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Prefrontal cortex and basal ganglia control access to working memory

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Our capacity to store information in working memory might be determined by the degree to which only relevant information is remembered. The question remains as to how this selection of relevant items to be remembered is accomplished. Here we show that activity in the prefrontal cortex and basal ganglia preceded the filtering of irrelevant information and that activity, particularly in the globus pallidus, predicted the extent to which only relevant information is stored. The preceding frontal and basal ganglia activity were also associated with inter-individual differences in working memory capacity. These findings reveal a mechanism by which frontal and basal ganglia activity exerts attentional control over access to working memory storage in the parietal cortex in humans, and makes an important contribution to inter-individual differences in working memory capacity.

Working memory capacity is an important factor for a wide range of cognitive abilities, including general fluid intelligence[1,2]. Recent studies of humans using functional magnetic resonance imaging (fMRI) and electroencephalography have identified a region in the parietal lobe where brain activity reflects the amount of stored visuo-spatial information[3,4]. Furthermore, subsequent studies have shown that when a working memory trial contains both relevant and irrelevant information, storage-related parietal activity for distractors is negatively correlated with working memory capacity, so that individuals with high working memory capacity are less likely to store irrelevant distractors, which would unnecessarily consume capacity[5]. This suggests that the extent to which only relevant information is stored is related to, and may form a basis for working memory capacity[5].

The neural basis for the control of access to working memory storage, the possible neural determinant of working memory capacity, is still unknown. It has been suggested that such control may stem from a bias signal from the prefrontal cortex[5], and recordings from the lateral prefrontal cortex of monkeys indicate that this region is involved in the selection of behaviorally relevant information[6]. However, the regions involved in such top-down control, and the relationship between their activity and working memory capacity, have not been investigated.

To address this, we conducted an fMRI study that was designed to identify activity associated with preparation to filter out irrelevant items that were presented during encoding in a visual-spatial working memory task. Task instructions were given before the presentation of the memory stimuli, a method that has been used previously to identify the neural correlates of various task sets (for example, see ref. 7), and that, in this study, enabled us to isolate top-down control processes from processes related to the encoding of stimuli into working memory.

In each trial the task instruction took the form of a geometric shape (a square or a triangle) that indicated whether yellow circles should act as distractors to be ignored (the 'distraction' condition) or target stimuli to be remembered (the 'no distraction' condition) in the subsequent working memory task (**Fig. 1**). In the distraction task, subjects needed to remember three red circles (targets) and ignore two yellow circles (distractors). In the no distraction task, the number of targets were either three (all red) or five (3 red circles and 2 yellow). Activity that was associated with preparation to filter out irrelevant items, before the processing of the memory stimuli, was identified by contrasting the instruction periods of the distraction task condition and the no distraction task condition.

RESULTS
Task difficulty
The inclusion of distractors increased task difficulty, as seen by the accuracy in trials of three target circles with and without distraction (accuracy was 80% ± 14% and 85% ± 11%, respectively, mean ± s.d.; paired t-test, $t = -2.3$; $P = 0.015$, $n = 24$). However, as the no distraction condition sometimes included trials with three and sometimes five targets, there was no difference in accuracy, on average, between the distraction and the no distraction conditions (80% ± 14% and 78% ± 10%, respectively, $n = 24$). Therefore, the task instruction did not predict differences in task difficulty.

Filtering set activity
'Filtering set activity' was defined as the difference in brain activity between the instruction periods of the distraction trials and the no distraction trials. Such activity was observed in three regions: bilaterally in the posterior part of the middle frontal gyrus (in and anterior to the precentral sulcus) and in left basal ganglia (with one local maxima in the putamen and one in the global pallidus) ($P < 0.05$, corrected for multiple comparisons). We determined the time course of activity at
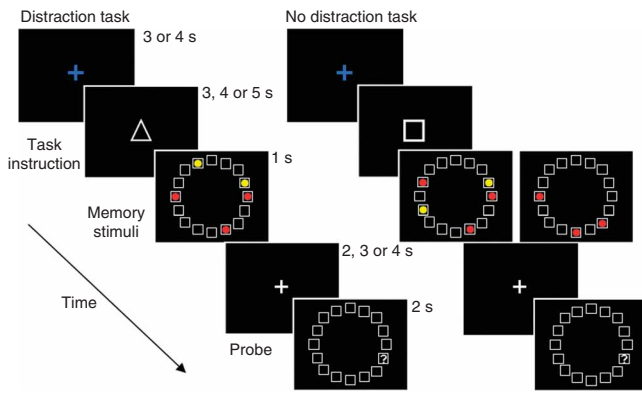
Figure 1 The distraction condition (one third of trials) and the no distraction condition (one third of trials) included in the scanning task (see the manuscript text). The remaining third of trials involved a no memory condition, indicated by a diamond, which followed the same format, but required participants to make a color judgment. The results of this task condition are not reported here.

the maxima for each region, averaged across sessions and subjects (**Fig. 2**). Activation peaked at 6 s after the onset of the instruction, which corresponds to the delay of the hemodynamic response. These results indicate that bilateral middle frontal gyrus and left basal ganglia are involved in the preparation to select the information that is to be stored in working memory. We next investigated the relationship between this preparatory activity and both working memory capacity and the storage of distractors.

Working memory capacity

We conducted a behavioral experiment outside of the scanner to establish each participant's working memory capacity. The procedure was the same as that used for the no distraction condition of the scanning task, except that trials always began with the presentation of a diamond and the grid contained three, four, five or six red circles. Participants were required to remember the positions of the circles and to indicate, via a button press, whether the probe position corresponded to one of these target positions (a yes or no response). Working memory capacity was estimated with the K-value, estimating how much information can be stored in working memory, using a standard formula[5,8]. For both the frontal and basal ganglia regions that showed filtering set activity (**Fig. 2**) we extracted the mean relative
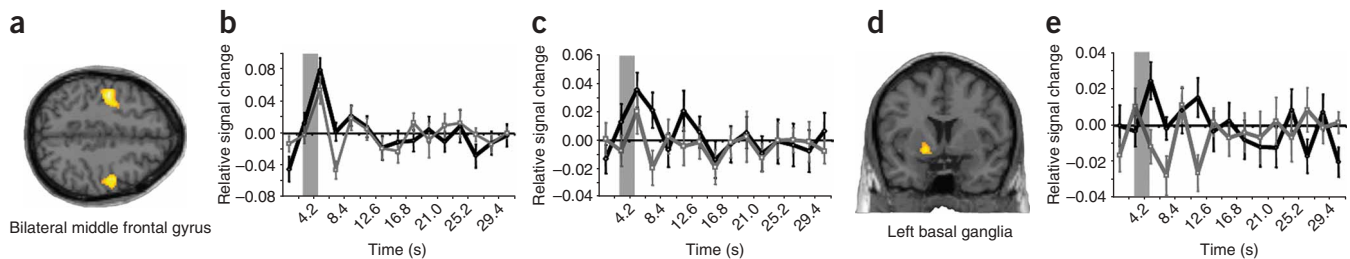
signal change from the distraction versus no distraction contrast, during the instruction period, for each participant, and correlated these values with working memory capacity (the average from the two prefrontal regions was used). There was a moderate, but significant, positive correlation between the mean filtering set activity in the prefrontal cortex and working memory capacity ($r = 0.35$, $P = 0.045$; **Fig. 3a**) and between the mean filtering set activity in the basal ganglia and working memory capacity ($r = 0.35$, $P = 0.042$; **Fig. 3b**).

The activity (mean beta values for the regressor) associated with the instruction for the no distraction condition did not correlate with working memory capacity (prefrontal cortex: $r = 0.20$, $P = 0.168$; basal ganglia: $r = -0.06$, $P = 0.391$). Therefore, it was specifically in the contrast between the distraction and no distraction conditions that prefrontal and basal ganglia activity correlated with working memory capacity.

The basal ganglia cluster contained local maxima located in the putamen and globus pallidus, respectively. Because these are functionally different parts of the basal ganglia circuit, separate correlation analyses were carried out on the values of mean relative signal change extracted from the maxima in the putamen and the maxima in the globus pallidus, revealing that, although activity in the putamen voxel did not significantly correlate with working memory capacity ($r = 0.27$, $P = 0.097$; **Fig. 3c**), the activity in the globus pallidus voxel did correlate with working memory capacity ($r = 0.57$, $P = 0.001$; **Fig. 3d**). Therefore, in line with our hypothesis, preparatory activity in the frontal regions and left basal ganglia (in particular, the globus pallidus) was significantly correlated with working memory capacity. We next investigated the relationship between preparatory filtering set activity and brain activity that is related to the storage of distractors.

Unnecessary storage activity

As previously mentioned, the extent to which irrelevant distractors are unnecessarily stored is reflected in event-related potentials that are recorded over load-sensitive lateral occipital and parietal lobes[5]. To identify such activity, we first located a load-sensitive parietal region by contrasting the activity associated with the encoding and storage of five circles (load 5) with that of three circles (load 3) in the no distraction task condition, considering the period between the onset of the circles and the onset of the probe stimulus. The maximum parietal difference was seen in the right posterior parietal cortex, which may correspond to the load-sensitive parietal region identified by previous studies[3–5]. We identified the medial/lateral (x), anterior/posterior (y) and dorsal/
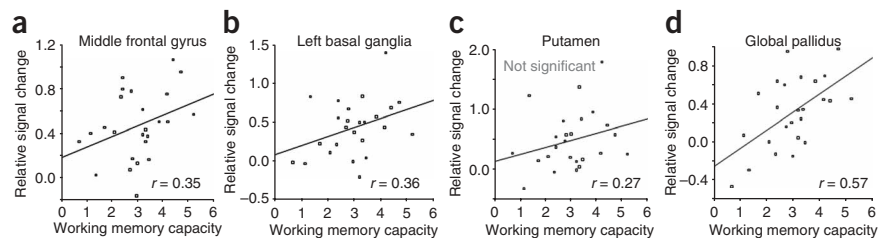

Figure 2 Preparatory filtering set activity. The results from the distraction versus no distraction contrast are shown for the task instruction period ($P < 0.05$, corrected for multiple comparisons). (**a–c**) Significant task-dependent differences were observed in bilateral middle frontal gyri (**a**, maximum at MNI coordinates in mm (x, y, z): –40, –12, 50 and 48, –10, 44). The time series of relative signal change are shown for signals at the peak of task-dependent differences in each cluster (**b**, left middle frontal gyrus; **c**, right middle frontal gyrus) for both distraction (shown in black) and no distraction (shown in gray) task conditions. (**d,e**) Significant task-dependent differences were also observed in left basal ganglia (**d**, maximum at –18, 6, –6), and the time series of relative signal change is also shown for the signal at the peak of task-dependent differences in this cluster (**e**). The error bars indicate s.e.m. and the shaded section represents the times at which the memory stimuli were presented (which varied between 3, 4 and 5 s after the onset of the instruction cue).

ventral (z) extremes of this activity, and converted these to Talairach coordinates. The cluster extent was $x = 24/59$, $y = -50/-77$ and $z = 36/51$, which corresponds closely with the previously identified load-sensitive parietal region[3] of $x = 17/29$, $y = -52/-69$ and $z = 38/54$ (personal communication, J.J. Todd & R. Marois, Vanderbilt Vision Research Center, Vanderbilt University).

If distractors are filtered effectively, the response to the distraction condition in the load-sensitive parietal area should be similar to that observed for load 3 of the no distraction condition (as both included three target stimuli). Conversely, if filtering is not effective, there should be greater activity in this region, reflecting the greater working memory load that is associated with the additional storage of distractors. Therefore, in the load-sensitive parietal cluster, we extracted values of mean relative signal change from the contrast between the distraction condition and load 3 trials of the no distraction condition for each participant, considering the period between the onset of the memory stimuli and the onset of the probe (corresponding to encoding and storage), as this should reflect the extent to which irrelevant distractors were unnecessarily stored.

We then correlated this parietal 'unnecessary storage activity' with the preparatory filtering set activity for the regions in which significant task-dependent differences had been observed (the prefrontal regions and the globus pallidus) during the preceding instruction period. A significant negative correlation was seen for the globus pallidus ($r = -0.50$, $P = 0.005$; **Fig. 4**), but not for the prefrontal regions ($r = -0.06$, $P = 0.387$), indicating that enhanced activity in the globus pallidus region was associated with fewer distractors being unnecessarily stored. Furthermore, the unnecessary storage activity was also negatively correlated with working memory capacity ($r = -0.43$, $P = 0.016$), which is consistent with the hypothesis that unnecessary storage accounts for the correlation between filtering set activity and working memory capacity. Filtering set activity in the globus pallidus was also significantly negatively correlated with the difference in accuracy between the distraction condition (three target circles and two distractors) and the no-distraction load-3 condition (three target

Figure 3 Correlations between working memory capacity and preparatory filtering set activity. (**a**–**d**) Correlations between working memory capacity and the mean relative signal change from the distraction versus no distraction contrast in the instruction period from frontal clusters (**a**, $P = 0.045$) and the basal ganglia (**b**, $P = 0.042$). Correlations are also shown for the maxima of the basal ganglia cluster in the putamen (**c**, −18, 6, −6; $P = 0.097$) and the globus pallidus (**d**, −12, −2, −8; $P = 0.001$).

circles) ($r = -0.40$, $P = 0.028$) during scanning, indicating that greater filtering set activity was linked to a reduced loss in accuracy associated with distracter presentation.

DISCUSSION

The present study identified the basal ganglia as being responsible for allowing only relevant information into working memory. Consistent with the theory that an individual's working memory capacity is determined by their ability to selectively filter irrelevant distractors[5], prefrontal and basal ganglia activity was a significant predictor of working memory capacity (measured in the absence of overt distractors), and basal ganglia activity significantly negatively correlated with parietal load effects that reflected the unnecessary storage of distractors. The present results therefore reveal a specific neural mechanism by which an individual's ability to exert control over the encoding of new information is linked to their working memory capacity[9–11], measured in the absence of overt distraction.

It has previously been suggested that individual differences in the efficiency with which items are filtered from working memory may stem from a bias signal emanating from the prefrontal cortex[5]. Here we show prefrontal activity that meets this criterion. The activity is associated with the preparation to filter items from working memory, consistent with a role for the prefrontal cortex as a control region[12,13]. The results also suggest that such a process is carried out in concert with the basal ganglia, presumably according to one of the previously described fronto-striatal loops[14].

The basal ganglia are activated during planning and set-shifting[15–17], and have been shown to be important in the pathophysiology of several diseases affecting sensory gating[18]. The globus pallidus is the output module of the basal ganglia and contains motor, limbic and associative regions, of which the latter is crucial for spatial attention[19]. Although it has been acknowledged that the basal ganglia is involved in working memory[20,21], such an involvement is not well understood. However, there is evidence for an involvement of the globus pallidus during working memory–guided movement sequencing[22], and electrophysiological studies in primates have indicated that globus pallidus activation is modulated by memory requirements during motor sequencing[23].

Furthermore, the basal ganglia have a high density of dopamine receptors, which are central to working memory[24]. Using the idea that dopamine can carry out a gating function by transiently strengthening the efficiency of inputs to the frontal cortex, and by extending models of disinhibitory gating in the motor domain, an interaction between the frontal cortex and the basal ganglia has been modeled[25]. In this model, the basal ganglia contribute a selective gating mechanism that disinhibits thalamocortical loops and the influence of incoming stimuli
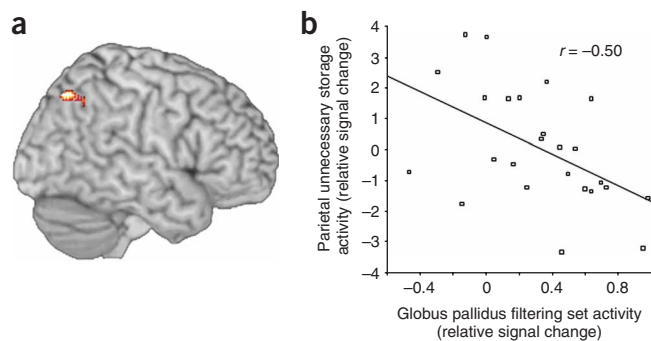
Figure 4 Correlations between preparatory filter set activity and unnecessary storage activity. (**a**) The right parietal region in which the load effect was observed from the contrast between load 5 and load 3 in the no distraction condition (maximum at 48, −66, 48). (**b**) The negative correlation between the relative signal change extracted from the globus pallidus voxel in the distraction versus no distraction contrast during the instruction period and the mean relative signal change from the distraction versus no-distraction load-3 contrast between onset of the circles and onset of the probe stimulus.

on the working memory system is regulated. Similarly, dopamine in the basal ganglia has been modeled as gating stabilization against distraction by enhancing select memories[26].

The present findings also address the question of the neural basis for the connection between attention and working memory. It is known that attention and working memory are closely connected (as well as being partly overlapping concepts), and working memory capacity correlates with the efficiency of controlled attention[9–11,27–29]. Such findings have led to the suggestion that attention can serve as a gatekeeper for working memory, by biasing the encoding of information toward items that are most relevant[10]. The present results provide a neural basis for such a gatekeeping function.

In conclusion, we have shown that activity in the prefrontal cortex and basal ganglia precedes the filtering of irrelevant items during the encoding of working memory. This preparatory activity predicts the extent to which only relevant information is stored, as reflected by parietal storage–related activity, and predicts inter-individual differences in working memory capacity. This activity therefore reveals a specific mechanism that could contribute toward an individual's working memory capacity.

METHODS

Participants. Twenty-five healthy participants (13 females, ages 19–33, right handed) gave informed consent to participate in the study, which was approved by the local ethics committee of the Karolinska Hospital (Forskningetikprovning).

Tasks and stimuli. In the tasks carried out during scanning, the assignment of geometric shapes to the distraction and no distraction task conditions was counterbalanced across participants so that comparisons between task instructions would not be confounded by differences in visual stimuli. The mean magnitude of the cosine of the angle between regressors (which is 1 for collinear regressors and 0 for orthogonal regressors) indicated that the activity associated with the presentation of the task instruction and that associated with the presentation of the stimulus array was sufficiently separated (0.046 in the distraction condition and 0.040 in the no distraction condition).

There were 16 positions in the grid. In the behavioral experiment, the grid subtended a visual angle of $20°$ both horizontally and vertically, and the minimum difference between circles was $4°$, from center to center. In the fMRI experiment, the grid subtended a visual angle of $11°$ both horizontally and vertically, and the minimum difference between circles was $2°$, from center to center. The instruction cues were presented for 3, 4 or 5 s. The stimulus array was shown for 1 s and was followed by a delay of 2, 3 or 4 s, and then the probe stimulus was displayed for 2 s.

In the behavioral experiment used to obtain a measure of working memory capacity for each participant, conducted at least 1 week before scanning, all parameters were the same as in the scanning procedure, but the experiment only involved the no distraction task. The geometric shape was always a diamond and target stimuli were three, four, five or six red circles (ten trials of each, yellow circles were never shown). On presentation of the probe stimulus, participants were required to make a button press with the index or middle finger of their right hand, depending on whether a circle had appeared at the location indicated (which was the case for half of the trials). When the probe stimulus was not in a target position, it was in a position adjacent to one of the target positions. The required response (yes or no) and the different durations of presentation of the diamond and both fixation crosses were distributed evenly across trials of each array size.

Visual working memory capacity was computed with the standard formula[5,8] $K = S \cdot (H - F)$, where K is the working memory capacity, S is the array size, H is the observed hit rate and F is the false alarm rate. This formula uses the false alarm rate to correct for guessing and assumes that if K items can be held in working memory, from an array of S items, the probed item would have been one of those held in memory on K/S of trials, so that performance will be correct on K/S of the trials. For each participant, we computed the K value for

each of the four array sizes and used the mean K of array sizes 5 and 6 as our measure of working memory capacity.

In the no distraction condition, the grid contained three red circles for half of the trials and three red circles with two yellow circles for the other half. The required response and durations of presentation of the instruction and both fixation crosses were distributed evenly across task conditions and the two load conditions. For each session, the stimulus configurations were generated pseudo-randomly, with the criteria that a maximum of two target items could be presented in adjacent locations and that one of the two yellow circles was always in a location adjacent to a red circle. The stimulus configurations were assigned to the different task conditions pseudo-randomly, but with the same assignment for each participant. In 60% of trials that occurred in the distraction condition, the probe appeared in a position that had been occupied by a distracter. Trials were presented pseudo-randomly (with the trial types also randomized) in an event-related design.

Before going into the scanner room, each participant completed one practice session of the scanning task (30 trials, ten of each condition). In the scanner, 22 of the 25 participants completed four sessions of 30 trials (ten trials of each condition), with the order of sessions being counterbalanced across participants. Button presses were recorded for all but one of the participants. Twenty-two participants completed all four sessions, two completed three sessions and one completed two sessions.

MRI acquisition. Images were acquired using a 1.5-T GE Signa scanner. T2*-weighted, gradient echo spiral echo-planar images were acquired with a repetition time of 2.1 s, an echo time of 40 ms, a flip angle of $76°$, 22 axial slices, 5-mm slice thickness, 220-mm FOV and a 64×64 grid. Each session lasted 7 min and involved the acquisition of 195 volumes. T1-weighted spin-echo images (FOV of 75 mm) were acquired in the same position as the functional images.

Data analysis. Preprocessing and statistical analysis were carried out with SPM5 (Welcome Department of Cognitive Neurology, http://www.fil.ion.ucl.ac.uk/spm/software/spm5). Preprocessing included slice-time correction, motion correction, normalization to the template EPI (interpolating to 2-mm cubic voxels) and spatial smoothing with an 8-mm Gaussian kernel. The models used a canonical hemodynamic response and its temporal derivative; however, to plot the time course of the preparation activity, we estimated the model again omitting the temporal derivative, and a finite impulse response (FIR) approach was used. From this model, maxima were located at Montreal Neurological Institute (MNI) coordinates –42, –10, 52, 48, –8, 42, and –16, –4, –6, and these voxels were used to plot time courses (shown in **Fig. 2**). The first model, used to identify filtering set activity, included separate regressors for each of the instruction conditions, a regressor for the presentation of the memory stimuli (duration 1 s, with a covariate of the number of circles presented), a regressor for storage (beginning at the presentation of the memory stimuli and ending at the onset of the probe, with a covariate for the number of circles to remember) and a regressor for the probe stimulus. A second model was used to investigate the unnecessary storage activity. In this model there were separate regressors for each of the instruction conditions and regressors for storage in the distraction condition, the no-distraction load-3 condition, the no-distraction load-5 condition, the no memory condition, and a regressor for the probe stimulus. In both cases, only trials that received a correct response were included in the model. Correlation analyses between fMRI data and behavioral outcomes (working memory capacity and filtering ability), as well as between preparatory activity and unnecessary storage activity, were carried out using SPSS for Windows (Rel. 11.5.0, SPSS) and the accompanying P values were determined by one-tailed analysis with the hypothesis that the preparatory filtering ability would determine working memory capacity and filtering ability.

Comparisons of interest were implemented as linear contrasts. The analysis was carried out individually, and contrast images for each subject were used in a second-level analysis, treating subjects as a random effect. For analysis of the instruction period, the statistical map was thresholded with a false discovery rate of $P < 0.05$, and differences were considered to be significant if they fulfilled the criteria of an extent threshold of 150 voxels and a corrected cluster level requirement of $P < 0.05$. To identify the parietal load-sensitive region, we

used a threshold of $P < 0.01$, uncorrected for multiple comparisons. This less stringent threshold was used because we had an a priori hypothesis for a load effect in this region, and the purpose of this analysis was only to identify the load-sensitive region for further analysis of unnecessary storage.

AUTHOR CONTRIBUTIONS
F.M. and T.K. designed the tasks and wrote the manuscript together. F.M. conducted the experiments and analyzed the data.

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