

Delayed discrimination of spatial frequency for gratings of different orientation: behavioral and fMRI evidence for low-level perceptual memory stores in early visual cortex

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Received: 3 September 2007 / Accepted: 1 April 2008 / Published online: 19 April 2008
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Abstract The concept of perceptual memory refers to the neural and cognitive processes underlying the storage of specific stimulus features such as spatial frequency, orientation, shape, contrast, and color. Psychophysical studies of perceptual memory indicate that observers can retain visual information about the spatial frequency of Gabor patterns independent of the orientation with which they are presented. Compared to discrimination of gratings with the same orientation, reaction times to orthogonally oriented gratings, however, increase suggesting additional processing. Using event-related fMRI we examined the pattern of neural activation evoked when subjects discriminated the spatial frequency of Gabors presented with the same or orthogonal orientation. Blood-oxygen level dependent BOLD fMRI revealed significantly elevated bilateral activity in visual areas (V1, V2) when the gratings to be compared had an orthogonal orientation, compared to when they had the same orientation. These findings suggest that a change in an irrelevant stimulus dimension requires additional processing in primary and secondary visual areas.

The finding that the task-irrelevant stimulus property (orientation) had no significant effect on the prefrontal and intraparietal cortex supports a model of working memory in which discrimination and retention of basic stimulus dimensions is based on low-level perceptual memory stores that are located at an early stage in the visual process. Our findings suggest that accessing different stores requires time and has higher metabolic costs.

Keywords Early visual cortex · fMRI · Perceptual memory · Delayed discrimination

Introduction

The concept of perceptual memory refers to the neural and cognitive processes underlying the storage of sensory information along such basic stimulus dimensions as spatial frequency, orientation, and motion, and is conventionally assessed in delayed discrimination tasks with a variable time interval between the two stimuli to be discriminated. The concept is related to, but not identical with the concept of visual working memory, referring to the number of visual items or categories that can be retained (Luck and Vogel 1997; Marois and Ivanoff 2005; Xu and Chun 2006), rather than the precision of the stimulus retention (Magnussen 2000; Magnussen and Greenlee 1999; Pasternak and Greenlee 2005). Brain imaging studies of visual perceptual short-term memory have revealed selective activation in occipital and parietal areas, suggesting that early cortical regions are involved (Cornette et al. 2001; Greenlee et al. 2000). The present paper reports direct evidence for such low-level perceptual memory mechanisms.

Psychophysical studies have shown, that the accuracy of delayed spatial discrimination is not affected by manipula-

Supported by: BMBF Project “Visuospatial Cognition” and Norwegian Research Council.

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tions of irrelevant stimulus dimensions. For example, spatial frequency discrimination thresholds were similar for parallel and orthogonal test and reference stimuli (Bradley and Skottun 1984; Magnussen et al. 1998). However, in the spatial frequency discrimination task, the choice reaction times are elevated for orthogonal as compared to parallel gratings with reaction times increasing linearly with orientation difference (Magnussen et al. 1998), suggesting that orientation and spatial frequency are not independently processed for perceptual discrimination. These findings are consistent with the hypothesis (Magnussen 2000; Magnussen and Greenlee 1999) that the delayed discrimination of basic visual features is based on the output of channels tuned to spatial frequency and orientation and performed by a serial search process operating in a neural network of the kind postulated by modular models of orientation and spatial frequency representation in V1, where anatomical and functional distance are correlated (DeValois and DeValois 1990; Maffei and Fiorentini 1977). A systematic effect of angular separation on reaction time for spatial frequency discrimination suggests that access to such feature-specific stores occurs as a serial process. Comparisons within mechanisms activated by both reference and test patterns would be fast, whereas comparisons across mechanisms would take place serially and require more time. Thus, the serial search time is related to distance in terms of similarity with respect to spatial dimensions rather than to the number of stimuli. The functional organization of representation of spatial frequency and orientation in the visual cortex, in which anatomical and functional distance are correlated, could yield equivalent effects as those evoked by display set size in visual and memory search tasks.

In the present paper we report an fMRI experiment designed to test the concept of cortical serial search within a network of channels tuned to spatial frequency and orientation (Magnussen 2000; Magnussen and Greenlee 1999). We investigated whether early visual cortex, or higher cognitive areas, are involved in the additional processing of the task-irrelevant stimulus properties indicated by prolonged reaction times for the discrimination of spatial frequencies with large orientation differences. We used functional MRI in a 3-T head scanner to determine the neural correlates of

delayed spatial frequency discrimination of centrally presented Gabor stimuli that either had the same or a different orientation. Accuracy and choice reaction time were recorded, allowing a comparison of the two response indicators of discrimination and memory.

Method

Subjects

Fourteen right-handed adults (5 male, 9 female), aged between 20 and 27 years (mean = 22 years), participated in the study. All participants gave their written informed consent. All had normal or corrected-to-normal vision and reported no prior psychiatric or neurological impairments.

Stimuli

Stimuli were created with Matlab 6.5.1 software (Math Works Inc., Natick, MA, USA) and presented with Presentation 9.13 software (Neurobehavioral Systems Inc., Albany, CA, USA). Stimuli were back-projected on a screen inside the scanner with a D-ILA LCD-projector (JVC Corp., Japan) with a frame refresh rate of 60 Hz. The screen size subtended $16.4^\circ \times 21.7^\circ$ of visual angle. Gabor stimuli had a diameter of approximately 6.5° of visual angle and were presented in center of the screen. Gabor patches had a maximum contrast close to 100%. The contrast of the Gabors was tapered with a Gaussian kernel (Gauss constant: 1.3°).

Procedure

In the experiment the participants had to decide whether two Gabor stimuli, which were presented sequentially and separated by a delay period, had the same or a different spatial frequency. The inter-stimulus interval between the reference and the test stimulus was 8 seconds. An example stimulus pair is depicted in Fig. 1 for a “different” trial.

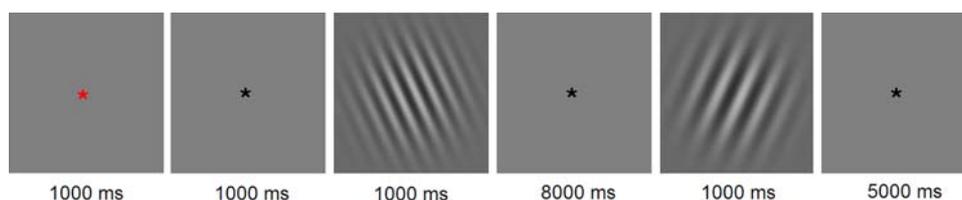


Fig. 1 Schematic depiction of a trial from the condition in which the test and the reference stimulus differed in orientation. Trials started with a red asterisk that informed subjects about the onset of a stimulus pair. After this a fixation point appeared that remained in the center of the screen for the rest of the trial. This was followed by the reference

Gabor that was shown in the center of the screen. The 8-s delay interval was presented afterward, followed by the test Gabor. During the following interval, the subject had to judge if the test and the reference stimulus had the same or a different spatial frequency and press the corresponding button

We measured spatial frequency discrimination for test and reference stimuli that matched or differed in orientation. The gratings either had the same spatial frequency or differed by $\pm 15\%$ across a frequency range of 3–9 c/deg (i.e., trial-by-trial jitter). The gratings were centered within a frame that subtended 13° of visual angle. In 50% of all trials both the reference and the test stimulus had the same spatial frequency, on the other trials the reference and test stimuli differed in spatial frequency. On half the trials both the reference and the test stimulus had the same orientation, on the other trials the reference and test stimuli had an orthogonal orientation. Trials were presented in random order and subjects were instructed to maintain central fixation throughout the experiment.

At the beginning of each trial, a red asterisk appeared for 1,000 ms in the center of fixation. This was followed for 1,000 ms by a black fixation point in the center of the screen. Then the reference grating appeared for 1,000 ms in center of the screen. During the following inter-stimulus interval of 8 s, only the fixation point appeared on the screen. After this the test grating appeared in the same location as the reference Gabor for 1,000 ms. Subjects then had to press a button with the index finger of their right hand if they thought that the test and the reference grating had the same spatial frequency. Another button was pressed with the middle finger of the right hand if they thought that the two spatial frequencies differed. Participants had been instructed to respond as quickly and as accurately as possible. After the offset of the test Gabor, a fixation point appeared for 5,000 ms. A schematic depiction of a trial in which the reference and the test stimulus differed, is depicted in Fig. 2.

Prior to the fMRI experiment subjects participated in a training session outside the scanner ($n = 32$ trials). In the fMRI experiment, each subject participated in one session that consisted of a total of 96 trials. Subjects responded by pressing the buttons of a Lumitouch (Photon Control, Burnaby, Canada) optical response device with their index

finger and the middle finger of their right hand. Reaction time and accuracy data were recorded and stored for offline analysis.

fMRI procedures

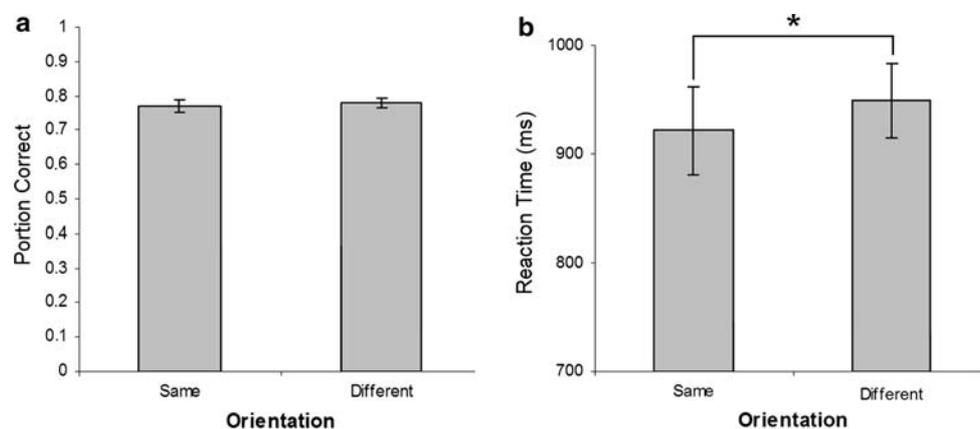
Blood-oxygen-level-dependant imaging data were acquired with a 3-Tesla Siemens Allegra head scanner (Siemens Inc., Erlangen, Germany) at the University of Regensburg. The scanner acquired echo-planar-imaging (EPI) sequences using fast gradients. A standard one-channel head coil was used. During T2* image acquisition 30 slices (whole brain) were scanned in ascending order. Time-to-repeat (TR) was 1,720 ms. Time-to-echo (TE) was set at 30 ms, with a flip angle of 90° . Voxel-size was set to $3 \times 3 \times 3$ mm. The field of view measured 192×192 mm. Trials in the experimental paradigm were synchronized with scanner pulses. Anatomical T1-weighted images were obtained using a MPRAGE pulse sequence (Magnetization Prepared Rapid Gradient Echo) with time-to-repeat (TR) of 2,300 ms, a time-to-echo (TE) of 3.93 ms, and a flip angle of 12° . A total of 176 slices were scanned, with isotropic voxels sized $1 \times 1 \times 1$ mm. The field of view had a size of 256×256 mm.

Data analysis

Reaction time and accuracy data were analyzed statistically with SPSS for Windows 12.0 software (SPSS Inc., Chicago, IL, USA). A repeated-measures ANOVA and a *T* test was conducted at a significance level of $P \leq 0.05$.

Images were pre-processed and statistically analyzed with SPM2, (<http://www.fil.ion.ucl.ac.uk/spm>), which runs in Matlab. Prior to pre-processing all obtained imaging data in DICOM format were transformed to ANALYZE file format. Functional data were slice timed, realigned, and co-registered to the anatomical image. Images were then normalized to a standard SPM2 template (Montreal

Fig. 2 **a** Mean accuracy measures for the conditions with “same” and “different” orientation. There is no statistically significant difference related to the orientation ($P = 0.688$). **b** Mean reaction times for the conditions with “same” and “different” orientation. There is a statistically significant difference related to the orientation, $P \leq 0.05$



Neurological Institute (MNI) Template) and smoothed with an 8-mm full-width half maximum (FWHM) isotropic Gaussian kernel.

Statistical evaluation consisted of modeling the onset times of the test Gabor-stimuli as events on individual first level. These onsets were modeled separately for each of the 2 conditions if the correct response was given. The relevant conditions were contrasted using T-statistics, generating the contrast images for second level evaluation.

For the random-effects group level statistics, *T* value maps were calculated with appropriate contrast images. The statistical maps were thresholded on clusterlevel at $P \leq 0.05$ (corrected for multiple comparisons, cluster-defining threshold $t = 2$). The reason we chose this threshold was the low *T* values detected at each individual voxel. We expected this finding because the differences between conditions were marginal since the paradigm had been optimized to render stimuli and task as identical as possible in order to attribute differing brain activity only to the difference in orientation of the test and reference stimulus. Nonetheless we expected a significant albeit very subtle effect of the difference in orientation, in a possibly spatially extended occipital area. We thus concentrated on cluster analysis in which many voxels in larger areas show small but similar differences. Also the cluster defining threshold is $P \leq 0.05$ corrected for multiple comparisons. Since it is a random effects analysis it is still very conservative. To visualize the results, the activations were overlaid on a normalized rendered image from one of the subjects.

Results

Behavioral data

The computation of each individual's performance revealed that all participants were able to discriminate the relevant stimuli reasonably well. Mean accuracy (portion of correct responses) for the two conditions was as follows: "same orientation": 0.77 (standard error of the mean, SE = 0.020); "orthogonal orientation": 0.78 (SE = 0.019); The results of a *T* test revealed no significant effect of the stimulus orientation on accuracy, $P = 0.688$.

Reaction times were computed for correct trials only and were as follows: same orientation, 922 ms (SE = 39.570 ms); different orientation: 948 ms (SE = 32.999 ms). A pair wise t-test revealed a significant effect for the factor orientation, $P \leq 0.05$. Accordingly, reaction times in the "same orientation" condition were significantly lower than in the "orthogonal orientation" condition in agreement with earlier psychophysical results (Magnussen et al. 1998), although the overall size of the effect is smaller. The reason why the reaction time differences in our experiment are

smaller is probably related to the fact that in the Magnussen et al. (1998) experiments the stimuli varied across four different orientations. This type of increased uncertainty/noise is likely to affect the memory performance and increase reaction time effects (Magnussen et al. 1996). The portions of correct responses and reaction times for the two conditions (averaged over all participants) are depicted in Fig. 2a and b.

The results of the present study confirm the previous behavioral findings (Bradley and Skottun 1984; Magnussen et al. 1998). First, the accuracy of delayed spatial discrimination is not affected by manipulations of irrelevant stimulus dimensions; spatial frequency discrimination thresholds are similar for parallel and orthogonal test and reference stimuli. Second, compared to discrimination of gratings with the same orientation, reaction times to orthogonally oriented gratings increase. The results show that accuracy and reaction time are uncorrelated measures of performance, suggesting that orientation and spatial frequency are not independently processed.

Functional MRI data

The contrast of the BOLD response associated with the presentation of the test stimulus to the intrinsic baseline led to bilateral activations in the dorsolateral prefrontal cortex (DLPFC), parietal lobe, lateral occipital cortex and early visual cortex, with a right hemispheric preponderance for the frontal and parietal regions. For our purposes, we focus on the comparison of activation across the two experimental conditions. The blood-oxygen level dependent (BOLD) fMRI revealed significant elevated activity bilaterally in visual areas V1 and V2 (BA 17 and BA 18) when the gratings to be compared had an orthogonal orientation, compared to when they had the same orientation. The left hemispheric cluster had its maximum at the Talairach coordinates 16-82-8 (cluster size 1,866 voxels) and the right hemispheric at the Talairach coordinates 46-58-2 (cluster size 1,338). No other brain areas showed a significant difference at this threshold. This differential activity, representing the mean differential contrasts for all participants, is depicted on a structural brain image of one of the subjects in Fig. 3. No significant activity was found for the inverse contrast in which we compared the activity arising in the same > different condition. To further elucidate the finding that parietal and frontal cortex are active during the presentation of the test stimulus, but not differentially sensitive for the orientation of the gratings, we conducted a region of interest analysis using "Marsbar" (Brett et al. 2002). Based on the activation patterns elicited by the test stimulus (parallel and orthogonal orientations) in comparison to the implicit baseline, we selected activation maxima of BOLD clusters in the frontal cortex (Brodmann area 46, Talairach

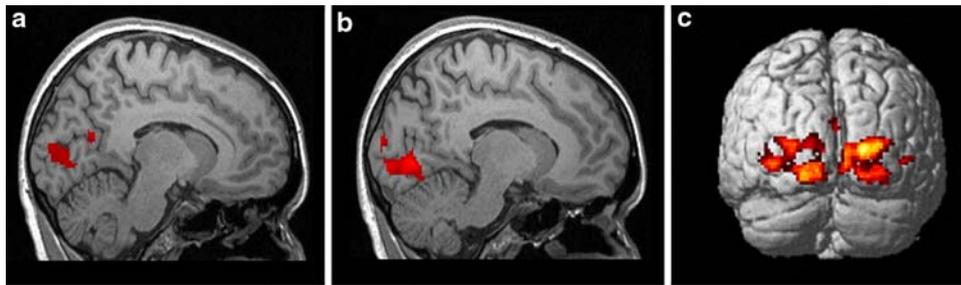


Fig. 3 Results of the event-related, random-effects group-analysis. Brain areas showing significant activation in the contrast “different orientation > same orientation” are shown by color-coded overlays. Significant clusters surpassing a threshold of $P \leq 0.05$ (corrected for

multiple comparisons, cluster-defining threshold $t = 2.0$) are presented. T values are overlaid onto an **a** MNI-normalized sagittal slice (Talairach plane $x = 10$), **b** MNI-normalized sagittal slice (Talairach plane $x = -10$), **c** MNI-normalized rendered template

coordinates 48, 42, 18), parietal cortex (Brodmann area 40, Talairach coordinates 44, -48 , 42) and occipital cortex (Brodmann area 18, Talairach coordinates 23, -89 , 6) as the center of three sphere-shaped regions of interest (ROI), with a diameter of 10 mm each. Right hemispheric ROI were chosen because of the stronger BOLD signal for the contrast ‘test stimulus > baseline’ on this side of the brain. The BOLD signal of the voxels in each ROI was averaged and the relative change of BOLD signal was computed in comparison to the average activity in these ROI for the entire fMRI measurement. The statistical comparison of the conditions with parallel and orthogonal test and reference stimuli only reached significance in the occipital ROI (See Fig. 4), thus confirming the results of the whole brain GLM analysis. We further conducted a linear correlation analysis comparing the differences in reaction time for the two conditions with differences in BOLD signal in the two occipital ROI for each individual subject. The results indicated that that the occipital BOLD activity correlated significantly with the differences in reaction time ($r = 0.796$, $P \leq 0.001$). This positive correlation between the difference in BOLD responses in the parallel and orthogonal orientation condi-

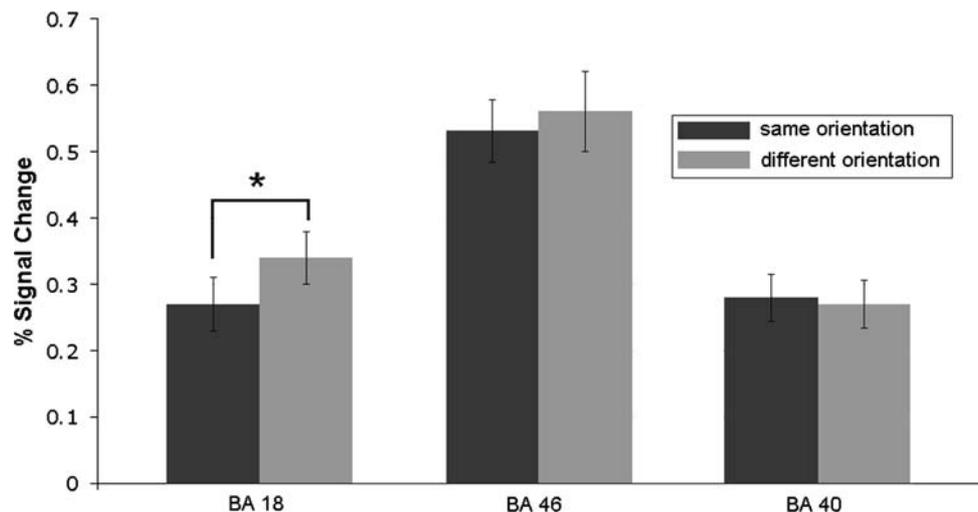
tions suggest the involvement of these brain regions in the memory task.

Discussion

The activation of low-level visual areas and the fact that no prefrontal and parietal activation was observed supports a model of perceptual memory in which discrimination and retention of basic stimulus dimensions is based on low-level perceptual memory stores that are located at an early stage in the visual process. It suggests that the retrieval of high-fidelity visual information requires activation of different stores, which in turn require more time and higher metabolic costs even if an irrelevant stimulus dimension has been changed.

Whereas the behavioral results of the present are compatible with other accounts of perceptual short-term memory (Wilken and Ma 2004), the functional imaging results support the model, so far based on behavioral data (Magnussen 2000; Magnussen and Greenlee 1999), that delayed discrimination is based on the output of channels

Fig. 4 Percent BOLD-signal change for Brodmann areas 18, 40 and 46 averaged separately over the two conditions (Error bars ± 1 SE). Only area 18 shows a statistically significant difference with respect to the orientation of the test grating ($P \leq 0.05$, paired t test with Bonferroni correction)



tuned to spatial frequency and orientation. A serial search process operates on a neural network of the kind postulated by modular models of orientation and spatial frequency representations in early visual areas, where anatomical and functional distance are correlated (DeValois and DeValois 1990; Maffei and Fiorentini 1977).

The finding that the task-irrelevant stimulus property “orientation” had no effect on the activity of the prefrontal and parietal cortices indicates that no mental rotation had been performed by the subjects, which would have led to activations in prefrontal and parietal regions (Hugdahl et al. 2006). The concept of mental rotation derives from the relationship between angular mismatch and reaction times and suggests a process that is analogous to physical rotation (Cooper and Shepard 1973); in such experiments observers report that they consciously perform a mental rotation task to compensate for the stimulus differences. No such strategies seem required in the selection of information on a single dimension like in the present experiments. There is also evidence from a lesion study indicating that mental rotation and orientation-invariant object recognition are dissociable processes (Farah and Hammond 1988).

Furthermore, the effect cannot be explained by neural adaptation (Grill-Spector and Malach 2001; Krekelberg et al. 2006), since adaptation effects in early visual cortex are very transient and would not survive an inter-stimulus interval of 8 s. Boynton and Finney (2003) used sinusoidal gratings to investigate adaptation effects with fMRI. Subjects viewed the gratings for 1 s, with inter-stimulus intervals of 0.125, 1, 3, and 7 s. The stimulus orientation could be, like in our experiment, either vertical or horizontal. Pairs had either the same orientation or were oriented orthogonally. They found that even after the short interval of 0.125 s, the relative orientation of the second stimulus had no differential effect on the fMRI response in V1 and V2. However, the amount of adaptation increased along the hierarchy of visual cortical areas (i.e., V3 and V4v). They found that psychophysically the adaptation had an effect on the detection threshold, which was evident up to 3 s after the offset of the adapting stimulus, but not after 7 s. Kourtzi and Huberle (2005) used closed contours rendered with Gabor elements, which varied in local orientation features, presented for only 300 ms. In contrast to Boynton and Finney, they were able to detect an adaptation effect in V1 and V2 but only for inter-stimulus intervals of 100 ms, but not 400 ms. Giving these results we would not expect any adaptation effects in the early visual cortex for our experiment, using an 8-s inter-stimulus interval and a stimulus duration of just 1 s. Furthermore, as reported in the results section we found the activity in the visual areas to be strongly correlated with the differences in reaction time, which implies a functional involvement in the memory process may be the cause for the difference in BOLD signal and not simply an adaptation effect.

Finally, the fact that activation differences in the parallel versus orthogonal grating comparisons were confined to low-level visual areas strongly suggests that the increase in choice reaction time observed for spatial frequency discrimination of orthogonal gratings is not associated with a more general higher-order decision process (e.g., Williams 1974).

In conclusion, our results suggest that the perceptual memory representations studied in delayed discrimination of orientation and spatial frequency are located quite early in the cortical processing streams. This hypothesis is corroborated by neuropsychological observations, which indicate that deficits in perceptual discrimination and recognition resulting from brain lesions are accompanied by parallel deficits in memory (Farah 1995; Greenlee et al. 1995; Zeki 1993). Our findings indicate that these circuits seem to have the dual function of precise sensory encoding and short-term storage of stimulus information. Experiments monitoring brain activity during visual imagery likewise suggest that the same areas are involved in perception and memory, including V1 (Farah 1995; Kosslyn et al. 1993; Pasternak and Greenlee 2005).

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