Orientation-specific adaptation to mentally generated lines in human visual cortex

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TITLE PAGE

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Running title: Neural adaptation induced by mental imagery

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Abstract

Previous studies have shown that prolonged inspection of a tilted visual pattern leads to changes in perception ("tilt after effect", TAE), as well as to a reduction of the neural activation evoked by this pattern ("neural adaptation"). In this fMRI study, we investigated whether such perceptual and neural adaptation can be induced solely by mental imagination. The subjects were asked to mentally generate tilted lines, after which they were presented test lines oriented in the same or the direction orthogonal to the mentally tilted lines. Subjects showed a TAE even after mental imagery ("mental TAE"). Furthermore, a significant orientation-specific adaptation occurred in extrastriate visual areas (V3-V4), showing a decreasing gradient of adaptation from areas V4 to V1. Both this neural adaptation and the individual size of the mental TAE correlated with performance in a behavioural task probing mental imagery. Thus, orientation-selective neurons in visual areas seem to be recruited by mental imagery, and the amount of recruitment correlates with the degree of success of mental imagery operations. The influence of mental imagery on perception and on the neural activity in extrastriate visual areas provides evidence for analogue coding of mental images.

Introduction

Prolonged inspection of visual patterns with a given orientation, colour, or motion, or even of human faces, causes noticeable perceptual changes, called visual after-effects. After prolonged inspection of tilted lines, subsequently presented test lines oriented close to the adapting orientation appear to be tilted in the opposite direction. This phenomenon is known as the tilt after-effect (TAE; Gibson & Radner, 1937).

Several studies investigated the neural mechanisms underlying visual after-effects (e.g. Wenderoth & Smith, 1999, Liu, Larsson & Carrasco, 2007). After prolonged inspection of tilted lines, a reduction of neural activation for subsequently presented test lines oriented close to the adapting orientation (neural adaptation) in contrast to orthogonal test stimuli was reported (Tootell et al, 1998). Orientation-selective adaptation, revealed by the fMRI response, has been described for the primary visual cortex and higher-order visual areas (Tootell et al, 1998; Liu, Larsson & Carrasco, 2007), or for the higher-order visual areas V3 and V4 only (Boynton & Finney, 2003). Long-term adaptation seems to reduce neural activity in primary visual cortex and higher visual areas (Fang, Murray, Kersten & He, 2005), whereas only V3A and V4 showed this response pattern with short-term adaptation (Fang, Murray, Kersten & He, 2005; Boynton & Finney, 2003).

In a previous study, we found that a perceptual TAE can be induced by visual mental imagery of tilted lines (Mohr, Linder & Sireteanu, 2008). This result suggests that orientation-selective neurons in visual areas are recruited for mental imagery. The influence of mental imagery on visual perception provides evidence for a coding of mental images similar to the coding of perception (Kosslyn, & Ochsner, 1994; perception-like theory of mental imagery), and homologies between the activation patterns associated with perception and imagery have indeed been documented in several functional imaging studies (Kosslyn, Ganis & Thompson, 2001; O'Craven & Kanwisher, 2000).

In the fMRI experiment described in this paper, we aimed to reveal the neural basis of the orientation-specific neural adaptation induced by behaviorally controlled mental imagery. We reasoned that if the mental imagery of tilted lines is based on the activation of orientation-selective neurons in early cortical visual areas, orientation-specific adaptation should be induced not only by the prolonged visual inspection of the real tilted lines, but also by the mental generation of these stimuli. We investigated whether the neural activity evoked by physically presented test lines after mental adaptation is reduced in contrast to the non-adapted condition.

Materials and methods

Participants

Fifteen subjects participated in the behavioural pre-experiment (6 men), twelve of them took part in the fMRI-study (5 men). All participants had normal or corrected-to-normal vision. Their mean age was 23.5 years (*SD* = 3.3 years). Written informed consent was obtained from each subject after the purpose of the study was explained. The study was performed in accordance with the Declaration of Helsinki.

Material

Visual stimuli were controlled by a personal computer triggered by the magnetic resonance (MR) tomograph. They were presented via a liquid crystal display projector (Sanyo PRO Xtrax Multiverse Projector, Japan) with dark background (0.30 cd/m^2). The stimuli were presented with the aid of Experimental Runtime System (ERTS, Berisoft), which also recorded the responses.

Design and Procedure

The maximum perceived orientation shift for the TAE illusion is realized when the testing and adapting angles are 15° apart (Clifford et al., 2000). We therefore designed a comparable psychophysical (see: behavioural experiment: TAE) and fMRI-design (see: FMRI-experiment: neural adaptation), where the subjects had to generate mentally four parallel lines (tilted + 15°).

FMRI-Experiment: neural adaptation

The subjects had to generate mentally four parallel lines into an empty circle (tilted + 15° vertically or + 15° horizontally, Fig. 1). The experiment was divided into two sessions, separated by at least five days. The sessions were identical in respect of the visual stimulation, only the imagined orientation differed. As an imagery control, the subjects were asked to decide if a dot presented inside the circle crossed one of the imagined lines (line-dot-crossing task). At the end of each trial, four parallel horizontal or vertical test lines were presented and the participants indicated which orientation they perceived (orientation decision, Fig. 1). Consequently, there are two different conditions: presentation of test lines oriented in a direction similar to the imagined ones (i.e. mental imagery of lines tilted + 15° vertically and presentation of vertical test lines; condition “adapted”) and presentation of orthogonal test lines (i.e. mental imagery of lines tilted + 15° vertically and presentation of horizontal test lines; condition “non-adapted”).

50 % of the participants completed two runs of the experiment with the mental imagery of four 15° from vertical tilted lines (session 1: vertical adaptation) within one day. After a pause of at least five days the experiment was repeated with the mental imagery of four lines tilted 15° from horizontal (session 2: horizontal adaptation). The pause was included to avoid interference of possible visual after-effects remaining from session 1. For the other 50% of the subjects, the order of these two sessions was reversed.

At the beginning of the experiment, a 10° diameter white circle was presented for four minutes on a grey background, surrounded by 32 dots (Fig. 1, pre-adaptation). The subjects were instructed to mentally generate four parallel lines connecting the four right upper and four left lower dots from vertical (condition: vertical adaptation at 15° clockwise from vertical, Fig. 1 dots indicated by V, letter not presented in the experiment). In the condition “horizontal adaptation” subjects had to mentally connect the four left upper and four right lower dots from horizontal by four parallel mentally generated lines (condition: horizontal adaptation at 15° clockwise from horizontal, Fig. 1 dots indicated by H, letter not presented in the experiment). Subjects were instructed that the width of the generated lines should be identical to the diameter of the dots. After a variable time interval (17.5, 19.5 or 21.5 sec, pseudo-randomized) an additional dot was presented inside the circle for 500 ms. The subjects were asked to press the right button when the mentally generated lines crossed the dot, otherwise they were required to press the left button (“line-dot crossing task”). In 50% of the cases the dot appeared “on” a mentally generated line, balanced over the four generated lines. In the other 50% of cases the dot appeared “off” the mentally generated lines, inside or outside the area delineated by the two outermost lines. Participants were instructed to resume the mental imagery of the lines of the indicated orientation after their response. There were 15 trials of the line-dot crossing task during each pre-adaptation experiment. We chose variable intervals for the presentation of the stimuli for the line-dot crossing task in order to reduce expectation and task preparation effects, and to enable a better separation of events in the subsequent fMRI experiment. The pre-adaptation was performed by the subjects inside the scanner directly before the beginning of the functional measurement.

After pre-adaptation, the actual fMRI experiment, consisting of two tasks, started. First, the circle with the surrounding dots was again presented to the subjects, this time for 17.5, 19.5 or 21.5 sec. As before, the subjects had to mentally generate lines connecting the opposite dots ("re-adaptation"). This was followed by the "line-dot-crossing-task: an additional dot was presented inside the circle for 500 ms and the subjects had to decide if the mentally generated lines crossed the presented dot. Afterwards four parallel vertical (50%) or horizontal (50%) test lines were presented in pseudo randomized order for 350 ms inside the circle. The participants were asked to report whether the test stimulus was oriented vertically or horizontally via button press ("orientation judgement"). The next trial started again with the presentation of a circle with surrounding dots, where the subjects had to mentally generate lines connecting the opposite dots ("re-adaptation", 17.5, 19.5 or 21.5 sec). Each session included 75 trials.

Behavioural experiment: TAE

In a pre-experiment the subjects performed the mental imagery task outside the scanner, in order for us to obtain the magnitude of the TAE of every subject by an adaptive stair-case paradigm. The TAE was measured outside the scanner to avoid differences of visual stimulation between participants in the fMRI-paradigm (Liu, Larsson & Carrasco, 2007). The behavioural experiment was divided into two sessions, separated by at least five days. The sessions were identical in respect of the visual stimulation, only the imagined orientation differed. As in the fMRI experiment the subjects had to mentally generate tilted lines into an empty circle (line-dot-crossing task).

After each trial of the "line-dot-crossing task" (7500 ms) four parallel test lines of different orientations were presented for 200 ms. Participants were asked to report whether the test stimulus was tilted clockwise or counter-clockwise with respect to their subjective vertical. The average of the last four points of a staircase was used for the estimate of the subjective vertical.

Participants completed 2 runs of the experiment with the mental imagery of +15° tilted lines (condition +15°) within one day. After a pause of at least five days, the experiment was repeated with the mental imagery of four lines tilted -15° (condition -15°). The pause was included, because after-effects have been shown to last for significant time-periods.

Mental imagery performance

The ability of the subjects to generate a mental image was measured by two tests. First, the performance in the "line-dot crossing task" was calculated for every subject in percent of correct responses. As a control for their ability to form mental images, the subjects were asked to complete the Vividness of Visual Imagery Questionnaire (Marks, 1973; VVIQ). The VVIQ consists of 16 items in which the participant had to generate a mental image by thinking about specific scenes and situations. Vividness of the mentally generated image was rated along a 5-point scale. The procedure was carried out for the 16 items with closed and opened eyes, respectively. The sum of the achieved scores was taken from both conditions ("eyes open" and "eyes closed"). The subjects reached a mean score of 112, *SEM* = 5.7, indicating a sufficient level of mental imagery ability.

FMRI

FMRI data were acquired with a Siemens 3 T Magnetom Trio MRT using a gradient echo EPI sequence (TR = 1400 ms; TE = 30 ms; flip angle FA = 80°, FOV = 210 x 210 mm^2, 23 axial slices covering the whole brain, slice thickness = 3 mm, distant factor = 25%, voxel size 3.3 × 3.3 × 3.3 mm^3). The subjects were tested in two functional scans with 906 volumes per scan on two different days. Each scan lasted 21.4 min. A high-resolution T1-weighted 3D anatomical MR data set was used for co-registration.

Retinotopic mapping

Visual cortical areas were identified for each subject, based on retinotopic polar mapping (DeYoe et al, 1996; Engel, Glover & Wandell, 1997; Sereno et al, 1995). The analysis of the retinotopic-mapping experiment was conducted using a cross-correlation analysis. We used the predicted haemodynamic signal time course for the first 1/8 of a stimulation cycle (corresponding to a 45° visual angle in the polar mapping experiment) and shifted this reference function successively in time (Muckli, Kohler, Kriegeskorte & Singer; 2005; time steps corresponded to the recording time for one volume, TR). Sites activated at particular polar angles were identified through selection of the lag value that resulted in the highest cross-correlation value for a particular voxel. The lag values obtained at particular voxels were encoded in pseudo-colour on corresponding surface patches (triangles) of the reconstructed cortical sheet. Based on the polar-angle mapping experiment, the boundaries of retinotopic cortical areas V1, V2, V3, V3A/B, V4 were estimated manually on the inflated cortical surface. We did not observe a consistent boundary between V3A and V3B; hence, we defined a visual area that contained both and labelled it V3a/b.

Data processing and statistical analysis

The data was pre-processed with BrainVoyager QX (Brain Innovation, Maastricht, the Netherlands). Data pre-processing included slice scan time correction with the first scan time within a volume used as a reference for alignment by sync-interpolation, three-dimensional motion correction, spatial smoothing with a 4 mm Gaussian kernel (full width at halfmaximum), temporal high-pass filtering to remove low-frequency non-linear drifts of three or fewer cycles per time course, and linear trend removal. Talairach transformation was performed for the complete set of functional data of each participant.

The statistical analysis of the BOLD (blood oxygenation level-dependent) signal variance was based on the application of multiple regression analysis to time series of task-related functional activation (Friston, et al, 1995). The general linear models (GLMs) were computed from the 48 *z*-normalized volume time courses (12 subjects x 4 runs). The BOLD effect was modelled by a two gamma hemodynamic response function for the physical test-stimulus onset (Friston et al, 1998).

Analysis was based on a random-effect GLM with 2 (adaptation: adapted and non-adapted) × 2 (line orientation: horizontal and vertical) predictors. Each condition included 75 trials. The obtained beta weights of each current predictor served as input for the second-level whole-brain random-effects analysis including a 2 x 2 factorial design. Due to our a priori hypothesis, a whole brain contrast for the test stimulus between “adapted” vs. “non-adapted” was calculated for all subjects with a threshold at $p < .001$, uncorrected for multiple comparisons. This contrast ensures that the activation due to the mental imagery task preceding the presentation of the physical test-stimuli in both “adapted” and “non-adapted” condition was subtracted from the BOLD-response. The statistical results were visualized through projecting 3D maps on the inflated surface reconstruction of a subject’s brain, including retinotopic mapping.

Regions of interest (ROIs)

The amount of adaptation was calculated for each visual area (V1, V2, ventral posterior area VP, V3, V3A/B, V4) identified by polar mapping separately for every subject. ROIs within each visual area were restricted to include only those voxels showing highly significant activation for presented horizontal and vertical lines by a subject, using a conservative threshold at $p < .01$, Bonferroni correction, but at least ≥ 20 voxels per ROI. We used this conservative criterion since we assume BOLD-adaptation induced by mental imagery to be retinotopically organized, and thus only wanted those parts of the visual cortex to be included in our calculation that were specialised to the visual field targeted by our mental imagery task. We calculated an adaptation index to quantify the reduction in response amplitudes (bold-peak for the test-stimulus) during the "adapted"- in contrast to the "non-adapted"- condition in a ROI: adaptation index AI = *(1- (BOLD_adapted / BOLD_non-adapted))* × 100. The AI indicates the relative % BOLD reduction in the "adapted" condition in comparison to the "non-adapted" condition.

Eye Movement Monitoring

All participants were trained outside the scanner to maintain proper fixation in all conditions of the experiment. We monitored horizontal and vertical saccades for the mental imagery and the orientation decision task in a pre-test (19 min) in a subgroup (N=6) of the participants (Electrooculography, recorded by BrainAmp amplifier, Brain Products GmbH, Gilching Germany). Subjects were able to maintain stable fixation throughout all conditions of the experiment. No significant difference was found for the number of saccades between the adapted (mean = 1.6, SE = .61) and non-adapted condition (mean = 1.8, SE = .58) in the pre-test, Z = .577, $p = .56$, N = 6. A Wilcoxon signed rank test for small sample sizes was used.

Results

Pre-experiment, behavioural data

In the pre-experiment we replicated the finding of a TAE induced by mental imagery with a staircase-design (*N* =15). The TAE shown in figure 2 is the average perceived orientation following adaptation to mentally generated clockwise and anti-clockwise adapters. The mental imagery of line orientation affected the perceived vertical in the eight subjects. When participants mentally generated the +15° orientation, the perceived vertical was shifted towards it, i.e., more than 0° (the objective vertical). Perceived orientation was less than 0° when subjects mentally generated the -15° orientation. The perceived vertical was highly significantly different between the two conditions, paired t-test $t(14) = 4.8$, $p < .01$. The mean influence of mental imagery on the perceived vertical was 1.2° (*SE* = .42). This is a somewhat smaller effect, in comparison to the impact of the prolonged adaptation to actually tilted lines in the literature. For example, Cruickshank and Schofield (2005) reported a TAE ranging from 1°- 4.5° for different kinds of visual adapting stimuli. However, the size of the present TAE is close to the amount of TAE induced by attention to one of two opposed orientations documented Liu, Larsson and Carrasco (2007, TAE of 1.6°).

The mean accuracy for the mental imagery "line-dot-crossing task" was 76%, *SEM* = 1.3, demonstrating that the mental imagery task is demanding but manageable. Furthermore, the amount of the TAE (difference in the perceived vertical for clockwise and anti-clockwise adapters) correlates with successful mental imagery operations in the "line-dot- crossing task", $r = .425$, $N = 15$, $p < .05$, two-tailed. Due to the small sample size of 15 subjects (12 for the fMRI-experiment) Kendalls Tau-b was used. This value is less likely to give distorted results when the assumptions for a parametric Pearson correlation are violated. There were no outliers for either the "line-dot-crossing task" or the TAE. This correlation underlines the assumption that the induced TAE is related to successful mental imagery.

MR-experiment, neural adaptation due to mental imagery

To detect outliers, we calculated the mean and standard deviation for the adaptation index (see methods) in each visual ROI for every subject. One subject was excluded from further analysis because the adaptation was outside of +/-2 standard deviations from the mean.

Whole brain contrast

Our hypothesis was that the neural response to the physically presented test lines in the "adapted" condition should be reduced in comparison to the "non-adapted" condition. A whole brain contrast "adapted vs. non-adapted" was calculated for all subjects with a threshold at $p \leq .001$, two-tailed, uncorrected for multiple comparisons.

The mental imagery of tilted lines modulated the orientation selective fMRI response in various occipital clusters. We observed significant adaptation in a cluster covering extrastriate VP-V4 (right hemisphere) and V3-V3a/b (bilateral) (Fig. 3A and table 1). As shown in the time course of the BOLD signal for these clusters, the test stimulus in the condition "adapted" evoked a significantly smaller response than the test stimulus in the condition "non-adapted". The clusters covering V3-V3a/b also showed a significant difference at a conservative threshold using the false discovery rate (Genovese, Lazar. & Nichols) $q(\text{FDR}) \leq .05$, cluster size > 10 voxels, whole brain contrast, paired *t*-test, corresponding to an uncorrected $p < .3 \times 10^{-5}$.

This pattern of results cannot be attributed to differences in the presented stimuli, because in both conditions they were physically identical. Hence, the effect of adaptation should be due to the influence of mental imagery. The interaction analysis between adaptation ("adapted" & "non-adapted") and test stimulus orientation ("horizontal" & "vertical") revealed no significant effects (threshold at $p \leq .001$, two-tailed, uncorrected for multiple comparisons). Thus, adaptation to the mentally imagined horizontally and vertically tilted lines was equal.

ROI- statistics reveal top-down gradient of adaptation

To investigate the amount of adaptation in the different visual areas, a region of interest analysis was performed. The differences in the BOLD peak for the two conditions (adapted vs. non-adapted) and for the ROIs in visual areas V1, V2, V3, V3a/b & V4 (identified for every subject by polar mapping, see methods) were contrasted by a 2×5 analysis of variance, repeated measurement. No significant main effect for the two conditions ($F(1,10) = 3.0$, $p > .1$) or the visual areas ($F(4,40) = .91$, $p > .4$) was found, but there was a highly significant interaction between the two factors, $F(4,40) = 6.1$, $p < .001$.

To evaluate the relationship between the adaptation effects and the different visual regions, we calculated an adaptation index AI for the areas V1, V2, V3, V3a/b & V4 (Fig. 4, see methods). The adaptation was defined as the percentage decrease in the BOLD signal peak for the test-stimulus in the “adapted” condition in comparison to the “non-adapted” condition. The resulting values showed a decreasing gradient of adaptation from V4 to V1 (Fig. 4). This was supported by a highly significant linear trend for the adaptation over the visual areas ($F(1,10) = 17.1$, $p < .01$). There was also highly significant reduction for the “adapted” condition in comparison to the “non-adapted” condition in the area V4, $t(10) = 5.1$, $p < .01$ and a significant effect in V3, $t(10) = 1.8$, $p \leq .05$, but not for V3a/b, V2 and V1 (revealed by post-hoc t-tests). The effect size for the difference in adaptation in V4 was about $d = 0.41$, (Cohen’s *d*), indicating a medium effect of adaptation.

The adaptation effect induced by mental imagery should be spatially specific and restricted to the retinotopic stimulus location in V1-V4 (= voxels with a significant BOLD-response to the vertical and horizontal test orientations in V1-V4). To investigate this assumption a second ROI-analysis was calculated for all voxels in a specific visual area which did not reach a significant activation for the vertical and horizontal test orientations at $p \leq .01$, Bonferroni correction in V1-V4.

The differences in the BOLD peak for the two conditions (adapted, non-adapted) and for the ROIs in V1, V2, V3, V3A/B & V4 were contrasted by a 2×5 analysis of variance, repeated measurement. No significant main effect for the two conditions ($F(1,10) = 1.1$, $p > .3$) or the visual areas ($F(4,40) = .9$, $p > .4$) was found, and there was no significant interaction between the two factors, $F(4,40) = 1.2$, $p > 2$. This result indicated that the reduction in BOLD-response for adapted orientations is restricted to the stimulus location and is less likely attributable to general attentional modulation in visual areas like stimulus novelty for orthogonal test stimuli.

A general challenge faced by adaptation analyses is how to distinguish the difference between stimulus-specific adaptation and a non-specific novelty effect to the non-adapted stimulus that could be attention driven. In the current experiment, suppose participants were imagining the target 'adapter' orientation; then, when the stimulus appeared, the mismatch between the imagined orientation and the actual physical orientation would have been a salient change, which by itself might have caused an increased BOLD response in higher visual areas like V4. To distinguish between a decrease of the adapted stimulus and an increase of the non-adapted, novel stimulus, we investigated the impact of adaptation over time. It is known that a longer adaptation duration produces larger after-effects and adaptations (e.g. Harris & Calvert, 1989), whereas novelty effects would be expected to attenuate, rather than increase, over time (e.g. Fabiani & Friedman, 1995). We therefore calculated the BOLD-response in bilateral V4 for the adapted and the non-adapted test-stimuli at the beginning (36 trials) and at the end of each experimental stimulation (36 trials, Fig. 3B). A 2×2 analysis of variance, repeated measurement was calculated (adapted vs. non-adapted × beginning vs. end).

We found significant main effects for adaptation (*F*(1,10) = 5, $p \leq .05$) and time (*F*(1,10) = 4.6, $p \leq .05$). Furthermore, the interaction between adaptation and time was significant ((*F*(1,10) = 4.5, $p \leq .05$). Post-hoc t-test showed a significant decrease in the BOLD-response for the “adapted” test-stimulus between the time points in the experiment ($t(10) = 3.2$, $p \leq .05$), but no change for the “non-adapted” stimulus ($t(10) = .9$, $p > .2$), ruling out a non-specific novelty effect.

Mental imagery and neural adaptation

To explore the relationship between neural adaptation in visual areas and mental imagery we correlated the accuracy in the mental imagery “line-dot-crossing task” with the amount of BOLD-adaptation (defined by the adaptation index AI = (1- (BOLD_adapted / BOLD_non-adapted)) × 100) in the defined visual ROIs. There were no outliers for either the “line-dot-crossing task” or the BOLD-adaptation. For one visual area we found positive correlations between the “line-dot-crossing task” and BOLD-adaptation: V4, $r = .59$, $p \leq .01$; for the other visual areas no significant correlation or trend occurred; two-tailed, N = 11, Kendalls Tau-b (fig. 4b).

Furthermore we did not find any significant correlation between the adaptation index AI in V4 and the subject’s scores in the VVIQ or the degree of the induced TAE outside the scanner (adaptation index V4 and VVIQ $r = -.243$, $p = .33$, adaptation index V4 and TAE $r = .21$, $p = .3$, N = 11, Kendall-Tau-b), which underlines the specificity of the observed correlation. Thus, we were able to demonstrate that mental imagery, probed by the “line-dot crossing task”, can induce two related adaptation effects, the perceptual TAE as well as neural adaptation in visual cortex.

Discussion

We investigated whether the tilt after effect observed after the mental imagination of tilted lines has a correlate in orientation-selective neural adaptation. Participants were asked to generate tilted lines mentally, after which they had to decide on the orientation of physically presented lines. The effects of adaptation were tested with functional magnetic resonance imaging. There was evidence for a decreasing gradient of adaptation from areas V4 to V1 after mental imagery. Furthermore, the performance of a mental imagery task ("line-dot-crossing") inside the scanner correlated positively with the amount of neural adaptation in V4 and with the size of the TAE during the behavioural pre-experiment.

Impact of mental imagery on visual perception

First, we replicated the induction of a TAE by mental imagery (Mohr, Linder, Sireteanu, 2008). The present data support the influence of mental imagery on other visual illusions like the Müller-Lyer illusion (Berbaum & Chung, 1981) or the subjective visual vertical (SVV) judgment under body tilt (Mertz & Lepecq, 2001; Mast, Kosslyn & Berthoz, 1999). Furthermore, the strength of this perception bias was related to successful mental imagery operations in the line-dot-crossing task, designed to probe the efficacy of mental imagery. This result underlines that the present mental imagery task is a useful tool to investigate the influence of mental imagery on adaptation effects. The influence of mental imagery on visual perception and perceptual accuracy provides evidence for analogue coding of mental images (Kosslyn et al., 1995).

Impact of mental imagery on neural adaptation

Repetition of a stimulus with a given orientation leads to a decrease of neural activity in visual areas. This effect was primarily observed in V1 (Tootell et al, 1998; Liu, Larsson &

Carrasco, 2007). We did not find an adaptation effect in V1 after mental imagery of line orientations. Instead, a clear adaptation effect occurred in extrastriate regions V3-V3A/B and VP-V4, calculated by a random-effects whole-brain contrast. Analysis of the individual ROIs confirmed that the amount of adaptation decreases from V4 to V1. There are several possible explanations for this result. First, there is evidence that the amount of adaptation in visual areas depends on the duration of stimulus exposure (Boynton & Finney, 2003; Krekelberg, Boynton & van Wezel, 2006; Fang, Murray, Kersten & He, 2005, for adaptation to faces see also Fang, Murray & He, 2007). Fang et al. (2005) found a neural adaptation effect in V1-V4 after long-term adaptation to an oriented pattern (5 seconds re-adaptation).

However, only V3A and V4 showed this effect after less intensive short-term adaptation (1 second re-adaptation). In the present mental imagery experiment, we used a long-term adaptation design (mean re-adaptation = 19.5 seconds). Nevertheless, we assume that the experience of tilted lines generated by mental imagery is less intensive and stable in time than the perception of physical lines, which may explain that only neurons in higher visual areas showed adaptation.

An alternative explanation for the missing adaptation effect in V1 is supported by the existence of the described adaptation gradient. The effort to generate and maintain mental images often involves the PFC (Formisano et al., 2002; Goebel et al., 1998; Mazard, et al, 2002; Mohr, Goebel, & Linden, 2006; Trojano et al. 2004). The mental imagery of tilted lines might be based on a top-down modulation from prefrontal cortex that first enters extrastriate areas and is not strong enough to produce significant neural adaptation in V1. A similar gradient with stronger effects in higher visual areas was reported for imagined visual motion by Goebel et al., 1998. This speculation is supported by our findings that the correlation between the neural adaptation and mental imagery accuracy is strongest for V4. The better the subjects performed the mental imagery task inside the scanner, the more they recruited orientation selective neurons in this area during mental imagery. Thus, V4 seems to play a central role in the utilization of occipital cortex for the generation of mental images. Self-reports about imagery experience (VVIQ) were not related to adaptation in visual areas, so the best predictor for adaptation in V4 is indeed the performance in the mental imagery line-dot-crossing task inside the scanner. Another important issue in fMRI-adaptation designs is how to distinguish the difference between stimulus-specific reduction of the BOLD signal and a possible non-specific novelty effect evoked by the non-adapted stimulus. In the present study, the mismatch between the imagined orientation and the actual physical orientation in the non-adapted condition could have been a salient change, which by itself might have caused a difference in the BOLD-response between the two conditions. However, we show that the neural response to the adapted stimulus in V4 decreases over time. Conversely, the BOLD-response to the non-adapted stimulus was not affected by the experimental stimulation over time, ruling out that the BOLD-adaptation was solely due to an increased BOLD-response to the non-adapted stimulus. Furthermore, non-specific novelty effects would have been reflected in activation of a wider network of frontal and parietal areas commonly associated with mismatch detection (Linden, 2005).

The amount of BOLD-adaptation in our experiment was highly significant for V4. The effect size (Cohen's *d* = .41*)*) indicates a medium effect of adaptation, but this effect was smaller in comparison to most fMRI adaptation effects after presentation of real physical stimuli at 3 Tesla (present study: V4 = .052 mean absolute %BOLD-signal change due to adaptation, and around .1 % for subjects with good mental imagery ability, corresponding to a relative change in adaptation of the BOLD-signal of 15% for good performers). For example, Larsson, Landy & Heeger (2006) demonstrated adaptation effects from .1 to .5 mean absolute % BOLD-signal over different visual areas. Montaser-Kouhsari et al. (2007) reported adaptation around .05 mean absolute %BOLD-signal change to physical presented illusory contour adapters in V1, more comparable to our signal changes induced by mental imagery in V4. However, it is important to notice that in the present adaptation design no physical adaptation stimuli were shown. It is known that sensory input activates visual areas more strongly than mental imagery (Ganis, Thompson & Kosslyn, 2004; Goebel et al., 1998). The present design is more comparable to cognitive experiments in the field of mental imagery and visual working memory. In such experiments, absolute %BOLD- signal changes at .05 only due to cognitive manipulation are common effects. For example Cui et al. (2007) demonstrated a mean activation of visual areas by mental imagery of .035% (absolute BOLD signal change, ranging from .11 to -.06), and Tomasi et al. (2007) showed a modulation of PFC activity (area 9, 46) by working memory of around .05% mean absolute BOLD signal change.

In summary, our results suggest that the mental imagery of tilted lines can bias the perception of orientations analogous to the TAE induced by prolonged inspection of tilted physical gratings. Furthermore, the results suggest that mental imagery of tilted lines used orientation-selective neurons located mainly in the extrastriate cortex, possibly recruited by top-down control and perhaps in conjunction with further attention processing. Our data are thus compatible with models of a picture-like analogue coding of mental images, based on the recruitment of the visual cortex (Kosslyn, & Ochsner, 1994).

An interesting direction of future research would be the investigation of psychophysical and neuroanatomical correlates of adaptation through mental imagery of more complex visual information like faces, motion or bodies. We assume that the recruitment of specialized neurons in the visual processing pathway and their adaptation is a general mechanism of mental imagery.

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References

Boynton, G.M., Finney, E.M., 2003. Orientation-specific adaptation in human visual cortex. J Neurosci. 23, 8781–8787.

Cavanna, A.E., Trimble, M.R., 2006. The precuneus: a review of its functional anatomy and behavioural correlates. Brain 129, 564-583.

Cruickshank, A.G., Schofield, A.J., 2005. Transfer of tilt after-effects between second-order cues. Spat Vis. 18, 379-397.

Cui, X., Jeter, C.B., Yang, D., Montague, P.R., Eagleman, D,M., 2007. Vividness of mental imagery: individual variability can be measured objectively. Vision Res. 47, 474-478.

DeYoe, E.A., et al, 1996. Mapping striate and extrastriate visual areas in human cerebral cortex. Proc Natl Acad Sci USA. 93, 2382–2386.

Engel, S.A., Glover, G.H., Wandell, B.A., 1997. Retinotopic organization in human visual cortex and the spatial precision of functional MRI. Cereb Cortex. 7: 181–192.

Fabiani, M., Friedman, D., 1995. Changes in brain activity patterns in aging: the novelty oddball. Psychophysiology, 32, 579-594.

Fang, F., Murray, S.O., He, S., 2007. Duration-dependent FMRI adaptation and distributed viewer-centered face representation in human visual cortex. Cereb Cortex., 17, 1402-1411.

Fang, F., Murray, S.O., Kersten, D., He, S., 2005. Orientation-tuned fMRI adaptation in human visual cortex. J Neurophysiol. 94, 4188–4195.

Friston, K.J. et al, 1995. Statistical parametric maps in functional imaging: a general linear approach. Hum Brain Mapp. 2, 189–210.

Friston, K.J. et al, 1998. Event-related fMRI: characterizing differential responses. Neuroimage 7, 30-40.

Formisano, E., Linden, D.E., Di Salle, F., Trojano, L., Esposito, F., Sack, A.T., Grossi, D., Zanella, F.E., Goebel, R., 2002. Tracking the mind's image in the brain I: time-resolved fMRI during visuospatial mental imagery. Neuron 3, 185-194.

Ganis, G., Thompson, W.L., Kosslyn, S.M., 2004. Brain areas underlying visual mental imagery and visual perception: an fMRI study.Brain Res Cogn Brain Res. 20, 226-241.

Genovese, C.R., Lazar, N.A., Nichols, T., 2002. Thresholding of statistical maps in functional neuroimaging using the false discovery rate. Neuroimage 15, 870–878.

Ghaem O. et al, 1997. Mental navigation along memorized routes activates the hippocampus, precuneus and insula. Neuroreport 8, 739–744.

Gibson, J.J., Radner, M., 1937. Adaptation, after-effect and contrast in the perception of tilted lines. J Exp Psychol. 20, 453-467.

Goebel, R., Khorram-Sefat, D., Muckli, L., Hacker, H., Singer, W., 1998. The constructive nature of vision: direct evidence from functional magnetic resonance imaging studies of apparent motion and motion imagery. Eur J Neurosci. 10, 1563-1573.

Harris, J.P., Calvert, J.E., 1989. Contrast, spatial frequency, and test duration effects on the tilt after effect: Implications for underlying mechanisms. Vision Research 29, 129–135.

Johnson, M.R., Mitchell, K.J., Raye, C.L., D'Esposito, M., Johnson, M.K., 2007. A brief thought can modulate activity in extrastriate visual areas: Top-down effects of refreshing just-seen visual stimuli. Neuroimage 37, 290–299.

Kosslyn, S.M., Ganis, G., Thompson, W.L., 2001. Neural foundations of imagery. Nat Rev Neurosci. 2, 635-642.

Kosslyn S.M., Ochsner, K.N., 1994. In search of occipital activation during visual mental imagery. Trends Neurosci. 17, 290-292.

Krekelberg, B., Boynton, G.M., van Wezel, R.J., 2006. Adaptation: from single cells to BOLD signals. Trends Neurosci. 29, 250-256.

Larsson. J., Landy, M.S., Heeger, D.J., 2006. Orientation-selective adaptation to first- and second-order patterns in human visual cortex. J Neurophysiol. 95, 862-881.

Linden, D.E., 2005. The p300: where in the brain is it produced and what does it tell us? Neuroscientist 11, 563-576.

Liu, T., Larsson, J., Carrasco, M., 2007. Feature-based attention modulates orientation-selective responses in human visual cortex. Neuron 55, 313-323.

Marks, D.F., 1973. Visual imagery differences in the recall of pictures. Br J Psychol. 64, 17-24.

Mazard, A. et al, 2002. Impact of fMRI acoustic noise on the functional anatomy of visual mental imagery. J Cogn Neurosci. 14, 172-186.

Mohr, H.M., Goebel, R., Linden, D.E., 2006. Content- and task-specific dissociations of frontal activity during maintenance and manipulation in visual working memory. J Neurosci. 26, 4465-4471.

Mohr, H.M., Linder, N.S., Sireteanu, R., 2008. Orientation-specific adaptation to mentally generated lines. Perception, ECVP abstract. 37, 9.

Montaser-Kouhsari, L., Landy, M.S., Heeger, D.J., Larsson, J., 2007. Orientation-selective adaptation to illusory contours in human visual cortex. J Neurosci. 28, 2186-2195.

Muckli, L., Kohler, A., Kriegeskorte, N., Singer, W., 2005. Primary visual cortex activity along the apparent-motion trace reflects illusory perception. PLoS Biol. 3, e265.

O'Craven, K.M., Kanwisher, N., 2000. Mental imagery of faces and places activates corresponding stimulus-specific brain regions. J Cogn Neurosci. 12, 1013-1023.

Tomasi, D., Chang, L., Caparelli, E.C., Ernst, T., 2007. Different activation patterns for working memory load and visual attention load. Brain Res. 1132, 158-165.

Sereno, M.I. et al, 1995. Borders of multiple visual areas in humans revealed by functional magnetic resonance imaging. Science 268, 889–893.

Suchan, B. et al, 2002. Hemispheric dissociation of visuo-spatial processing and visual rotation. Cogn Brain Res. 136, 533–544.

Tanji, J., Hoshi, E., 2008. Role of the lateral prefrontal cortex in executive behavioural control. Physiol Rev. 88, 37-57.

Tootell, R.B. et al, 1998. Functional analysis of primary visual cortex.V1 in humans. Proc Natl Acad Sci USA. 95, 811-817.

Tootell, R.B., Reppas, J.B., Dale, A.M., Look, R.B., Sereno, M.I., Malach, R., Brady, T.J., Rosen, B.R., 1995. Visual motion aftereffect in human cortical area MT revealed by functional magnetic resonance imaging. Nature 11,139-141.

Trojano, L., Linden, D.E.J., Formisano, E., Goebel, R., Sack, A.T., Di Salle, F., 2004. What clocks tell us about the neural correlates of spatial imagery. European Journal of Cognitive Psychology 16, 653-672.

Wenderoth, P., Smith, S., 1999. Neural substrates of the tilt illusion. Aust N Z J Ophthalmol. 27, 271-274.

Figure captions

Fig. 1. Example of a trial in the fMRI experiment. During mental imagery the subjects were instructed to mentally generate 4 lines connecting the dots tilted 15° clockwise from vertical (V, letter not presented in the experiment) or horizontal (H, letter not presented in the experiment). After pre-adaptation, a dot was presented inside the circle. The subjects had to decide if the mentally generated lines crossed the presented dot. Afterwards, subjects performed an orientation decision (horizontal-vertical).

Fig. 2. The effect of mental imagery on the tilt after-effect ($N = 15$). The figure shows the difference between the perceived and the objective vertical (0°) orientation after the mental imagery of +15° or -15° tilted lines from vertical. Error bars are ±1 SEM across observers.

Fig. 3. A; Random-effects GLM for “adapted” versus “non-adapted” ($N = 12$). Below, time courses of clusters covering bilateral V3-V3a/b and VP-V4. Red, “adapted“; yellow, “non-adapted“; $p < 0.001$, uncorrected, visualized on the inflated surface of a subject’s brain. **B**; Time courses for bilateral V4, during the beginning and the ending of the experimental stimulation. Red, “adapted“; yellow, “non-adapted“.

Fig. 4. A; Amount of BOLD-adaptation induced by mental imagery for the visual areas V1-V4, adaptation index AI = *(1- (BOLD_adapted / BOLD_non-adapted))* × 100. A highly significant decreasing linear trend could be found for the adaptation in the visual areas from V4-V1, $F(1,10) = 17.1$, $p < .01$. **B**; Correlation of the AI in bilateral V4 and the percentage of correct decisions in the “Line-dot crossing task”, a test of the subjects’ ability to mentally generate a tilted line.

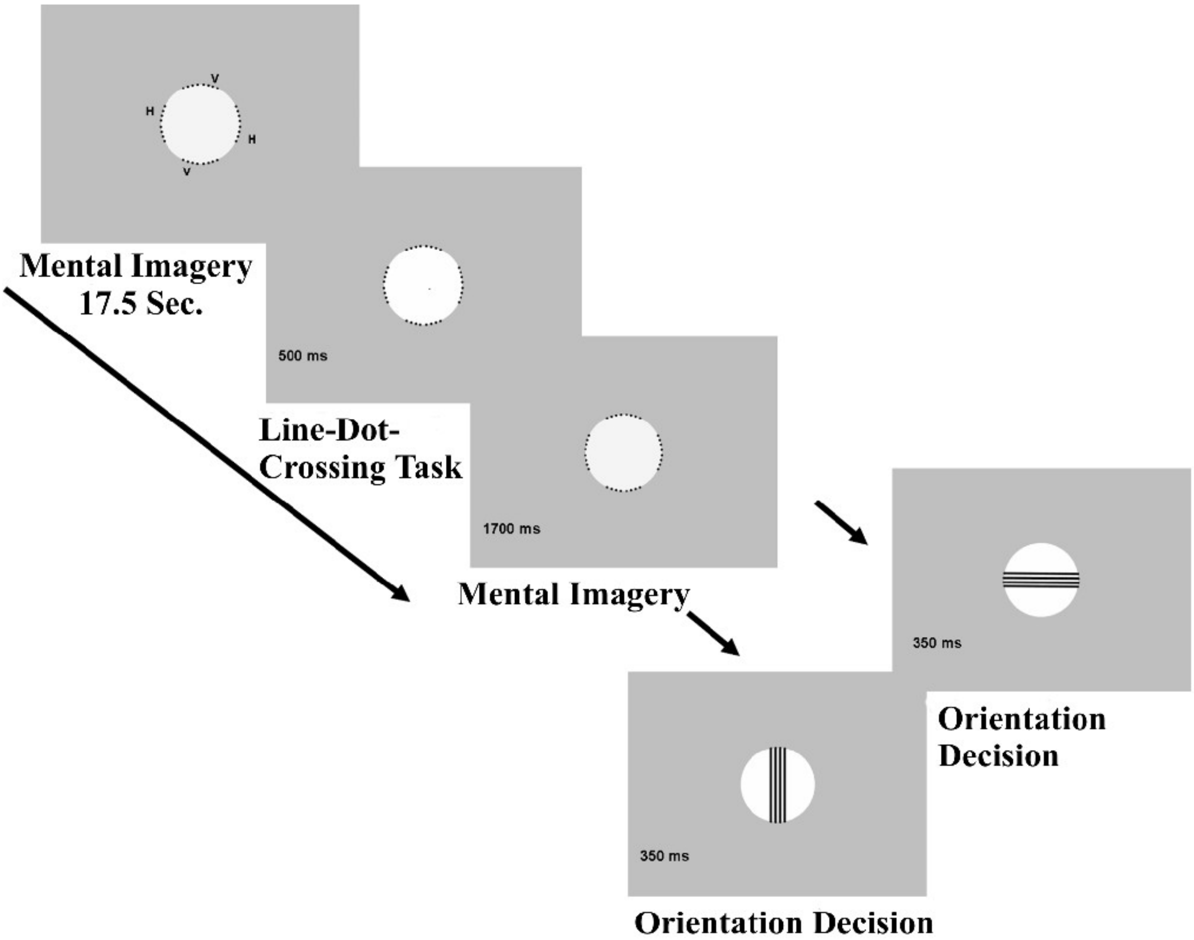
Tables

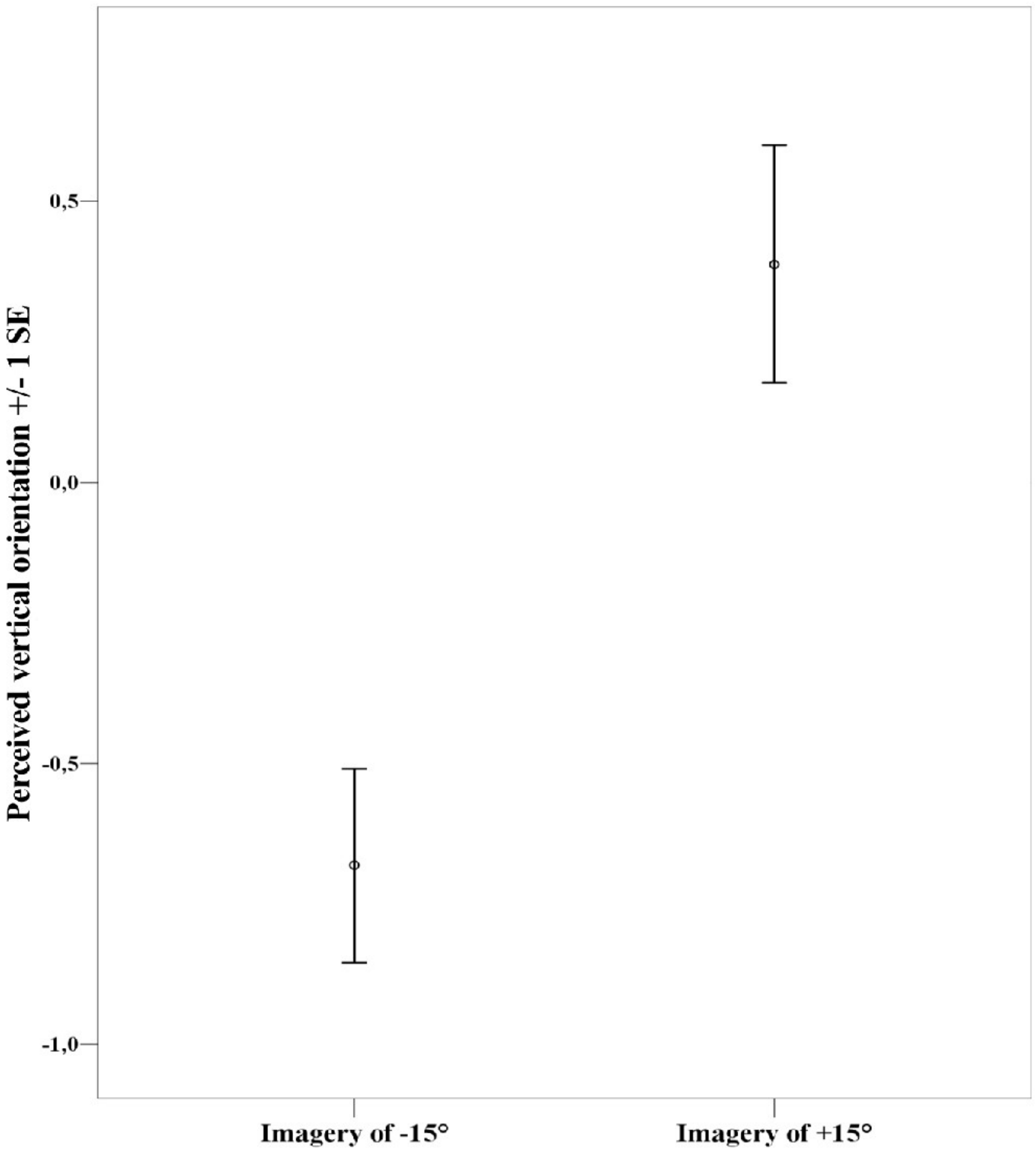
Table 1.

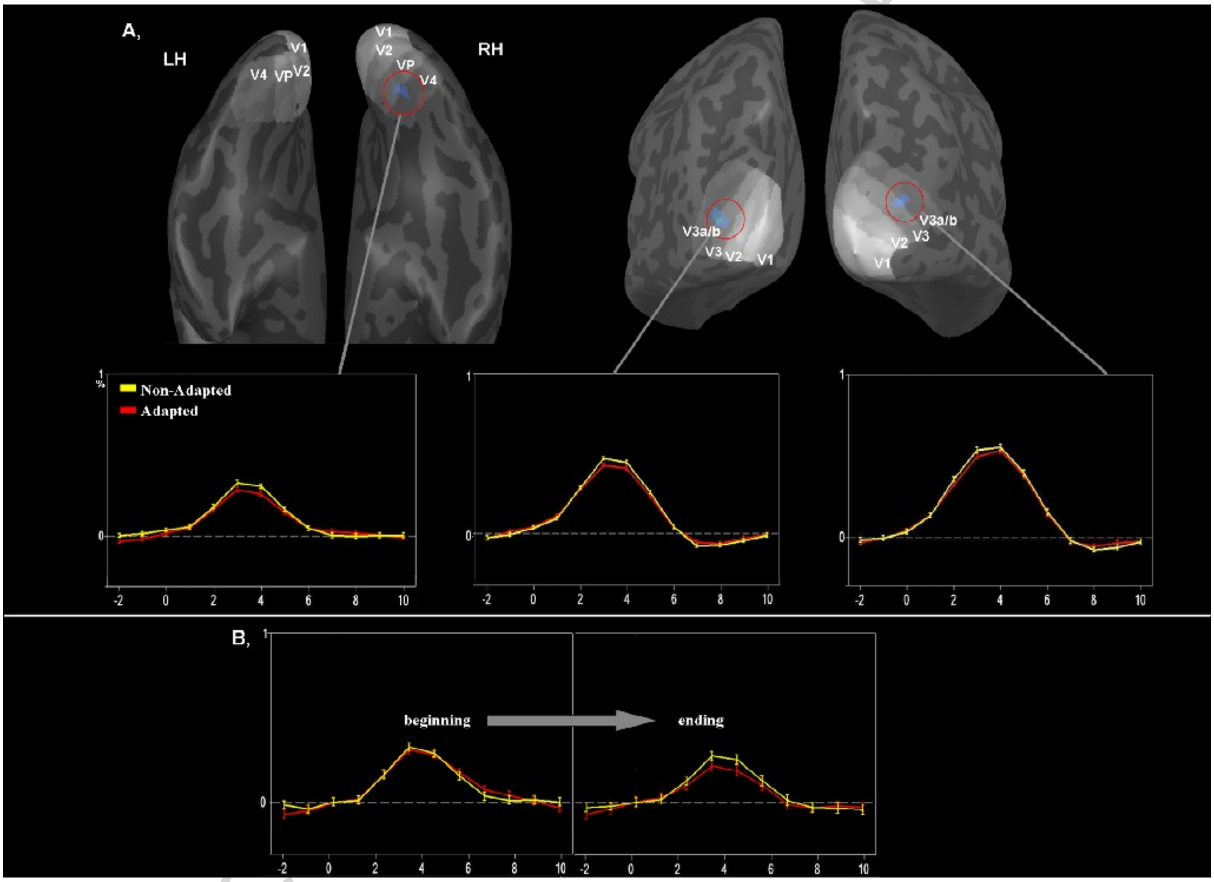
Regions associated with contrast of interest “adapted” < “non-adapted”.

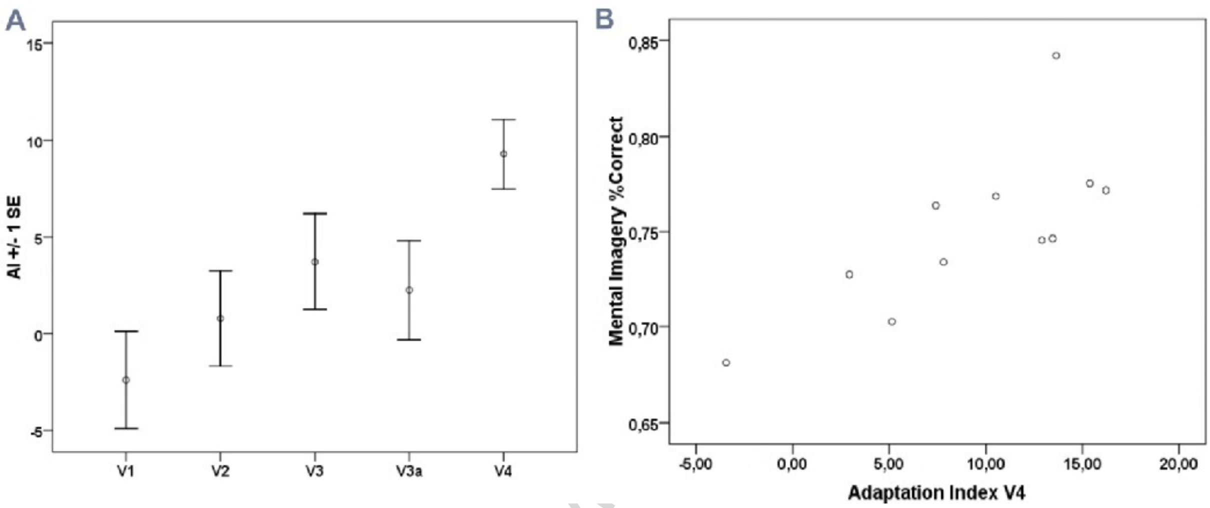
Area	**Hem.**	**x**	**y**	**z**	Cluster size
Middle occipital Gyrus / BA 18 /V3-V3a/b	LH	-24	-88	3	204
Middle occipital Gyrus / BA 19/ V3-V3a/b	RH	27	-87	11	30
Lingual Gyrus / BA 18/VP-V4	RH	20	-77	-7	20

Centers of mass and cluster sizes Hem. = hemisphere, (LH = left hemisphere, RH = right hemisphere); *x, y, z* = Talairach coordinates; Cluster size is provided in mm^3, random effect, $p < .001$, uncorrected, $N = 11$. For the contrast “adapted” > “non-adapted” no significant activation occurred at the given threshold.


V
H
H
V
Mental Imagery
17.5 Sec.
500 ms
Line-Dot-
Crossing Task
1700 ms
Mental Imagery
350 ms
Orientation
Decision
350 ms
Orientation Decision


Perceived vertical orientation +/- 1 SE
0,5
0,0
-0,5
-1,0
Imagery of -15°
Imagery of +15°


A,
LH
RH
V1
V2
V4
VP
V1
V2
VP
V4
V3a/b
V3
V2
V1
V3a/b
V3
V2
V1
1
%
0
Non-Adapted
Adapted
-2
0
2
4
6
8
10
B,
beginning
ending


A
15
10
5
0
-5
AI +/- 1 SE
V1
V2
V3
V3a
V4
B
0,85
0,80
0,75
0,70
0,65
Mental Imagery %Correct
-5,00
0,00
5,00
10,00
15,00
20,00
Adaptation Index V4