 and 32.2 cd/m^2 , respectively. In all experiments subjects were instructed to maintain gaze on a central fixation square subtending a 0.25° visual angle present for the entire duration of each experiment. In all experiments, moving dots ($N = 200$) were presented within a 20° (diameter) circular field centered on the fixation square, with a 1.6° (diameter) circular blank region around the fixation point. Dots subtended 0.15° in diameter and had a limited lifetime of seven frames. Behavioral responses were collected by means of mouse button presses.

During the psychophysical experiments visual stimuli were presented at 75 Hz on a 21" Syncmaster 1100 mb CRT monitor (Samsung Electronics, Seoul, Korea); the monitor was the only light source in the room. Eye movements were recorded in these sessions using an iView X™ HI-Speed eye tracker (Sensomotoric Instruments, Berlin, Germany) at a sampling rate of 240 Hz. The eye tracker also served as a head rest that fixed the viewing distance at 50 cm.

During the fMRI experiment visual stimuli were projected onto a translucent screen located at the back of the scanner bore using a Panasonic PT-D3500E DLP projector (Matsushita Electric Industrial Co., Osaka, Japan) at a refresh rate of 75 Hz. Stimuli were viewed from inside the magnet through a mirror attached to the head coil with a viewing distance of 58 cm. Head motion was minimized using foam padding.

General procedure

The experimental protocol consisted of a training phase and two testing phases, one before and another after training (see Fig. 1). Training comprised six 1:00 h sessions of psychophysical testing during which subjects performed the speed discrimination task. Each observer underwent four different testing steps before training: a retinotopic mapping scanning session to identify the boundaries of retinotopically organized regions of visual cortex, a psychophysical testing session to estimate motion coherence detection thresholds, an electroencephalography session, and an fMRI scanning session. Electroencephalography data are not presented in the present work. The same set of experiments (with the exception of retinotopic mapping) was repeated after training to evaluate training-induced changes in performance and brain activity. The post-training sessions

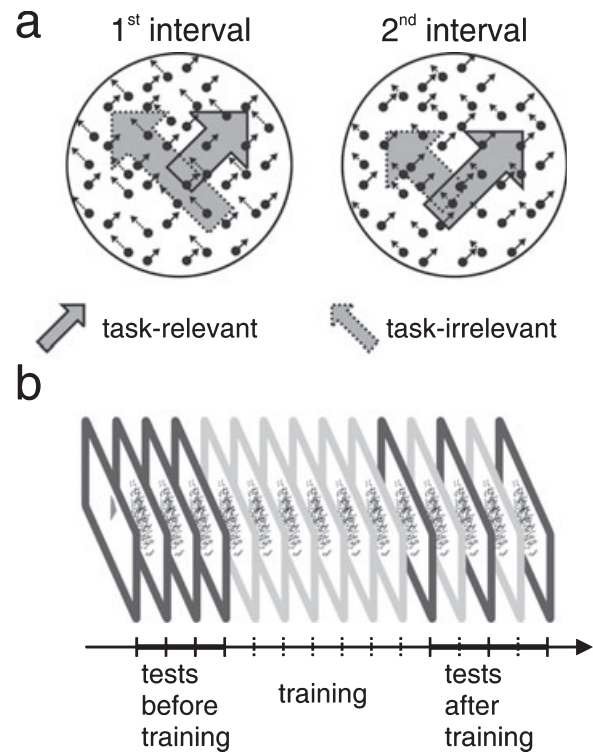


FIG. 1. Schematic representation of the stimuli during training and the experimental procedure. (a) Transparent random dot motion display used for training on the speed discrimination task. One of the motion directions was task-relevant and the other direction was task-irrelevant throughout training. The different lengths of the arrows indicate that dot speed was different in the two intervals in the case of both task-relevant and task-irrelevant directions. (b) The experimental protocol consisted of a training phase and two testing phases, one before and another after training. Training comprised six 1:00 h sessions of psychophysics during which subjects performed a speed discrimination task. Before training, the test phase included: (i) an fMRI retinotopic mapping session to localize the retinotopic visual cortical areas; (ii) psychophysical measurement of motion coherence detection thresholds; (iii) an event-related potential recording session and (iv) an fMRI scanning session. In the test phase after training there was no retinotopic mapping and the psychophysical, fMRI and electroencephalography measurements were separated by a top-up training session.

were separated by two additional 'top-up' learning sessions to ensure that learning was maintained. Each test session was performed on a different day and their order was randomized across subjects. Each psychophysical testing session and training session lasted for 1:00 h, whereas fMRI experiments lasted for 1.5:00 h.

Training

On each training day, subjects performed a series of two-interval forced choice speed discrimination tasks. In each trial the two 500 ms stimulus presentation intervals were separated by a 200 ms inter-stimulus interval. The next trial was initiated by the subject's response button press with an inter-trial interval jittered between 300 and 500 ms. Each interval contained two populations of spatially superimposed dots moving in a direction either $+45^\circ$ or -45° tilted from the upward direction (Fig. 1). Subjects were instructed to attend to dots moving in one of the directions (task-relevant direction) while simultaneously ignoring dots that moved in the orthogonal direction (task-irrelevant direction). They were asked to indicate which of the two intervals contained faster motion in the task-relevant direction. The speed of the task-relevant direction was fixed for one of the two

intervals (at $6^\circ/\text{s}$), whereas that of the other interval was varied using a QUEST adaptive staircase procedure (Watson & Pelli, 1983) arriving at a value providing 75% correct performance. The speed of the task-irrelevant motion also differed between the first and second trials (a random speed jitter between 6 and $7^\circ/\text{s}$). Every training session consisted of eight experimental blocks of 80 trials each. Task-relevant and task-irrelevant directions were randomized across subjects but kept constant across training sessions.

Testing motion coherence detection threshold

Motion coherence thresholds were acquired for three motion directions within the same block, two directions similar to those of the training ($\pm 45^\circ$ from the upward direction) and a third, downward (180°) control direction. A single trial consisted of two 250 ms stimulus presentation intervals, separated by a 250 ms interstimulus interval. The next trial was initiated by the subject's response button press with an inter-trial interval jittered between 200 and 300 ms. The order of the intervals was randomized across trials and motion coherence for each direction was varied independently by using the QUEST adaptive staircase procedures to converge at 75% correct performance in 60 steps. Two staircases (one starting at 0% and the other starting at 100% coherence) were randomly interleaved within an experimental block for each motion direction. Data were analysed with repeated-measures ANOVA with factors of test session (before training and after training) and task relevance (task-relevant and task-irrelevant) for each experiment.

Functional magnetic resonance imaging experiments

Subjects performed a two-interval forced choice speed discrimination task during scanning. A single trial lasted 1875 ms and consisted of two 300 ms intervals of moving dots (separated by 300 ms interstimulus interval) followed by a 950 ms period for response. Subjects were instructed to indicate which of the two intervals contained faster motion. The speed was fixed for one of the intervals at $6^\circ/\text{s}$, whereas for the other it was adjusted (based on pilot testing) so that the subject's performance was around 75% correct during scanning. Trials were organized into blocks. During a single block of eight trials the direction of motion of the dots was kept constant at either $+45^\circ$ or -45° . One run comprised a pseudo-randomized and balanced presentation of four 15 s blocks of each motion direction, interleaved with 13 15 s blocks of static dot display as rest periods. Six runs were performed in an experimental session.

Functional magnetic resonance imaging data acquisition and analysis

The magnetic resonance imaging scanning was performed at the MR Research Center (Szentágotthai J. Knowledge Center, Semmelweis University, Budapest, Hungary) on a 3 Tesla Achieva scanner (Philips, Best, The Netherlands) equipped with an eight-channel SENSE head coil (Philips, Best, The Netherlands). High-resolution anatomical images were acquired in all of the imaging sessions using a T1-weighted three-dimensional turbo field echo sequence yielding images with a $1 \times 1 \times 1$ mm resolution. During the retinotopic mapping session T2*-weighted functional images were acquired using an echo planar imaging sequence, with 23 slices oriented parallel to the calcarine sulcus (64×64 image matrix; $3.4 \times 3.4 \times 3$ mm resolution; TR, 1200 ms; TE, 30; FA, 75° ; FOV, 220 mm, ascending non-interleaved acquisition order). During the main experimental session, 46 transverse slices were acquired with an EPI sequence (80×80 image matrix; $2.75 \times 2.75 \times 2.75$ mm resolution; TR,

3000 ms; TE, 30; FA, 75° ; FOV, 220 mm, ascending interleaved acquisition order).

Data analysis was performed using BrainVoyager QX (v. 1.74; Brain Innovation, Maastricht, The Netherlands) and custom time series analysis routines written in MATLAB v. 7.1. The three anatomicals were homogeneity corrected, coregistered and then averaged to provide a better grey and white matter contrast. Images were then normalized to Talairach coordinates, segmented and inflated to provide a three-dimensional reconstruction of the grey and white matter boundary. All of the processing steps were performed using BrainVoyager QX.

Region of interest selection: retinotopic mapping and human MT+ complex functional localizer task

Retinotopic mapping was implemented using the standard traveling wave method (Engel *et al.*, 1994; Sereno *et al.*, 1995; DeYoe *et al.*, 1996). The polar angle was mapped with a slowly rotating ($8.3^\circ/\text{s}$) phase-reversing wedge stimulus (30° wide) extending from the center of gaze to 10° in the periphery. Eccentricity was mapped in a similar fashion by estimating the phase of the response to a slowly expanding or contracting ($0.35^\circ/\text{s}$) stimulus annulus with a width of 1.25° . Based on the activation maps five retinotopic visual areas were delineated for the region of interest (ROI)-based analysis: V1, V2, V3, V4v and V3a.

The fMRI sessions before and after training included a localizer scan, based on which human MT+ complex was identified. Subjects viewed a stimulus consisting of 12 15 s intervals of moving dots interleaved with 11 15 s epochs of randomly plotted dots. The reference stimulus was windowed by the aperture in which the stimuli appeared in the experimental scans and contained either uncorrelated motion or a correlated motion flow field with the direction of motion changing every 3 s. The speed of the moving dots was $6^\circ/\text{s}$.

A general linear model with two boxcar regressors was applied to the time series of the blood oxygen level dependent (BOLD) signal from the functional localizer scans; the regressors marked temporal epochs of coherent motion and incoherent motion. Each of the boxcar regressors was then convolved with a prototypical hemodynamic response function (mixture of two gamma functions with an initial peak at 6 s and a later undershoot peaked at 16 s, with a 6 : 1 ratio between the early and the late gamma functions). The human MT+ complex was defined as a contiguous group of voxels lateral to the parietal-occipital sulcus and beyond the retinotopically organized visual areas that exhibited a larger response during epochs of motion compared with epochs of static dots.

Region of interest analysis

To evaluate the fMRI responses obtained in the main experiment (in each subject) we extracted time-course data locked to stimulus onset and averaged over blocks from each ROI and for each condition. A canonical hemodynamic response function (described above) was convolved with boxcar regressors (reflecting the onset of the trials) to model the hemodynamic response for prolonged (block-type) stimulation. With a single free parameter this function was fitted to the averaged fMRI responses for each subject and condition separately. The free parameter was a scaling factor and was taken as the measure of response magnitude for each condition for all subsequent analyses.

In order to make comparison of activations between different scanning sessions (before and after training) possible, we derived normalizing factors for each area and scanning session. The normalizing constants were calculated from the data acquired during the independent functional MT+ localizer scans in a similar way as the response magnitudes for the main experiment. Thus, the normalizing

constants for a given ROI represent the average response magnitudes to coherent and incoherent motion in that region. We were able to estimate these values for eight subjects because data acquired during the reference scans of two subjects after training were not reliable due to excessive head motion. To increase the reliability of the estimates (the calculation of the constants are based on single scans), the normalizing values were averaged across the subjects.

The normalized magnitude $RN_{session}^{area}$ is calculated according to the formula

$$RN_{session}^{area} = (R_{session}^{area} / N_{session}^{area}) \bar{N}^{area}$$

where $R_{session}^{area}$ is the uncorrected response magnitude for each condition, scanning session, subject and region, $N_{session}^{area}$ is the normalization factor for each region and scanning session and \bar{N}^{area} is an average normalization constant for each region (averaged across the scanning sessions before and after training).

For statistical analysis of the difference between response magnitudes in different conditions we used repeated-measures ANOVA with test session (before training and after training), task relevance (task-relevant and task-irrelevant) and ROI (V1, V2, V3, V4v, V3A and MT+) as factors. We also performed planned contrasts to evaluate pairwise differences between conditions.

Eye movement data analysis

We calculated the mean eye position, saccade frequency and cumulative saccade amplitudes using an interactive computer program. Saccade detection was performed by a velocity threshold algorithm (velocity threshold 50°/s). The algorithm detected saccades greater than 0.2°. Artifacts like drifts or blinks were identified by visual inspection and removed. The program yielded estimates of amplitude of each saccade. We calculated the frequency (ratio between number of saccades and total number of trials) and cumulative amplitude of gaze shifts (Kimmig *et al.*, 2008), which occurred during the visual stimulus presentation separately for the different motion directions. We compared these values between the different conditions using repeated-measures ANOVA and Student's *t*-test.

Results

During training, observers were presented with two fields of spatially superimposed moving dots (Fig. 1); they had to discriminate the speed of dots moving in one direction while simultaneously ignoring dots that moved in an orthogonal direction (i.e. a task-irrelevant distractor). As shown in Fig. 2, speed discrimination thresholds gradually improved as a result of training. Comparison of the performance during the first six blocks of training (speed discrimination threshold 0.58°/s) with the performance during the last six blocks of training (speed discrimination threshold 0.49°/s) revealed a significant learning effect ($t_9 = 4.48$, $P < 0.002$). These data demonstrate that the training sessions were sufficient to improve the efficiency of processing basic visual attributes such as stimulus speed.

Effect of training on motion detection thresholds

We next investigated how training on a speed discrimination task affects perceptual sensitivity to different motion directions by measuring motion detection thresholds for three different directions before and after training (i.e. the motion coherence required for threshold performance). The three tested directions included the two

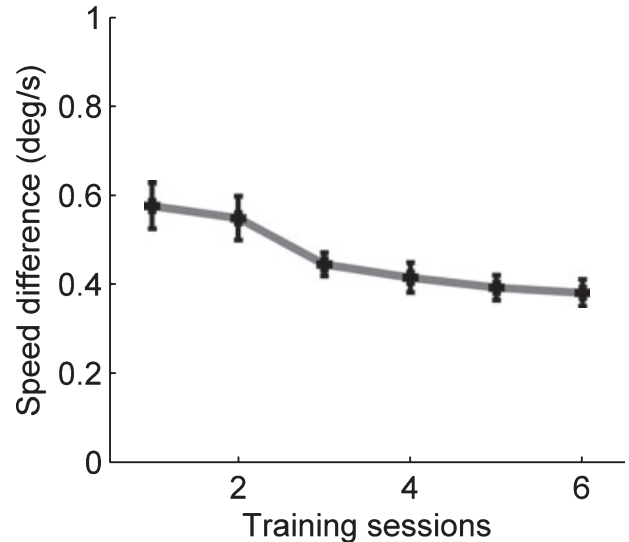


FIG. 2. Motion speed discrimination performance during training. Speed discrimination thresholds gradually improved as a result of training. Error bars indicate \pm SEM.

directions that were present during training (+45° and -45°) as well as a control direction that was equidistant from them (180°, downward). The results revealed that training had a strong effect on the observers' performance (Fig. 3). A repeated-measures ANOVA showed no significant main effect of test session (before and after training, $F_{1,9} = 1.21$, $P = 0.3$); however, there was a significant main effect of task relevance (task-relevant and task-irrelevant, $F_{1,9} = 30.7$, $P < 0.001$) and a significant interaction between these variables ($F_{1,9} = 58.2$, $P < 0.001$). Before training (Fig. 3, left side), there was no difference in motion detection thresholds for the two directions that were present during training ($t_9 = 0.04$, $P = 0.966$); however, both of these directions had higher thresholds than the control direction. The increased sensitivity for the control direction might be explained by

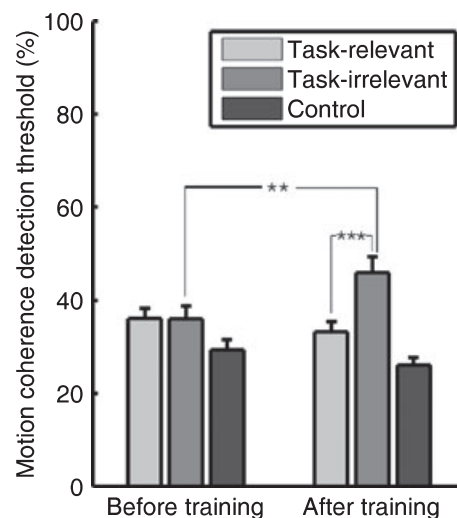


FIG. 3. Perceptual sensitivity for the different motion directions. Before training, there was no difference between the motion coherence detection thresholds for the directions that were task-relevant and task-irrelevant during training as well as for a control direction. After training, sensitivity for the direction that was task-irrelevant during training was strongly reduced. Error bars indicate the SEM. ** $P < 0.01$; *** $P < 0.001$.

the fact that it was a cardinal direction (downward), for which transparent motion detection has been shown to be better than for non-cardinal motion directions (Greenwood & Edwards, 2007). However, the motion coherence threshold for the task-relevant direction was significantly lower than the threshold for the task-irrelevant direction (Fig. 3, right side) after training ($t_9 = -8.33$, $P < 0.0001$). Furthermore, a comparison of the motion coherence thresholds before and after training revealed that thresholds for the task-relevant direction decreased non-significantly ($t_9 = 0.89$, $P = 0.396$), whereas thresholds for the irrelevant direction significantly increased ($t_9 = -8.33$, $P < 0.001$). The threshold for the control direction also underwent a non-significant decrease ($t_9 = 1.13$, $P = 0.289$), further supporting the observation that training decreased sensitivity to motion in a direction that was continuously present as a task-irrelevant distractor during training. Importantly, in our motion coherence detection experiment the three motion directions were presented randomly within a block and observers were required to indicate which of the two temporal intervals contained coherent motion. Thus, our design ensured that a possible learning-induced bias to choose the task-relevant rather than the task-irrelevant direction in case of uncertainty can be excluded as an explanation of the results of our motion coherence detection experiment.

For all experimental conditions subjects were instructed to maintain eye-gaze on the small fixation point at the center of the display. However, to verify that subjects were able to maintain fixation and that there was no differential pattern of fixations for different motion directions, we tracked the eye position of subjects while they were performing the motion coherence detection task. We did so for five randomly chosen subjects in the sessions before and after the training period. Trials were binned based on motion direction and we calculated the mean eye position (x and y values) for the period when the motion stimulus was present on each trial. We found no significant differences in the mean eye position for the three different motion directions (main effect of direction: before training, $F_{2,8} = 1.83$, $P = 0.221$; after training, $F_{2,8} = 0.506$, $P = 0.621$), indicating that there was no systematic bias in eye position induced by the direction of the motion stimulus (also see Fig. S1 in Supporting information). Furthermore, additional analysis using ANOVA showed that there were no significant differences between the three motion directions in the saccadic frequency (main effect of direction: before training, $F_{2,8} = 1.628$, $P = 0.255$; after training, $F_{2,8} = 1.613$, $P = 0.259$) and in the cumulative saccadic amplitude (main effect of direction: before training, $F_{2,8} = 0.301$, $P = 0.748$; after training, $F_{2,8} = 0.676$, $P = 0.535$).

Effect of training on functional magnetic resonance imaging responses

Before and after training, fMRI responses within the visual cortex were measured to motion directions that were task-relevant and task-irrelevant during training. The two different directions were presented in separate blocks (i.e. no distractors were present). Observers performed a two interval speed discrimination task during fMRI scanning. Speed discrimination performance before training was slightly better for the task-relevant direction compared with the task-irrelevant direction; this difference was magnified after training (Fig. 4). However, ANOVA revealed no significant main effect of test session (before and after training, $F_{1,9} = 0.193$, $P = 0.67$) and, even though there was a significant main effect of task relevance (task-relevant and task-irrelevant, $F_{1,9} = 15.0$, $P < 0.003$), the interaction between these variables was not significant ($F_{1,9} = 1.41$, $P = 0.265$). These data show that training did not significantly increase the

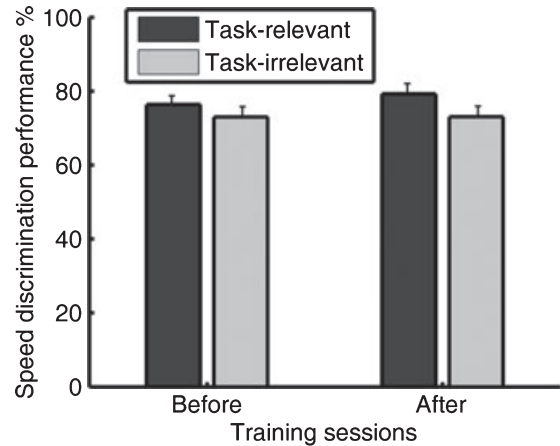


FIG. 4. Motion speed discrimination performance during the fMRI scanning sessions. Error bars indicate the SEM.

difference in speed discrimination performance between the task-relevant and task-irrelevant directions during scanning. The apparent discrepancy between these results and the significant improvement of speed discrimination performance measured during training might be explained by the fact that during training the speed of the task-relevant motion direction had to be discriminated in the presence of a task-irrelevant distractor direction, whereas during scanning only one motion direction was present during each trial.

In a separate scanning session carried out before training, we defined ROIs in early retinotopic visual cortex as well as the human MT+ complex using standard independent functional localizer tasks (Engel *et al.*, 1994; Sereno *et al.*, 1995; DeYoe *et al.*, 1996; Tootell *et al.*, 1997). We then performed an ROI-based analysis of the fMRI data obtained in the main experiment. The fMRI results revealed that, before training, the magnitude of the fMRI responses evoked by the two motion directions were similar (Fig. 5). However, after training, fMRI responses evoked by the task-irrelevant direction were smaller than responses evoked by the task-relevant direction. A repeated-measures ANOVA revealed no significant main effect of test session (before and after training, $F_{1,9} = 0.06$, $P = 0.817$), no significant main effect of task relevance (task-relevant and irrelevant, $F_{1,9} = 1.78$, $P = 0.215$) but a significant interaction between these variables ($F_{1,9} = 8.76$, $P = 0.016$). After training, a strong reduction of fMRI responses evoked by the task-irrelevant direction compared with responses evoked by the task-relevant direction (Fig. 5) was observed in ROIs V2, V3, V3A and MT+ (for all ROIs $P < 0.023$; the significance threshold corrected for multiple comparison: $P = 0.033$ corresponding to a false discovery rate of 0.05), whereas in ROIs V1 and V4v the difference between the fMRI responses to task-relevant and task-irrelevant directions did not reach the significance level (V1, $P = 0.051$; V4v, $P = 0.11$).

Although training did not significantly increase the difference in speed discrimination performance between the task-relevant and task-irrelevant directions during scanning, it is possible that the difference between the fMRI responses to task-relevant and task-irrelevant directions might be the result of the small difference in speed discrimination performance. To exclude this possibility, an additional analysis was performed to formally test the relationship between speed discrimination performance and fMRI responses. We divided the fMRI data from each subject into two median split subgroups based on speed discrimination performance. One subgroup contained the fMRI data from runs with the best speed discrimination performance and the other subgroup contained fMRI data from runs where performance in

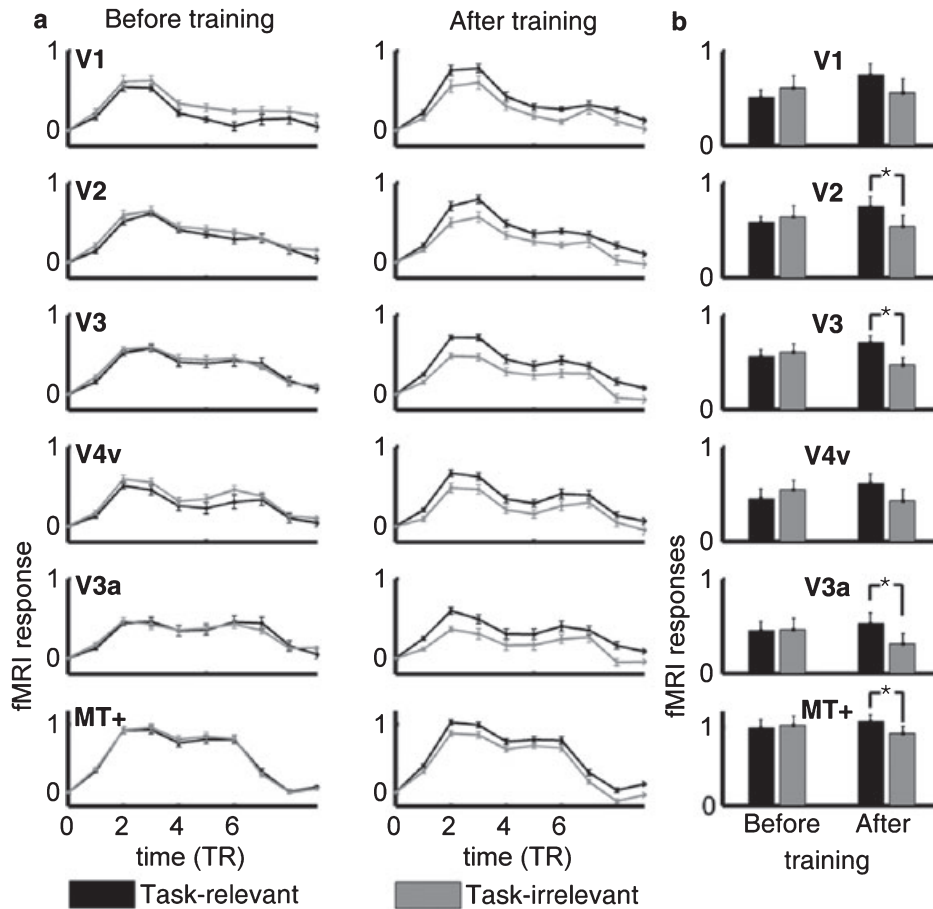


FIG. 5. Effect of learning on the fMRI responses. fMRI responses to the task-relevant and task-irrelevant directions before and after training. (a) Time-courses and (b) response amplitudes of the fMRI responses in different visual cortical areas. Values on the ordinates represent: (a) percent BOLD signal change and (b) calculated model fitting weights (in arbitrary units, see Materials and methods). Error bars indicate the SEM. * $P < 0.05$.

the speed discrimination task was poor. ANOVA revealed a significant difference in the speed discrimination performance between these subgroups (good and poor, $F_{1,9} = 61.2$, $P < 0.001$); no significant main effect of test session (before and after training, $F_{1,9} = 0.084$, $P = 0.778$) and no significant interaction between these variables ($F_{1,9} = 0.848$, $P = 0.381$). Importantly, however, we found no significant differences in the fMRI responses between these two subgroups: no main effect of test session (before and after training, $F_{1,9} = 0.43$, $P = 0.528$), no significant main effect of performance (good and poor, $F_{1,9} = 0.05$, $P = 0.82$) and no significant interaction between these variables ($F_{1,9} = 0.44$, $P = 0.522$). These results provide further support that the difference between the fMRI responses to task-relevant and task-irrelevant directions found after training is primarily due to a difference in the strength of neural responses to these two directions as a result of training and not due to the difference in the discrimination performance between the two directions during scanning.

Although the present study was not designed to investigate across-session effects, normalization of the fMRI responses of each cortical region obtained in the main conditions with the magnitude of fMRI responses to the MT+ localizer provides an opportunity to compare the fMRI responses to the task-relevant and task-irrelevant directions before training with those obtained after training (see supporting Fig. S2). In the case of task-relevant direction, normalized data showed a trend of increased neural responses in the early visual cortical areas after training compared with that before training; however, this difference was

significant only in the primary visual cortex ($P = 0.0037$; the corrected significance level: $P = 0.0167$ corresponding to a false discovery rate of 0.05). However, a comparison of the fMRI responses to the task-irrelevant direction before and after training showed that learning resulted in a significant reduction of the fMRI responses in areas MT+ and V4v ($P = 0.0025$ for MT+ and $P = 0.01$ for V4v; the corrected significance level: $P = 0.0167$ corresponding to a false discovery rate of 0.05).

Although we did not track eye position during scanning while the subjects performed a speed discrimination task, the results of our control experiment speak against the possibility that the difference between the fMRI responses to the task-relevant and task-irrelevant directions could be explained by a difference in the pattern of fixations. The experimental procedure in the control experiment was the same as that in the main experiment with the exception that there were no fMRI scans before and after training. Instead, the eye position of the observers was recorded outside the scanner using the same stimuli and the same speed discrimination task that were used during scanning in the main experiment. Eye position data from trials with task-relevant and task-irrelevant direction were separated and binned. We calculated the mean eye position (x and y values) for the period when the motion stimulus was present on each trial. We found no significant differences in the mean eye position for the two different motion directions (main effect of direction: before training, $F_{1,3} = 0.49$, $P = 0.533$; after training, $F_{1,3} = 2.24$, $P = 0.231$), indicating that there was no systematic bias in eye position induced by the

direction of the motion stimulus. Furthermore, additional analysis showed that there were no significant differences between the three motion directions in the saccadic frequency (effect of direction: before training, $t_4 = -1.967$ $P = 0.121$; after training, $t_4 = 1.055$ $P = 0.35$) and in the cumulative saccadic amplitude (effect of direction: before training, $t_4 = -1.902$ $P = 0.13$; after training, $t_4 = 0.414$ $P = 0.67$).

Importantly, the motion coherence detection results obtained during the control experiment revealed that training led to similar learning effects as those in the main experiment, i.e. thresholds were slightly reduced for the task-relevant direction and increased for the task-irrelevant direction. ANOVA showed no significant main effect of test session (before and after training, $F_{1,3} = 0.23$, $P = 0.659$); however, there was a significant main effect of task relevance (task-relevant and task-irrelevant, $F_{1,3} = 11.97$, $P < 0.041$) and a significant interaction between these variables ($F_{1,3} = 14.38$, $P < 0.032$). Thus, the results of our control experiment suggest that reduced fMRI responses to the task-irrelevant direction as compared with the task-relevant direction cannot be explained by a difference in the fixation patterns between the two directions.

Discussion

Our findings provide evidence that learning results in increased detection thresholds for task-irrelevant features during training. This learning-induced sensitivity decrease was specific for the feature that served as a distractor during training as the detection threshold for a control direction that was not present during training slightly decreased (rather than increased) after training. The observation of a small non-significant increase in sensitivity to task-relevant motion in the present task is consistent with previous reports showing improved perceptual performance for visual features that were task-relevant during training (Ramachandran & Braddick, 1973; Fiorentini & Berardi, 1980; Ball & Sekuler, 1982; Karni & Sagi, 1991; for review see Fahle & Poggio, 2002). However, recent studies also suggest that learning results in increased sensitivity for subthreshold task-irrelevant visual features presented concurrently with the task-relevant information during training (Watanabe *et al.*, 2001, 2002; Seitz & Watanabe, 2003), whereas suprathreshold task-irrelevant features are not affected by training (Tsushima *et al.*, 2008). These findings apparently conflict with our observation of reduced sensitivity for task-irrelevant information. However, several key differences between the studies might explain this discrepancy. First, the task-irrelevant stimulus used by Watanabe and co-workers was spatially separated from the task-relevant stimulus during training. Second, the target and distractor stimuli were very different (alphanumeric characters and moving dots, respectively), suggesting that task-relevant and task-irrelevant stimuli were processed by at least partially distinct regions of visual cortex: one region specialized for processing shape/letter information and the other for processing visual motion. Due to the distinctiveness of the relevant and irrelevant stimuli, it seems likely that the irrelevant stimulus did not strongly interact or interfere with target processing. In the present study, however, task-relevant and task-irrelevant stimuli were spatially overlapping and structurally similar (i.e. both were moving dot patterns). Therefore, the stimuli were probably competing for access to the same neural processing mechanisms, which would be expected to drastically increase the amount of competition. We therefore posit that the learning-induced suppression of distractors (as opposed to enhancement as reported by Watanabe and co-workers) may only be observed when the task-irrelevant information strongly interferes with the processing of task-relevant information and thus must be suppressed by attention during training.

The possibility that the strength of distractor suppression during training might affect learning has also been invoked (Tsushima *et al.*, 2008) to explain why learning leads to increased sensitivity for subthreshold but not for suprathreshold task-irrelevant information. For example, attentional suppression of task-irrelevant information is less pronounced when the distractor is a very weak, subthreshold signal compared with when it is suprathreshold (Tsushima *et al.*, 2006). Thus, learning may result in increased sensitivity for subthreshold distractors but not for suprathreshold distractors because only the latter must be suppressed during training (and this suppression should attenuate any positive consequences of learning) (Tsushima *et al.*, 2008). The results of the present study take this logic one step further and show that, in cases when there is direct interference between task-relevant and task-irrelevant information that requires strong attentional suppression, training will actually produce decreased sensitivity for the task-irrelevant information.

We also found that learning results in decreased fMRI responses evoked by the task-irrelevant motion direction compared with the task-relevant motion direction throughout the visual cortex. The strongest learning effects were observed in the extrastriate visual cortical areas V2, V3, V3a and MT+, the latter two of which are known to be involved in visual motion processing (Huk & Heeger, 2002; Nishida *et al.*, 2003; Kamitani & Tong, 2006; Serences & Boynton, 2007a,b). An important question is whether the observed reduction in fMRI responses associated with task-irrelevant stimuli can be explained by learning-induced changes in performance in the speed discrimination task that was performed during scanning (even though statistical analyses revealed no significant learning effects on performance in the speed discrimination task in the absence of distractors during scanning). To test this possibility, we investigated the relationship between speed discrimination performance and fMRI responses. We found no significant differences in the fMRI responses between runs with the best speed discrimination performance and runs where performance in the speed discrimination task was poor. These findings suggest that the difference between the fMRI responses to task-relevant and task-irrelevant directions found after training in the present study cannot be explained by the difference in the speed discrimination performance between the two directions during scanning.

Therefore, we propose that the learning-induced modulation of fMRI responses might be a combined effect of increased neural responses to the task-relevant direction and decreased neural responses to the task-irrelevant direction after training. Importantly, we also suggest that the learning-induced modulation of neural responses to task-relevant and task-irrelevant directions is not restricted to the trained task condition but affects processing of these directions generally in a task-independent manner. This interpretation is in agreement with the results of our behavioral experiments showing a strong learning effect in an untrained motion coherence detection task.

Previous research has shown that the effect of perceptual learning on fMRI responses depends on several factors, including task and testing conditions as well as the time during learning when fMRI responses are measured (Kourtzi *et al.*, 2005; Carmel & Carrasco, 2008; Yotsumoto *et al.*, 2008). These results imply that there are multiple mechanisms by which learning can modulate fMRI responses. In accordance with this, comparing fMRI responses after training with those before training suggests that the site and mechanisms of learning-induced facilitation of the task-relevant information and suppression of the task-irrelevant information might be different. In particular, we found that fMRI responses to the motion direction that was task-relevant during training are enhanced in the

primary visual cortex. However, learning-induced suppression of fMRI responses to the motion direction that was present as a distractor during training was most pronounced in the motion selective human area MT+ and was absent in earlier cortical areas, such as the primary visual cortex. We propose that the observed reductions of fMRI responses in MT+ might reflect suppressed neural responses to the task-irrelevant direction, which is supported by recent findings showing that decreases in BOLD activity in early visual cortex are associated with decreased neural activity (Shmuel *et al.*, 2006). Importantly, previous research provided evidence that neural responses in human area MT+ are sensitive to motion coherence and are associated with the perceived strength of the global coherent motion signal (for review see Serences & Boynton, 2007b). Based on this, it is tempting to suggest that decreased neural responses in human area MT+ to the motion direction that was task-irrelevant during training might underlie the learning-induced suppression of perceptual sensitivity for this direction found in our psychophysical experiments. At the same time, it is important to point out that, in addition to the learning-induced modulation of the strength of direction selective neuronal responses, changes in either the receptive field tuning properties of direction selective neurons or the readout of the visual cortical neuronal responses could also contribute to the observed behavioral learning effects. For example, previous neurophysiological studies provided evidence for sharpening of neuronal responses to the trained feature with learning in the macaque visual cortex (for recent review see Hoffman & Logothetis, 2009). Narrowing of the tuning curves, however, leads to a smaller fraction of cells being active for any given stimulus and thus would lead to a decreased BOLD signal (Carmel & Carrasco, 2008; Hoffman & Logothetis, 2009). Therefore, in the case of the present study, an explanation based on sharpening of neuronal responses would predict decreased fMRI responses to the task-relevant direction, which is not supported by the results of our fMRI experiment. Unfortunately, to our knowledge, the possibility that learning might also modulate the receptive field tuning properties of neurons responsible to features that are present as distractors during training or might modify the readout of their responses at the higher stages of perceptual decision level processing has not been investigated before. Therefore, further research is required to explore whether these neural mechanisms might also contribute to learning-induced suppression of perceptual sensitivity to the task-irrelevant direction found in the present study.

It has been proposed that increasing the efficacy of noise exclusion might be a crucial component of perceptual learning and that it is achieved by improving the extraction of the visual information that is relevant for the trained task via reweighting or retuning of the perceptual template that is used to arrive at a decision (Doshier & Lu, 1998, 1999; Li *et al.*, 2004; Lu & Doshier, 2004). Our findings suggest that a learning-induced decrease in neural responses to a competing task-irrelevant feature represents one of the mechanisms underlying such reweighting of the perceptual templates due to learning. To explain the effect of training on the task-irrelevant information, Seitz and Watanabe (2005) proposed a model suggesting that perceptual learning involves a diffuse reinforcement signal that leads to long-lasting improvement of information processing for all stimuli presented concurrently with the task-relevant information during training, even if the stimulus is a task-irrelevant distractor. This model, however, fails to account for the present observation of a learning-induced suppression of distractor information. We suggest that learning-induced suppression represents an important mechanism underlying more efficient distractor exclusion after training and should be incorporated into models of perceptual learning.

Supporting information

Additional supporting information may be found in the online version of this article:

Fig. S1. Representative fixation patterns of one of the subjects during the motion coherence detection threshold measurements after training in the case of the three different motion directions.

Fig. S2. Effect of learning on the fMRI responses.

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Abbreviations

fMRI, functional magnetic resonance imaging; ROI, region of interest; BOLD, blood oxygen level dependent.

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