Long-term memory prepares neural activity for perception

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Past experience provides a rich source of predictive information about the world that could be used to guide and optimize ongoing perception. However, the neural mechanisms that integrate information coded in long-term memory (LTM) with ongoing perceptual processing remain unknown. Here, we explore how the contents of LTM optimize perception by modulating anticipatory brain states. By using a paradigm that integrates LTM and attentional orienting, we first demonstrate that the contents of LTM sharpen perceptual sensitivity for targets presented at memory-predicted spatial locations. Next, we examine oscillations in EEG to show that memory-guided attention is associated with spatially specific desynchronization of alpha-band activity over visual cortex. Additionally, we use functional MRI to confirm that target-predictive spatial information stored in LTM triggers spatiotopic modulation of preparatory activity in extrastriate visual cortex. Finally, functional MRI results also implicate an integrated cortical network, including the hippocampus and a dorsal frontoparietal circuit, as a likely candidate for organizing preparatory states in visual cortex according to the contents of LTM.

Our expectations shape how we see the world. From the earliest pioneers in perception (e.g., ref. 1), it has long been appreciated that past experience guides perceptual processing and decision-making. Indeed, the statistical regularities of the environment, extracted over past experience and coded in long-term memory (LTM), provide a rich source of predictive information that could be exploited to optimize perception for goal-directed behavior (2–4).

Studies of selective attention provide an important framework for understanding the dynamic changes in neural processing that optimize perceptual analysis for goal-specific input. In particular, influential theories suggest that modulations in baseline neural activity in sensory cortex bias perceptual processing in favor of behaviorally relevant information (5–7). For example, a cue stimulus that provides information about the likely location of a target triggers a shift in baseline activity for neurons that represent the cued position (8–11), thereby increasing the neural sensitivity for subsequent stimulation at the attended region of space (10, 11). However, in everyday life, we rarely enjoy the benefit of explicit cues to guide our attention. More typically, we must rely on our own past experiences, stored in LTM, to build the predictions that shape perception for goal-directed behavior.

Despite the obvious biological relevance of experience-based perceptual biasing, few studies have directly examined how memory influences attentional control. Studies of contextual cueing (2) demonstrate a close relationship between past experience and visual search efficiency: search times decrease with repeated exposure to the same stimulus configurations, even when repetitions are not explicitly processed (12). Contextual cueing effects are particularly compelling for detail-rich naturalistic scenes (13; see also ref. 14), and when memory-predicted information is presented before the search array (15), thereby serving as a preparatory cue (16).

Memories for naturalistic scenes could provide a rich context for preparing the visual system for processing task-relevant information. Critically, LTM for naturalistic scenes is extremely high-capacity: with relatively little effort, observers can remember details for hundreds of individual scenes (17), including precise object identities (18) and locations (16) uniquely associated with each scene. By contrast, arbitrary associations used in explicit cueing paradigms are presumably maintained online in working memory, and therefore limited by the same capacity constraints.

Extending upon such findings leads to the intriguing idea that past experience facilitates perception by integrating mechanisms of memory and preparatory attention (see also refs. 19, 20). According to this hypothesis, high-capacity memory systems could modulate baseline activity to optimize subsequent perception for memory-predicted input (16, 21). In this study, we explored this hypothesis by using an experimental paradigm in which memories for natural scenes can be used to guide preparatory shifts in spatial attention (16). Importantly, this protocol also allows us to separate memory-guided attentional preparation from target processing, as well as the mnemonic processes associated with initial LTM encoding. First, participants perform a learning task in which they search for a specific target stimulus embedded within a large set of naturalistic visual scenes (Fig. 1*A*). Across a number of training sessions, participants establish robust memories of the target locations in target-present scenes. For target-absent scenes, there is no specific spatial location to learn. On the following day, participants then perform a covert-orienting task guided by the contents of LTM (Fig. 1*B*). Whereas standard covert-orienting tasks use explicit spatial cues to direct the focus of attention (22), in this memory-guided version, previously learned scenes are used to direct spatial attention in preparation for target detection. Scenes that previously contained a search target during the learning task provide a valid memory cue that can be used to predict the target location for the detection task. In contrast, scenes that did not contain a target scene during learning constitute a memory-neutral cue that does not provide any predictive information regarding the likely location of the subsequent target stimulus.

We used complementary methods to chart the temporal and spatial characteristics of preparatory visual activity triggered by memory cues. Exploiting the fine temporal resolution of EEG, we found that memory predictions for left or right hemifield targets desynchronized oscillatory activity in contralateral visual cortex. This shift in oscillatory activity at posterior electrode sites is consistent with a relative shift in neural sensitivity to bias information processing at memory-predicted locations (23–27). Functional MRI (fMRI) further demonstrated increased neural activity at subregions of extrastriate visual cortex that were contralateral to the cued hemifield, including in V3a and V4. Moreover, whole-brain analysis of the fMRI data further impli-

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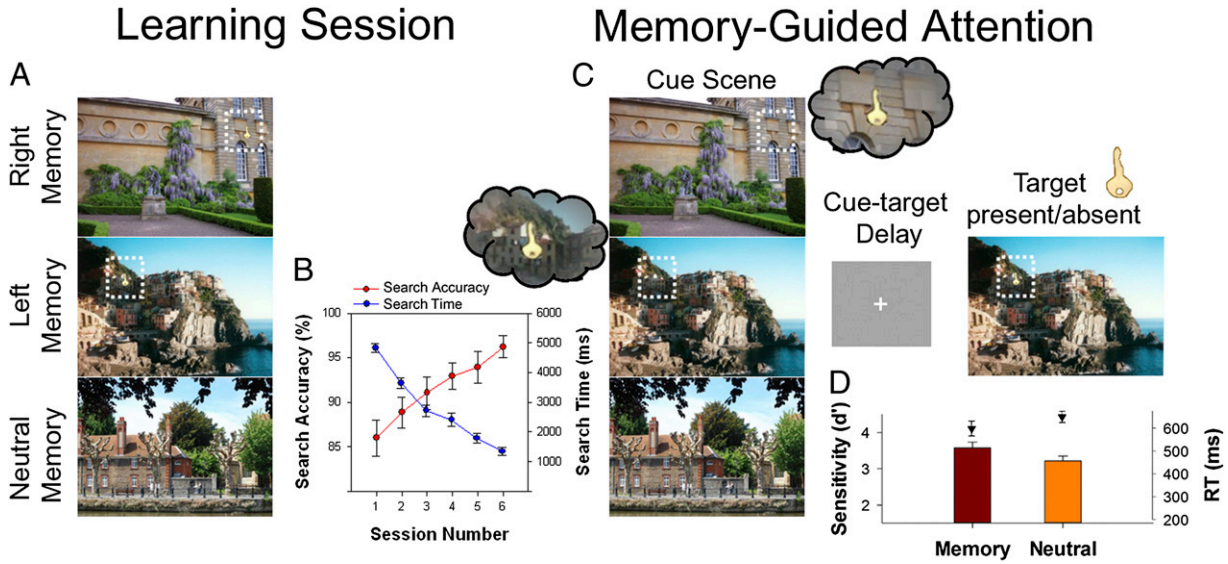

Fig. 1. Experimental protocol for memory-guided attention. (*A*) In both EEG and fMRI experiments, participants first completed a learning task in which they searched for a target stimulus that was embedded within naturalistic scenes. Targets were presented on the right (Right Memory), left (Left Memory) or not at all (Neutral Memory). (*B*) Over repeated sessions, participants found, and learned, the location of target stimuli. The learning profile from the EEG experiment is plotted for search accuracy (left *y* axis, red) and search time (right *y* axis, blue) as a function of training session number (*x* axis). (*C*) On the following day, participants performed an attention task in which scenes from the initial learning task were used to cue the location of a subsequent target. The first scene was always presented without the target stimulus, whereas the second scene contained a target on 50% of trials. On target-present trials, previously learned locations were 100% predictive of the subsequent target location. Consequently, valid memory cue scenes could be used to predict the precise location of the subsequent target, whereas memories for neutral cues contained no task-relevant spatial information. (*D*) Behavioral data are shown for the EEG experiment, with sensitivity (left *y* axis, bars) and RT (right *y* axis, triangles) plotted as a function memory condition (memory vs. neutral). Detection sensitivity was higher for spatially predictive memories, and RTs were shorter. Error bars represent ±1 SEM.

cated an integrated network of brain areas, including hippocampus and dorsal frontal and parietal cortices, as a likely control system for memory-guided shifts in preparatory attention.

Results

Establishing Target-Predictive Memories. Behavioral analyses of the learning task for the EEG experiment confirmed that participants were able to establish robust memories for the spatial locations at which target stimuli were presented (Fig. 1*B*). Not only did participants find more keys throughout the learning task, but search times also decreased over the course of learning, demonstrating that participants could use their memories of the target location to reduce the search demands. The same pattern of results was also observed during the learning session of the fMRI experiment (Fig. S1). Overall, these data replicate the learning profile observed previously (16), thereby further validating this search-based learning task as a useful method for establishing robust memories for specific locations within a large set of naturalistic scenes, which can then be used to guide behavior. Final recall accuracy, assessed after the subsequent orienting task, further confirmed that the learning task yields robust memories for target locations. On average, participants could explicitly recall the correct location of target stimuli on 80% (±4.5%, SEM) and 77% (±2.5%, SEM) of trials following EEG and fMRI experiments, respectively.

Orienting Task: Memory Predictions Increase Perceptual Sensitivity. During the subsequent orienting task, detection sensitivity (d′) for targets embedded within naturalistic scenes was strongly influenced by the content of LTM. To quantify the influence of memory-guided attention on perception, we compared sensitivity for targets presented after a valid memory cue to sensitivity for targets following neutral memory cues. Valid trials were only included in these analyses if the target location was found during the initial learning task, and if the location of the target was also accurately recalled during the explicit memory test that was completed at the end of the experimental session. Positive cueing effects were evident in both EEG and fMRI experiments [EEG, $d'_{mem} = 3.5$, $d'_{neut} = 3.1$, $t_{15} = 3.3$, $P < 0.005$ (Fig. 1*D*); fMRI, $d'_{mem} = 3.0$, $d'_{neut} = 2.1$, $t_{15} = 7.0$, $P < 0.001$]. These reliable changes in perceptual sensitivity clearly demonstrate that memory-guided preparatory attention directly influences perceptual sensitivity. In addition, we also found that targets presented at memory-predicted locations were detected with shorter response times (RTs) than those presented at memory-neutral locations [EEG, $RT_{mem} = 590$ ms, $RT_{neut} = 649$ ms, $t_{15} = 4.2$, $P = 0.001$ (Fig. 1*D*); fMRI, $RT_{mem} = 822$ ms, $RT_{neut} = 972$ ms, $t_{15} = 3.2$, $P = 0.006$], thereby replicating previous evidence for RT cueing effects for memory-guided attention (15, 16; see also ref. 21).

Preparatory Neural Activity: Contralateral Alpha Desynchronization. Time-frequency analysis of the EEG data recorded after the presentation of a valid memory cue, but before the target scene, identified a significant reduction in power at the alpha-band frequency range in posterior electrodes that were contralateral to the learned location (Fig. 2). Initially, we performed a fast Fourier transformation to estimate the frequency of the alpha band in each participant, identified as a distinct peak in power between 8 and 12 Hz (mean, 9.8 Hz; range, 9–11 Hz). These individual alpha-frequency estimates were then used for all subsequent analyses. Statistical analyses were restricted to a time-window spanning 650 ms to 750 ms after cue onset, which corresponds to at least 100 ms before the onset of the earliest possible presentation of the time-jittered target. Fig. 2*A* shows the distribution of cue-related differences in alpha power within this time window projected across the scalp surface, clearly illustrating the concentration of cue-specific alpha desynchronization around posterior electrodes overlaying the visual cortex contralateral to the memory-predicted location. Statistical analyses were performed at electrode sites PO7 and PO8, which have previously been as-

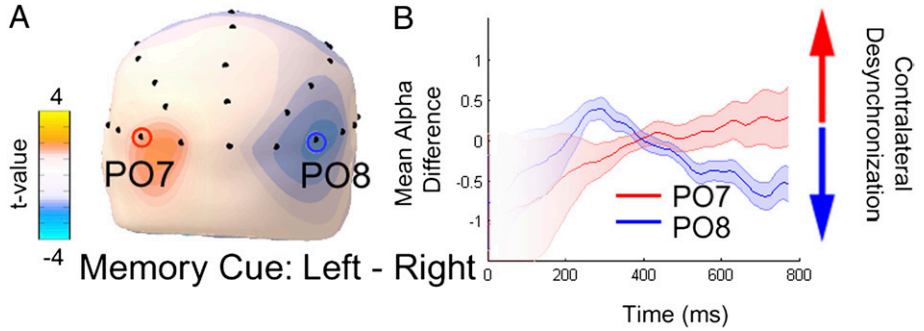

Fig. 2. Memory predictions trigger contralateral alpha-desynchronization in posterior electrodes. (*A*) EEG recordings demonstrate that memory cues trigger spatially specific desynchronization of alpha-band oscillations in posterior electrodes, including PO7/PO8. The scalp topography of cue-specific differences (left – right cue; 650–750 ms) in alpha power is shown projected across a 3D scalp surface. (*B*) Time-course analysis of alpha power in lateralized posterior electrodes, PO7 (in red) and PO8 (in blue), illustrates how contralateral desynchronization emerges at approximately 400 ms after the cue onset. Positive values reflect contralateral desynchronization in the left hemisphere, whereas negative values reflect desynchronization in the right hemisphere, and shading represents ±1 SEM.

sociated with alpha desynchronization during explicitly cued attention tasks (e.g., refs. 11, 26, and 28). A repeated-measures ANOVA, with factors for electrode side (left vs. right) and cue side (left vs. right) revealed a significant interaction, which reflects contralateral desynchronization ($F_{1,15} = 3.0$, $P = 0.039$; no main effects, $P > 0.1$). The temporal evolution of contralateral alpha desynchronization is illustrated in Fig. 2*B*, which plots the difference in alpha power associated with left and right cues as a function of time and electrode side. For the left hemisphere, positive values reflect contralateral desynchronization whereas negative values reflect desynchronization in the right hemisphere. This index of differential alpha power shows evidence of contralateral desynchronization after approximately 400 ms.

Preparatory Neural Activity: Lateralized Biases in Blood Oxygenation Level-Dependent fMRI. To complement the results of EEG analyses, we also used fMRI to examine the functional neuroanatomy of memory-guided attentional orienting. As in the EEG experiment, participants learned specific spatial locations for a large set of naturalistic visual scenes 24 h before performing the memory-guided orienting task. However, for this fMRI experiment, the delay between cue and target onset was extended, with variable jitter, to allow us to dissociate activity elicited by the cue and target stimuli. For each participant, we constructed regression functions for each event type of interest, including valid memory cues for left and right visual field (*Materials and Methods* includes full details). Parameter estimates were then assessed at the group level via random-effects analyses. To examine spatially specific preparatory activity, we first interrogated the parameter estimates for the cue-related response to left and right spatial locations in left and right visual cortices (Fig. 3*B*). For illustration, statistical maps were projected onto the flattened occipital surface. In both visual cortices, activity was greater for memory cues that predicted targets in the contralateral visual field, relative to cues for ipsilateral targets. To assess more directly how memory-predictions modulated activity across the visual hierarchy, we extracted cue-specific preparatory activation profiles from predefined regions of interest (ROIs) for visual areas V1, V2v, V2d, V3v, V3d, V3a, and V4 (*Materials and Methods*). Contrast values were extracted while preserving the critical spatial relationship to the memory cue: in left-hemisphere visual areas, cue specificity was indexed by contrasting right vs. left memory cues, whereas in right visual areas, values were extracted from the left vs. right contrast. Accordingly, positive values reflect a relative increase in activity at visual areas representing spatial locations contralateral to the memory-predicted location (Fig. 3*C*). A one-way ANOVA revealed a main effect of ROI ($F_{6,114} = 15.5$, $P < 0.001$). Follow-up analyses confirmed significant preparatory biases according to memory cue for V3v ($t_{19} = 3.8$; $P = 0.008$), V3a ($t_{19} = 5.3$, $P < 0.001$), and V4 ($t_{19} = 5.0$, $P < 0.001$; Bonferroni-corrected, $P > 0.05$ in all other comparisons).

As noted earlier, we used long and varied cue-target stimulus onset asynchrony in this fMRI experiment so we could separate activity associated with the memory cue from the neural response to target stimuli. As this separation is critical to our

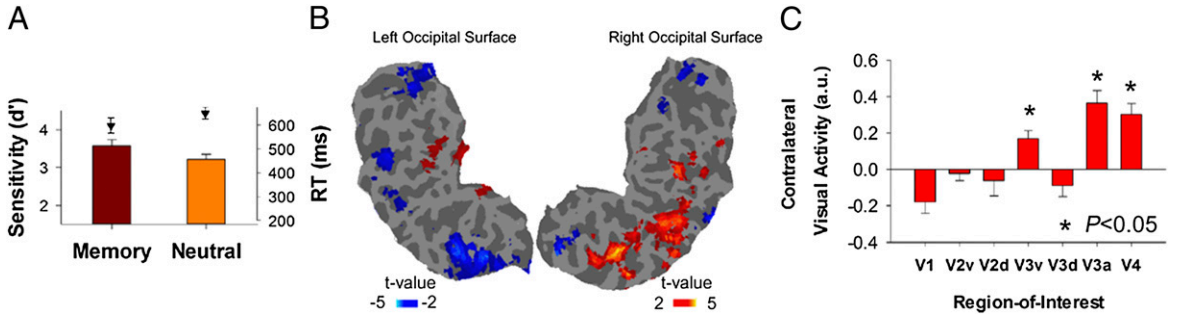

Fig. 3. Memory predictions increase BOLD-related activity in contralateral visual areas. (*A*) Behavioral analysis of fMRI experiment confirmed that detection sensitivity was enhanced for targets presented at memory-predicted locations, relative to memory-neutral locations. Detection sensitivity (left *y* axis, bars) and RT (right *y* axis, triangles) are plotted as a function memory condition (memory valid vs. neutral). (*B*) Analysis of the BOLD response revealed evidence of spatially specific biases in preparatory visual activity: memory cues elicited increased activity in contralateral subregions of visual cortex, particularly in extrastriate visual areas. Data contrasting left vs. right views are shown on the occipital surface, extracted and flattened using Freesurfer (*Materials and Methods*) (*C*) Spatially specific cue-related activity is shown for specific visual areas (text provides details). Error bars represent ±1 SEM.

analyses of preparatory activity, we performed subsequent control analyses to confirm that preparatory activity associated with the cue was not contaminated by target-related activity. First, we tested for any evidence of lateralized differences in visual activity patterns associated with neutral memory cues for trials within which left or right target stimuli were subsequently presented. If target-related activity had contaminated our valid memory cue effects, a similar profile should also be observed even when the cue is not associated with a target-predictive location in memory. ROI analyses did not reveal any evidence for spatially specific activation contralateral to the subsequent target location ($P > 0.29$ for all comparisons, uncorrected for multiple comparisons; Fig. S2). More importantly, direct statistical comparison between the preparatory bias associated with the valid memory cue and the equivalent contrast performed on neutral memory cues confirmed that contralateral activity was specific to valid memory cues. Analysis of variance, with factors for validity (valid vs. neutral) and ROI (V3v vs. V3a vs. V4) revealed a significant main effect for validity (valid > neutral: $F_{1,19} = 21.6$, $P < 0.001$; Fig. S3) and no other significant terms.

For an additional control, we also tested whether a similar pattern of biases could be observed on trials that contained no spatially specific differences in sensory stimulation. At the first level, we separated the valid memory cue data according to the presence or absence of a subsequent target. Next, we assessed parameter estimates at the group level in a repeated-measures ANOVA, with factors for target presence (absent vs. present) and ROI (V3a vs. V3v vs. V4). There was a significant main effect of ROI ($F_{2,38} = 3.9$, $P < 0.031$), but no other significant terms, suggesting that the pattern of lateralized preparatory activity was not dependent on the presence or absence of the subsequent target stimulus. From the results of these control analyses, we can be confident that lateralized activation biases reflect preparatory neural states triggered by spatial predictions stored in LTM.

Preparatory Neural Activity: Control Network. Similar to the results of the EEG study, the pattern of lateralized changes in preparatory visual activity measured with fMRI strongly resembled changes in pretarget activity observed following an explicit cue that directs the focus of spatial attention (e.g., ref. 8). However, instead of an explicit cue directing attention to one or other hemifield, in our study, the cue stimulus does not intrinsically signal any useful spatial information. Rather, these cues trigger stored memories for task-relevant spatial locations, which in turn guide attention. In this section, we explore the neural substrate for directing preparatory biases from spatial predictions stored in LTM.

Previously, Summerfield and colleagues (in 2006; ref. 16) observed increased activity for frontal and parietal brain areas during experimental trials containing memory-valid cues. The network of high-level brain areas closely resembled control areas previously described in the attention literature (8, 29–32), suggesting that memory-guided attention could operate through a similar neural mechanism. However, because the previous design did not enable dissociation of cue-related and target-related activity, it was not possible to rule out an alternative explanation that activity in the frontoparietal network was elicited by target-related processes, such as stimulus-driven attentional capture, perceptual decision-making, and/or response generation. As demonstrated in the previous section, the long and variable cue-target stimulus onset asynchrony used in this experiment now allows us to test directly the extent to which activity specific to memory predictions was also specific to memory cues.

A whole-brain analysis contrasting the parameter estimates for valid vs. neutral memory cues revealed a network of frontal and parietal brain areas, including intraparietal sulcus (IPS) and frontal eye field (FEF; Fig. 4*A*). In contrast, no significant clusters were identified for the comparison between target events following valid or neutral memory cues. Next, more detailed analyses were performed on frontal and parietal ROIs based on coordinates for IPS and FEF that were previously reported for memory-guided attention (16). Condition-specific beta parameters estimated for each ROI in each participant were assessed via a repeated-measures ANOVA, with factors for memory validity (valid vs. neutral), event (cue vs. target) and ROI (IPS vs. FEF). Main effects were observed for ROI (IPS > FEF: $F_{1,19} = 26.4$, $P < 0.001$) and validity (valid > neutral: $F_{1,19} = 16.8$, $P = 0.001$). Most importantly, there was also a validity-by-event interaction ($F_{1,19} = 15.9$, $P = 0.001$; Fig. 4*B*) caused by significant validity effects associated with cue ($P < 0.001$), but not with target events ($P = 0.87$). There were no other significant ANOVA terms ($P > 0.05$). These results confirmed that memory-related differences in frontoparietal activity were associated with attentional preparation triggered by the cue, rather than by target-related processes.

In the previous study of Summerfield et al. (16), valid-memory trials also elicited more activity in the left hippocampus than neutral-memory trials. Although we could not be sure that this differential response was related to cue, and not target-related processing, memory-specific hippocampal activity is consistent with the hypothesis that the hippocampus provides an important interface linking predictions stored in LTM with frontoparietal control mechanisms that can selectively modulate preparatory activity in visual areas according to memory predictions. Because the design of the present fMRI experiment separates activity associated with cue and target, we can now confirm that activity in the left hippocampus is triggered by the presentation of the cue scene, rather than during target processing. Parameter estimates were extracted from an ROI defined according to the results of the previous and submitted to a two-way repeated-measures ANOVA, revealing a main effect for event (cue > target: $F_{1,19} = 15.1$, $P = 0.001$; Fig. 4*C*). Although there were no other significant terms ($P > 0.05$), the overall pattern of results clearly resembled the pattern observed for frontoparietal brain areas with a trend for a validity effect associated with cues but not targets.

Discussion

Exploiting past experience to guide future behavior is probably one of the most general optimizing principles in neuroscience (3),

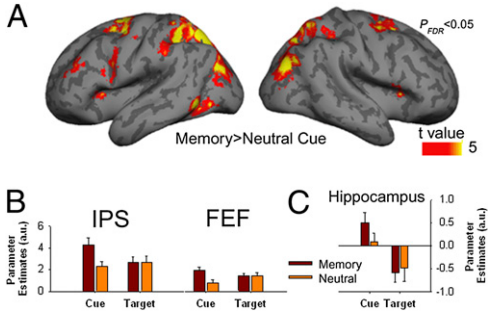

Fig. 4. Control network for memory-guided attention. (*A*) Whole-brain analyses revealed a network of parietal and frontal brain areas that are more active in response to valid memory cues, relative to memory-neutral cues (valid > neutral, $P_{FDR} < 0.05$). (*B*) More specific ROI analyses focused on activation profiles within key nodes of an attentional network, IPS and FEF, that were previously associated with memory-guided orienting (16). Beta parameter estimates are plotted as a function of memory condition (valid vs. neutral) and event type (cue vs. target). Validity effects were specific to the cue event in both ROIs. (*C*) Data were also analyzed for the hippocampus, defined according to the coordinates from Summerfield et al. (16), which are also shown as a function of memory condition (valid vs. neutral) and event type (cue vs. target). Hippocampal activity was specific to cue events, and there was a trend for a validity effect for cues but not targets. Error bars represent ±1 SEM.

critically underlying adaptive and intelligent behavior. Here we address the important link between predictions derived from past experience and another fundamental optimizing principle, attentional control. In two complementary experiments, we demonstrate how past experiences could shape perception via shifts in baseline visual activity to optimize sensory analysis of task-relevant information. The fMRI results also implicated an extended network of brain areas, including the hippocampus and key nodes of a dorsal frontoparietal network, as a likely candidate for memory-guided control over visual cortex.

Memory Predictions Optimize Preparatory Visual Activity for Target Detection. Past experience facilitates perception: following a valid memory cue, perceptual sensitivity was enhanced at memory-predicted spatial locations. Previously, we demonstrated that the contents of LTM reduce response latencies for stimuli presented at memory-predicted locations (16). However, in the present study, we now demonstrate that past experiences directly modulate perceptual sensitivity. This raises the important question: how do predictions, stored in LTM, fine-tune perceptual sensitivity?

Exploiting the high temporal resolution of EEG, we first demonstrate that memory cues trigger a shift in lateralized power of neural oscillations in the alpha band. In posterior electrodes overlying visual cortex, alpha power decreased when memory cues predicted target locations on the contralateral side of space, relative to predicted ipsilateral targets. This pattern of lateralized changes in alpha-band neural oscillations at memory-predicted locations closely resembles changes in preparatory oscillations that are elicited by explicit perceptual cues (23–27). Specifically, a cue stimulus that directs attention to the left or right side of space elicits a relative bias in neural oscillations at posterior electrodes, which can be characterized by increased power over ipsilateral visual areas, relative to alpha desynchronization in contralateral visual cortex. Although it can be difficult to disentangle the direction of relative changes in alpha power (33), ipsilateral alpha is tightly coupled to trial-by-trial variations in perceptual sensitivity (28), providing important evidence that alpha-band oscillations are important for suppressing task-irrelevant information processing. Similarly, artificial induction of lateralized biases in alpha-band oscillations can also induce a corresponding shift in perceptual bias. Transcranial magnetic stimulation (TMS), delivered at 10 Hz to visual cortex, impairs subsequent processing of visual input from the contralateral visual field, and correspondingly, facilitates processing for ipsilateral visual input (24). Overall, these results are consistent with theoretical models that suggest that oscillations in the alpha range suppress neural processing (28, 34). Accordingly, selective desynchronization could release specific neural populations from baseline suppression resulting in a relative increase in processing efficiency within alpha-desynchronized neural ensembles.

Dynamic shifts in alpha power provide a plausible neurophysiological mechanism for fine-tuning the sensitivity of visual cortex to bias information processing at spatial locations that are most likely to be behaviorally relevant. The results of this experiment provide evidence that shifting the balance of alpha-band oscillations in visual cortex could also mediate perceptual optimization according to past experience. By using naturalistic scenes, attentional orienting in this study exploits high-capacity brain mechanisms for LTM. Participants were able to learn locations for a large number of scenes with relatively few exposures. In this study, we were careful to control for differences in the "memorizability" of scene locations by counter-balancing stimuli across participants. However, future modifications of this experimental design could directly manipulate the strength, and/or accuracy of location memories to identify activity patterns that are strongly coupled to the quality of memory.

Previous fMRI experiments that used explicit perceptual cues to direct the focus of spatial attention have also revealed a pattern of preparatory biases in visual cortex that complements contralateral alpha desynchronization observed in EEG. Visual activity, index by changes in the blood oxygenation level-dependent (BOLD) fMRI response, increases when attention is directed to the contralateral visual field, relative to ipsilateral shifts of attention (8). Dynamic changes in the cue-related BOLD response in visual cortex also predict perceptual sensitivity (10, 35), and perceptual sensitivity is also enhanced when TMS is used to induce transient elevations in the BOLD response at spatially specific subregions of visual cortex (36). Finally, similar shifts in baseline activity are also observed for nonspatial preparatory attention (37, 38), consistent with a general mechanism of attentional control that selectively preactivates neural subpopulations that code for cue-predicted information (6).

Similar dynamics observed in the present study demonstrate that memory predictions can also preactivate neural subpopulations in visual cortex that code information that is most likely to be relevant to behavior. The results of the fMRI experiment also provide important neuroanatomical insights that were beyond the scope of the EEG experiment. Modulations in the BOLD response were most evident in ventral visual areas V3 and V4, as well as V3a in the dorsal visual cortex. There was little evidence of contralateral BOLD increases for earlier visual areas, including V1 and V2. Although it is possible that LTM is unable to modulate early visual cortex, other factors particular to this experiment could also account for the null effect in V1/V2. For example, preparation for the target object used in this experiment could preferentially modulate neural populations in higher visual areas (38), compared with preparatory activity for more basic visual features, such as orientation, previously observed in V1 (10). The lack of early visual modulation could also be attributed to differences in the precise spatial location between scenes, as there might have been insufficient overlap in the preparatory response to yield a significant average across trials in early retinotopic cortex.

Relationship Between Shifts in Alpha Power and BOLD Response. By using complementary methodologies, the results of the current study highlight the relationship between shifts in alpha power and BOLD responses in visual cortex (39, 40). In previous attention studies, both mechanisms have been associated with preparatory biases corresponding to the focus of covert spatial attention (8, 23), as well as corresponding changes in perceptual sensitivity (10, 11). The present study provides important confirmation of the functional relationship between these two measures across near-identical experimental contexts. The only difference between the EEG and fMRI experiment was the delay between cue and target stimuli. Consequently, lateralized shifts in visual activity observed in EEG and fMRI are both likely to reflect neurophysiological mechanisms for optimizing perceptual sensitivity according to task-relevant spatial predictions.

Top-Down Control for Memory-Guided Preparatory Biases. Without reference to past experience, the cue stimulus used in the memory-guided orienting task provides no predictive information. This lack of intrinsic spatial cueing by the visual input raises the important question: how do memory predictions modulate preparatory activity in visual cortex?

Feedback from dorsal subregions of frontal and parietal cortices, including IPS and FEF, is an attractive candidate (41–43). Numerous fMRI studies of attention implicate these high-level brain areas as key nodes in an attention network that provides dynamic modulation of visual cortex (7, 44–46). In the present experiment, we successfully dissociate activity relating to cue and target events, allowing us to confirm that valid memory cues activate IPS and FEF more than neutral memory cues. Importantly, there was no difference between memory conditions during target processing. Frontoparietal activity that is specific for valid memory

predictions could provide top-down modulation of visual cortex, resulting in preparatory biases that would optimize target processing. However, top-down feedback from a putative attention network is unlikely to be sufficient for memory-guided orienting. More likely, an additional memory signal is also required for attentional modulation to reflect predictions stored in LTM.

Previously, we proposed that the hippocampus provides a crucial interface linking past experience with attentional orienting systems to optimize perception (16). In our previous study, hippocampal activity was higher for valid relative to neutral memory trials; however, as mentioned earlier, it was not possible to dissociate activity related to the cue or target. In the present study, the hippocampus was more active during the cue period, relative to target processing, consistent with the hypothesis that hippocampal memory signals provide important information during memory guided orienting. We further suggest that memory signals from the hippocampus could be integrated within frontoparietal cortex, which in turn generates the appropriate top-down attentional signal to modulate preparatory visual activity.

Recent studies highlight the importance of oscillatory dynamics in forming functional connections between distant brain areas (47), including hippocampus and prefrontal and visual cortices (48). It will be important for future studies to identify how brain areas for memory, attention, and perception are coupled during memory-guided attention. Moreover, further studies could test the critical involvement of frontoparietal cortex in memory-guided orienting by using TMS to disrupt key nodes of the attention network. Previously, Summerfield et al. (16) found that memory-guided orienting could facilitate reaction times to memory-predicted targets even with a very short cue period (100 ms). Rapid attention effects could reflect direct connections between medial temporal lobe memory structures and visual cortex; whereas modulation via the frontoparietal network could trigger attentional modulations in visual cortex over a more extended time range.

Overall, the results of these experiments provide convergent evidence that memory-guided attention is mediated via the hippocampus and attention-related frontoparietal network. This control network could orchestrate spatially specific activation biases observed in visual cortex to optimize perception for behaviorally relevant stimuli. Therefore, we propose that the neural mechanisms previously associated with externally cued attentional orienting also shape ongoing perceptual processing according to past experience stored in LTM (see also refs. 49, 50), and that the hippocampus provides the crucial link between past and future goals during memory-guided attention. This network provides a plausible neurophysiological basis for ongoing processes that continuously shape activity in perceptual brain areas according to our past experiences, rendering our perception of the world unique and inherently personal (1).

Materials and Methods

EEG Experiment. ***Participants.*** Participants were 16 healthy right-handed volunteers (seven male, nine female; mean age, 25 y) with normal or corrected-to-normal vision. All participants gave written informed consent before testing, and were financially reimbursed for their time. Experimental protocols were approved by the University of Oxford Central University Research Ethics Committee.

Experimental protocol. The experiment was conducted over three sessions performed separately on consecutive days (16). Over the first 2 d, participants performed a learning task to establish long-term memories for specific spatial locations within a large set of naturalistic scenes. Next, participants performed a memory-guided orienting task while we acquired EEG data.

Learning task. During the learning task, participants viewed 192 naturalistic scenes repeated in random order over six blocks. Scene stimuli were similar to those used by Summerfield et al. (16), consisting of photographs of different indoor or outdoor views. Scenes were prepared using Matlab, and subtended 22° × 17° of visual angle at a viewing distance of 100 cm. Half the scenes contained a target stimulus (a small gold key 15 × 29 pixels in size, equivalent to 0.3° × 0.7°), located in either upper or lower quadrants of the right or left side of the picture. In the remaining 96 scenes, no target was present. Participants were instructed to explore the scenes overtly (freely moving their eyes) to search for the embedded targets. To indicate when a target was found, participants clicked the left button of a mouse, and then moved a cursor (a small white box) onto the target before clicking the left mouse button again. If the participant made no response, the program moved onto the next scene after a variable interval, which decreased in length between blocks: 16 to 24 s in block 1, 12 to 20 s in block 2, 12 to 20 s in block 3, 10 to 18 s in block 4, 10 to 18 s in block 5, and 8 to 16 s in block 6. Furthermore, to reduce the discrepancy in exposure time between the scenes with targets present and absent, the presentation durations of the scenes without targets were calibrated according to the participant's reaction times for locating targets in target-present scenes. The presentation time for target-absent scenes was randomly drawn from the last five reaction times in target-present scenes, with 2 s added to account for cursor manipulation time.

Participants were instructed to locate as many targets as they could over the six learning blocks, and to memorize their locations when they had been found. The order of presentation of scenes was randomized in each block for each version. The target presence, and location, within each scene was counterbalanced across participants. Eye movements were recorded by using an infrared eye-tracking system (ISCAN).

Memory-guided orienting task. One day after completing the learning task, participants performed the memory-guided orienting task while we recorded EEG data. Similarly to standard overt visual orienting tasks (22), participants were cued to attend covertly to a specific spatial location before the presentation of a target stimulus. However, in contrast to typical visually guided orienting tasks, the cue does not directly provide predictive spatial information in the memory-guided orienting task, but rather, predictive spatial information is retrieved via LTM.

Each trial commenced with a cue stimulus (100 ms) that was valid or neutral with respect to the associated spatial information stored in LTM. Valid memory cues were scenes for which participants had encoded into LTM a specific target location during the learning task; whereas neutral memory cues were scenes for which there was no specific spatial information stored (i.e., no target had been present during the learning task). The validity of the memory cue was verified by accurate spatial recall during a subsequent explicit memory task (described later). Scenes that had contained a target during the learning task, but which were not associated with explicit location memories—either because the target had remained undetected during the learning task, or because the exact location of the target had since been forgotten—were excluded from behavioral and EEG analyses. Cue offset was followed by a gray fixation screen presented for a variable delay, randomized between 750 and 1,150 ms, followed by a probe screen for 200 ms. The probe screen was always the same scene just presented as the memory cue, but this time with an additional target stimulus on 50% of trials. As in the learning task, these targets were a small gold key. However, because the presentation of the target screen was brief (200 ms), and participants performed the detection task covertly, the key stimuli were larger (25 × 49 pixels; equivalent to 0.6° × 1.1°) relative to the visual scene (22° × 17°) in the orienting task. Targets were always presented at the same location as in the learning task within valid memory scenes or at a randomized location within the neutral scenes. Target presence, location, and relation to its appearance in the learning task (valid or neutral) were counterbalanced across participants. Participants could respond within a 1,000-ms time window after the probe scene disappeared. After feedback, the next fixation screen indicated the start of a new trial. Eye movements were monitored by using an infrared eye-tracking system (ISCAN). Presentation (version 10; (Neurobehavioral Systems) was used for all aspects of experimental control, including stimulus presentation, recording behavioral responses and synchronizing experimental timing with the EEG recordings.

Explicit memory task. Immediately after performing the orienting task, participants performed an explicit memory task to determine which scenes were associated with accurate memories for the target locations identified during the initial learning task. The procedure was almost identical to that of the learning task; all 192 scenes were presented sequentially, and in a randomized order. However, unlike the memory task, the target stimulus was always absent. Therefore, rather than searching for the target, participants indicated whether they could recall the presence of the key stimulus in each scene via a mouse-button click, and then if possible, the precise location of the remembered target location by moving the cursor to the remembered location and clicking again. Participants were also instructed to rate the confidence in their responses using a three-point scale. Each scene was

considered to be associated with a valid target memory location if the final click was within a 150-pixel radius (3.4°) of the target location.

Event-Related Potential Recording and Analysis. The EEG was recorded continuously by using NuAmp amplifiers (Neuroscan) from 33 scalp sites by using Ag/AgCl electrodes mounted on an elasticized cap, positioned according to the International 10-20 system (American Electroencephalographic Society, 1991). The montage included seven midline electrode sites (FZ, FCZ, CZ, CPZ, PZ, POZ, and OZ) and 14 sites over each hemisphere (FP1/FP2, F7/F8, F3/F4, FT7/FT8, FC3/FC4, T7/T8, C3/C4, TP7/TP8, CP3/CP4, P7/P8, PO7/PO8, PO3/PO4, and O1/O2). Additional electrodes were used as ground and reference sites and for recording the electrooculogram (EOG). The right mastoid was used as the active reference. Data were then rereferenced offline to the algebraic average of the right and left mastoids. The horizontal EOG was recorded bipolarly with one electrode on the side of one eye and the other electrode on the other side of that eye directly next to the nose. Vertical EOG data were recorded bipolarly with one electrode under the right eye and FP2 used as the other vertical EOG. The signal was digitized at a sampling rate of 1,000 Hz. Data were recorded with a low-pass filter of 200 Hz and with no high-pass filter (dc). Digital codes were sent to the EEG recording computer to mark the presentation of the cue and target stimuli in each trial type.

Offline, the EEG was then low-pass filtered (40 Hz) and epoched to the presentation of the cue stimuli. Epochs started 500 ms before and ended 1,000 ms after the stimulus presentation. Epochs containing excessive noise or drift (±100 mV) at any electrode were rejected. Trials with blinks and large saccades (±50 mV), identified through the horizontal and vertical EOGs, were excluded; additional visual inspection was used to remove trials with any residual artifacts or eye movements. Epochs were baselined from 0 to 50 ms after stimulus presentation.

Time-frequency analysis was performed in Fieldtrip (Donders Institute for Brain, Cognition and Behavior) by using a multitaper method with default parameters. All analyses were performed on alpha power. During initial preprocessing in NeuroScan, a fast Fourier transformation was first used to estimate the frequency of the alpha band in each participant. Individual alpha frequency was identified by a distinct peak in power between 8 and 12 Hz (mean, 9.8 Hz; range, 9–11Hz). To avoid contamination from event-related responses to the cue or target stimuli, statistical analyses were restricted to a time window spanning 650 ms to 750 ms after cue onset. This conservative time window corresponds to at least 100 ms before the onset of the earliest possible presentation of the time-jittered target.

fMRI Experiment. ***Participants.*** Participants were 20 right-handed volunteers with normal or corrected-to-normal vision and no history of neurological or psychiatric illness (9 male, 11 female; mean age, 21 y). Participants were also screened for MRI contraindications, and provided written informed consent before testing. Volunteers were financially reimbursed for their time, and all experimental protocols were approved by the Hertfordshire Local Research Ethics Committee.

Experimental protocol. The experimental protocol was extended across two consecutive days. Again, participants performed the learning task before the orienting task in the fMRI scanner. As a result of an equipment failure during the fMRI experiment, button-press responses were not recorded in five participants, therefore, behavioral analyses were performed on the remaining 15 participants (eight male, seven female; mean age, 21 y). Presentation (version 10; Neurobehavioral Systems) was used for all aspects of experimental control, including stimulus presentation, recording of behavioral responses, and synchronization of experimental timing with scanner-pulse timing during fMRI.

Learning task. The learning task used to train participants for the fMRI experiment was almost identical to the learning task described earlier for the EEG experiment, with the following exceptions. Stimuli were 120 naturalistic scenes repeated in random order over five blocks. Scenes were the same as those used by Summerfield et al. (16), consisting of photographs of different indoor or outdoor views. Scenes were prepared by using a graphics editor package (Paint Shop Pro 5; Jasc; 1,000 × 750 pixels in 32-bit color), and subtended 28° × 21° of visual angle at a viewing distance of 80 cm. Eighty scenes contained a target stimulus (a small gold key 12 × 23 pixels in size, equivalent to 0.3° × 0.7°), located anywhere within the right or left side of the picture. In the remaining 40 scenes, no target was present. If the participant made no response, the program moved onto the next scene after a variable interval, which decreased in length between blocks: 16 to 24 s in block 1, 12 to 20 s in block 2, 8 to 16 s in block 3, 4 to 12 s in block 4, and 2 to 10 s in block 5.

Memory-guided orienting task. The orienting task was identical to that used in the EEG experiment, with a few exceptions. Most importantly, for the fMRI experiment, the temporal structure of the orienting task was manipulated to allow us to separate the neural response to cue and target stimuli. Specifically, the intervals between the onsets of cue and target stimuli, and between successive trials, were long and variable (2–12 s), thereby reducing the correlation between condition-specific regression functions used to model the hemodynamic response. These long intervals were distributed logarithmically to shorten the total duration of the experiment and to keep temporal expectations constant. Participants were instructed to indicate whether they had detected the target stimulus at the end of each trial by pressing one or other of two buttons on an MRI-compatible button box. Overall, there were 120 trials, 40 of which contained neutral memory cues. Cue stimuli on the remaining 80 trials were classified valid memory cues if the target location was found during the learning task, and if participants could explicitly recall the learned location during the subsequent memory test. Trials with cues for which target-predictive memories could not be verified (i.e., were not learned and/or recalled during the explicit memory test) were modeled separately. Before scanning, participants performed a short practice session of the memory-guided orienting task, which contained only novel scenes. Participants were instructed to refrain from head movements and eye movements throughout the scanning session. Central fixation was confirmed in six participants by using an MRI-compatible eye-tracking system (ASL 504 LRO eye tracking system; Applied Sciences Laboratory). Eye-tracking data were analyzed offline by using ILAB version 3.6.4 (51). Participants maintained fixation within 3° of central fixation on at least 95% of trials. Most importantly, there was no relationship between the observed eye position during valid memory trials and the location of the learned target stimulus. Specifically, there were no differences within any participant between the horizontal eye position recorded during left or right memory cue trials ($P > 0.05$).

Explicit memory task. Performed immediately after scanning, the explicit memory task was identical to task used in the EEG experiment described earlier, except that confidence rating was not collected. As in the EEG experiment, scenes were considered to be associated with a valid target memory location if participants could indicate the correct location within a 150-pixel radius.

Image acquisition. Functional images were acquired with a 3-T Siemens Tim Trio MRI system using a 12-channel head coil. Stimuli were back-projected by using a Hitachi CP-X80 LCD projector onto a translucent screen that participants viewed through mirrors. Images were acquired using echo-planar T2*-weighted imaging (echo time, 30 ms; repetition time, 3 s), consisting of 45 axial slices of 3 mm (3 mm^3 voxel size) in a 64 × 64 acquisition matrix (192 × 192-mm field of view). The acquisition matrix was positioned to cover the entire cortex and cerebellum. The first four image volumes were collected in the absence of any task to allow the signal to reach a steady state, and were excluded from further processing and analysis. High-resolution anatomical images (1 × 1 × 1 mm) were also acquired for each participant by using a T1-weighted magnetization-prepared rapid gradient-echo sequence (field of view, 192 × 192 mm; 176 sagittal slices).

Image processing and analysis. The imaging data were analyzed by using statistical parametric mapping (SPM5; Wellcome Trust Centre for Neuroimaging). Images were corrected for slice timing, and jointly realigned and unwarped by removing variance caused by susceptibility-by-movement interactions (52). The anatomical scans were realigned to the mean functional image, and then both types of images were transformed into a standardized space by using the default Montreal Neurological Institute template provided by SPM 5. The resulting functional images were spatially smoothed using an 8-mm Gaussian kernel. The time series was also temporally filtered using a high-pass filter (128 s) to remove signal drift across the scanning session, and corrected for autocorrelations using the AR(1) model in SPM5. The neural responses to events of interest were modeled using the canonical HRF. Separate regression functions were used to model cue events according to event type, including valid and neutral conditions, for left- and right-sided targets. Cues for which a target-predictive memory could not be confirmed were modeled separately by a regressor of no interest. Target events were modeled by regression functions for target present and absent scenes preceded by left- and right-associated memory cues, or neutral memory cues. Again, a separate regressor of no interest captured variance associated with target scenes that followed a cue that could have been associated with a specific location, but that was forgotten or never found during the learning task. Finally, movement parameters were also used to construct six regressors to model variance caused by head movements during scanning.

Specific contrasts were then entered to the second-level random-effects analyses. First, we examined spatially specific preparatory activity by contrasting beta parameters for left and right valid memory cues. Contrast maps were then projected onto the surface of occipital cortex using Freesurfer, and corrected for multiple comparisons [i.e., false discovery rate (FDR)]. ROI analyses were also performed by using MarsBar.[†] To avoid circular inferences (53), visual ROIs were defined on independent data. Specifically, ROIs for each visual area were taken from a previous study that combined retinotopic maps from 11 participants, each normalized to the standard Montreal Neurological Institute template (54). Control analyses were also performed to ensure that spatially specific activity was triggered by memories, rather than target stimuli. To compare cue-related activity on target-present and target-absent trials, we performed another first-level analysis, this time separating cues according to the presence or absence of target stimuli. Again, these data were assessed at the group level with a second-level analysis at specific ROIs.

Finally, we also examined activity specific to valid memory cues, relative to neutral cues. Beta parameters estimated at the first level were averaged across laterality, yielding the critical contrast: valid memory cue vs. neutral memory cue. The statistical map was projected across the whole cortical surface in Freesurfer, and FDR-corrected for multiple comparisons. Again, to avoid circular inferences, ROIs were selected by using previously identified neuroanatomical coordinates. Specifically, we examined the event-related response to cues and targets as a function of cue validity within spherical ROIs centered on coordinates for the left hippocampus (−30, −15, −18 mm, r = 3 mm), FEF (left, −27, −3, 51 mm, r = 10 mm; right, 33, 6, 51 mm, r = 10 mm) and IPS (left, −27, −63, 51 mm, r = 10 mm; right, 27, −66, 45 mm, r = 10 mm) previously identified by Summerfield et al. (16).

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