Research Report

Attentional modulation of repetition attenuation is anatomically dissociable for scenes and faces

Do-Joon Yi[a], Todd A. Kelley[b], René Marois[c], Marvin M. Chun[a],*

[a]Department of Psychology, Yale University, 2, Hillhouse Ave., PO Box 208205, New Haven, CT 06520-8205, USA
[b]Department of Psychological and Brain Sciences, Johns Hopkins University, Baltimore, MD 21218, USA
[c]Department of Psychology, Center for Integrative and Cognitive Neuroscience, and Vanderbilt Vision Research Center, Vanderbilt University, Nashville, TN 37203, USA

ARTICLE INFO

ABSTRACT

Repeating a stimulus generally leads to a decreased response in neural activity compared to that for novel items. This neural attenuation provides a marker for stimulus-specific perceptual encoding and memory that can be detected using functional magnetic resonance imaging (fMRI). Although previously assumed to occur automatically whenever a stimulus is repeated, recent studies have begun to show that the repetition attenuation effect is task-specific and modulated by attention. Here, we demonstrate that attention is crucial for obtaining neural attenuation even after extensive stimulus repetitions. Furthermore, the effect of attention on attenuation is anatomically dissociable for stimuli that have relatively segregated neural representations in high-level perceptual cortex. To manipulate attention, we used overlapping scene and face images, and asked subjects to attend to either category. In a scene-sensitive cortical region known as the parahippocampal place area (PPA), significant attenuation in the fMRI BOLD signal was observed for the attended repeated scenes (relative to attended novel scenes), while no attenuation was observed for ignored repeated scenes or attended repeated faces against their respective novel image baselines. Conversely, in the face-sensitive region known as the fusiform face area (FFA), significant attenuation was observed for attended repeated faces, but not for ignored repeated faces or attended repeated scenes. An additional control experiment ruled out alternative explanations based on global signal level reductions due to inattention. Thus, attention actively governed when neuronal activity was attenuated to repeated perceptual input, and such attenuation was specific to the cortical regions that actively represent the attended category of stimuli.

© 2006 Elsevier B.V. All rights reserved.

1. Introduction

Prior exposure to a stimulus facilitates subsequent perception of the same stimulus, a benefit known as perceptual priming.

The neural basis of such priming has been the focus of much neuroimaging research, which has typically revealed a reduction in neural activity to repeated stimuli compared to novel stimuli (Maccotta and Buckner, 2004; Buckner et al., 1995, 1998;

Grill-Spector and Malach, 2001; Squire, 1992; Yi and Chun, 2005). These learning-related changes in neural activity have been denoted as the repetition suppression, adaptation, or attenuation effect. A commonly accepted model for such repetition-induced reductions is that learning causes the pruning of neural activity that poorly represents a stimulus's features, resulting in a smaller, but more selective population of neurons to support perceptual memory (Desimone, 1996; Wiggs and Martin, 1998). Another viable interpretation is that attenuation may occur if the entire population of selective neurons is less active to repeated images (Henson and Rugg, 2003).

Such learning properties are highly adaptive and useful as they allow the perceptual system to process recurrent stimuli more efficiently, and they also enable rapid orienting to novel visual events (Stern et al., 1996; Desimone, 1996). However, there is too much information from the visual environment for sensory systems to fully encode (Chun and Marois, 2002; Marois and Ivanoff, 2005). Rather, some selection should occur to achieve an adaptive balance between the need to encode new stimuli (plasticity) and to maintain existing connections (stability) in neural circuitry (Grossberg, 1980; Yi and Chun, 2005).

Powerful attentional mechanisms in the brain regulate which information is selected and processed more extensively (Kanwisher and Wojciulik, 2000; Kastner and Ungerleider, 2000). Naturally, such attentional mechanisms should play a role in regulating which information is learned and which is not. Learning should occur only for attended information and not for unattended information, otherwise the brain would be overwhelmed with information to encode (Rock and Gutman, 1981; Jiang and Chun, 2001).

As evidence for these considerations, researchers have begun to demonstrate attentional modulation of learning-related attenuation effects to repeated perceptual events. First, there is growing evidence that repetition attenuation is actively modulated by the task that the subject is engaged in (Henson et al., 2002). For example, it is important that subjects perform the same task across repetitions; if subjects perform different tasks for otherwise identical pairs of stimuli across trials, then repetition attenuation is not observed (Dobbins et al., 2004). Moreover, simple instruction of what to attend to modulates repetition attenuation. Using stimuli that were spatially segregated (Eger et al., 2004) or could be segregated with spatial attention (Murray and Wojciulik, 2004), fMRI studies have shown that the attenuation occurred for attended information and not for unattended information. Such attentional modulation occurred even for attended and unattended stimuli that overlap in the same location. Using composite images of overlapping scene and face stimuli, Yi and Chun (2005) demonstrated that attenuation for repeated scenes only occurred when the scenes were fully attended. Yi and Chun further showed that attention was necessary during both the initial presentation and during repetition, suggesting that attention is required for both encoding and retrieval.

The present study has two aims. The first is to provide a strong test of attentional modulation of attenuation effects. Prior studies typically used event-related designs in which repetitions occurred unpredictably within a trial or across several trials. Typically, only one or two repetitions were tested in the studies that involved attention or task modulation. Such event-related designs solidly demonstrated the lack of attenuation for unattended stimuli, ruling out expectancy effects and other confounds. However, it is conceivable that low stimulus repetition rates are inadequate for revealing attention-independent attenuations of activation. Hence, the present study employed a blocked design in which the stimuli were repeated up to 16 times within 32-s-long blocks. This blocked design yields highly robust levels of repetition attenuation (Grill-Spector et al., 1999). The question is whether attention would still gate neural attenuation when the 16 repetitions are actively ignored across the blocked presentations.

The second aim of this study is to examine the anatomical specificity of attentional modulation of learning-related neural attenuation, as prior studies had not compared different stimulus categories in separate ROIs. To this effect, we designed the experiment and stimuli as shown in Fig. 1. The stimuli consisted of overlapping scenes and faces, which both confer multiple advantages for studying neural plasticity using fMRI. First, several researchers have argued that scenes and faces are processed in dissociable cortical regions (Kanwisher et al., 1997; Epstein and Kanwisher, 1998, McCarthy et al., 1997; Aguirre et al., 1996; Puce et al., 1996) (but see Haxby et al., 2001; Tarr and Gauthier, 2000). Second, stimulus repetition decreases activity in these cortical areas (Ishai et al., 2004; Epstein et al., 1999; Yi and Chun, 2005; Yi et al., 2004). Finally, attention can enhance perceptual processing to one category over the other (O'Craven et al., 1999).

We first localized the PPA and the FFA in each subject to functionally define regions of interest (ROI) within which we probed attentional modulation of learning-related activity. Second, we instructed subjects to selectively attend to either scenes or faces within blocks of trials that presented scene-face composite images. Finally, we independently varied whether the attended or ignored stimuli set consisted of 32 novel or 2 cycling images in a factorial design. The difference in neural activity for novel and cycling images provides a measure of repetition attenuation. Each of the cycling images was repeated every 2 s, so our method provides a robust, sensitive test of short-term memory, akin to that measured using fMRI (Grill-Spector et al., 1999) or electrophysiology (Miller et al., 1991, 1993).

For the attended stimuli, we predict attenuated activity for repeated (cycling) scenes relative to novel scenes in the PPA, and for repeated faces relative to novel faces in the FFA. Critically, if attention modulates stimulus-specific learning within specialized cortical areas, then no such attenuation should be observed for repeated scenes in the PPA when the scenes are ignored, and for repeated faces in the FFA when the faces are ignored. Furthermore, a novel aspect of our design is that it enables us to establish the selectivity of attentional modulation of neural attenuation. Namely, we hypothesize that scene repetition should not affect activity in the FFA and that face repetition should not affect activity in the PPA. In sum, we measured learning-related neural attenuation for attended and ignored stimuli, while holding retinal stimulation constant across all comparisons.

Because ignoring a visual stimulus reduces the overall level of neural activity for that input, it is possible that the predicted
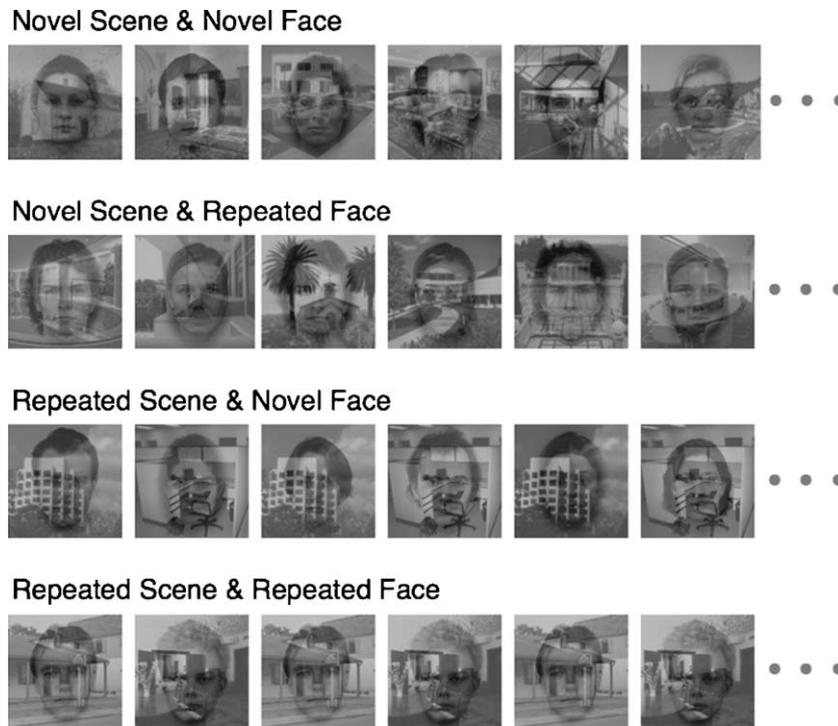
Fig. 1 – Composite scene-face stimuli and experimental design. Participants attended to either scenes or faces in alternating blocks. Within each attention condition, scenes were either novel or repeated and faces were either novel or repeated.

lack of adaptation for ignored stimuli may result from a scaling effect; namely, the lower BOLD signal levels may prevent us from observing attenuated activity. Thus, one must convincingly rule out such potential floor effects (Avidan et al., 2002). In prior studies, computational analyses indicate that the lack of attenuation during unattended conditions cannot be simply attributed to reduced levels of neural activity (Murray and Wojciulik, 2004). Moreover, by perceptually degrading the stimuli to reduce the corresponding neural response using low-pass filtering, Yi and Chun (2005) demonstrated that the lack of attenuation during inattention cannot be attributed to lower levels of BOLD signal. Here, we conducted an additional control experiment to further confirm that the predicted lack of attenuation for unattended stimuli cannot be attributed to floor effects in the BOLD response.

2. Results

2.1. Behavioral

Attended items were remembered better than unattended items. At the end of the scanning session, subjects rated whether each image was presented earlier during the main experiment using a three-option scale, where 1 was yes, 2 was maybe, and 3 was no. Subjects recognized attended images more confidently than unattended images ($M = 1.69$ vs. 2.06, $F(1, 12) = 41.15$, $P < 0.0001$). The ratings for unattended images did not differ from that for novel images that were never presented to subjects before (2.06 vs. 2.18, $F(1, 12) = 2.64$, $P > 0.1$).

We also analyzed the recognition task data as a function of whether the images came from novel image blocks or repeated image blocks. As one may expect, the ratings were better for attended repeated scenes than attended novel scenes (1.55 vs. 1.82, $F(1, 12) = 15.50$, $P < 0.003$). There was also a trend that approached significance for ignored repeated scenes to be recognized better than ignored novel scenes (1.97 vs. 2.16, $F(1, 12) = 4.31$, $P < 0.07$). The latter may reflect some residual familiarity with some repeated scenes that were inadvertently attended. Overall, the main point is that attended scenes were recognized more confidently than ignored scenes, replicating Yi and Chun (2005).

2.2. Neuroimaging

We localized the PPA bilaterally in all 13 subjects, the right FFA in 12 subjects, and the left FFA in nine subjects (see Experimental procedures and Fig. 2). Given the well-established laterality of face processing to the right hemisphere (Puce et al., 1996; De Renzi, 1997; Kanwisher et al., 1997) and also to maximize comparability between the PPA and FFA, we first focused our analyses to the right hemisphere ROIs (see Epstein et al., 2003). For completeness, the results from the left hemisphere ROI's will follow next (see also Table 1).

2.2.1. Parahippocampal place area (right hemisphere)
The percent signal change data were analyzed with a $2 \times 2 \times 2$ ANOVA using attention (scene or face), scene repetition (novel or repeated), and face repetition (novel or repeated) as the three factors. As reported before (O'Craven et al., 1999; Yi and Chun, 2005), there was a significant effect of attention with
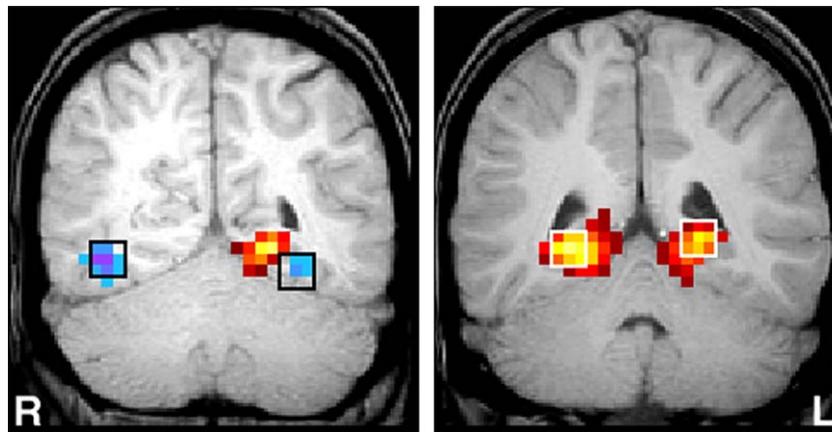
Fig. 2 – The FFA ROI (black outline) and PPA ROI (white outline) shown for a representative subject. Statistical parametric maps (P < 0.0001, uncorrected) on coronal T1 images show anatomically specific responses to either faces (bluish) or scenes (yellowish). Each ROI was defined as the voxel with the peak difference and its eight surrounding voxels.

higher responses in the PPA when scenes were attended compared to when faces were attended, $F(1,12) = 72.25$, $P < 0.00001$.

Fig. 3 (top left) shows significant attenuation in the PPA for repeated scenes when scenes were task-relevant and attended, but not when scenes were ignored during the face attention task. There was a main effect of scene repetition, $F(1,12) = 7.10$, $P < 0.05$, and a significant interaction between attention and scene repetition, $F(1,12) = 21.14$, $P < 0.001$. Critically, attentional modulation of learning in the PPA was specific to scene stimuli. The main effect of face repetition was not significant, $P > 0.2$ (Fig. 3 top right). Rather, there was a trend for increased responses in the PPA to attended scenes when faces were repeated, based on the marginally significant interaction between attention and face repetition, $F(1,12) = 3.84$, $P = 0.074$. It may have been easier to attend to scenes when the unattended face features repeated than when they were always novel, as revealed by the significant difference between repeated faces and novel faces in the background when scenes were attended, $t(12) = 2.82$, $P < 0.05$. Neither the two-way interaction between scene repetition and face repetition nor the three-way interaction reached significance, all P's > 0.1.

2.2.2.   Fusiform face area (right hemisphere)

We observed analogous trends for attentional modulation of face-learning activity in the FFA. The percent signal change data were also submitted to the same $2 \times 2 \times 2$ ANOVA employed for the PPA with attention, scene repetition, and face repetition as factors. Mirroring the scene attention responses in the PPA, there was a significant main effect of attention for face responses in the FFA, $F(1,11) = 6.01$, $P < 0.05$.

As shown in Fig. 3 (bottom right), repeating attended faces produced significant attenuation but repeating ignored faces did not. This observation was supported by a marginally significant interaction between attention and face repetition, $F(1,11) = 4.21$, $P = 0.065$. There was significant attenuation for attended repeated faces compared with attended novel faces, $t(11) = 2.58$, $P < 0.05$. The three-way interaction between attention, scene repetition, and face repetition was also marginally significant, $F(1, 11) = 4.13$, $P = 0.067$, further supporting the pattern that attenuation in the right FFA only occurred for attended repeated faces and not for ignored repeated faces, or for attended or ignored repeated scenes. Unlike the PPA data, the interaction between attention and the non-preferred category, in this case, scene repetition, was not significant (see Fig. 3 bottom left), $F(1, 11) = 1.41$, $P = 0.261$. The

Hemisphere	ROI	Attention	Novel scene		Repeated scene	
			Novel face	Repeated face	Novel face	Repeated face
Right	PPA	Scene	0.79 (0.05)	0.79 (0.06)	0.41 (0.04)	0.59 (0.05)
		Face	0.29 (0.06)	0.31 (0.04)	0.31 (0.08)	0.18 (0.05)
	FFA	Scene	0.71 (0.07)	0.60 (0.07)	0.50 (0.04)	0.62 (0.08)
		Face	0.73 (0.06)	0.80 (0.04)	0.91 (0.07)	0.65 (0.06)
Left	PPA	Scene	0.47 (0.04)	0.49 (0.04)	0.20 (0.03)	0.33 (0.05)
		Face	0.01 (0.06)	0.06 (0.05)	0.00 (0.06)	0.00 (0.03)
	FFA	Scene	0.54 (0.07)	0.51 (0.06)	0.32 (0.05)	0.37 (0.08)
		Face	0.59 (0.07)	0.56 (0.05)	0.71 (0.08)	0.52 (0.04)

Table 1 – Percent signal change for each condition in each ROI (standard error of the mean in parentheses)
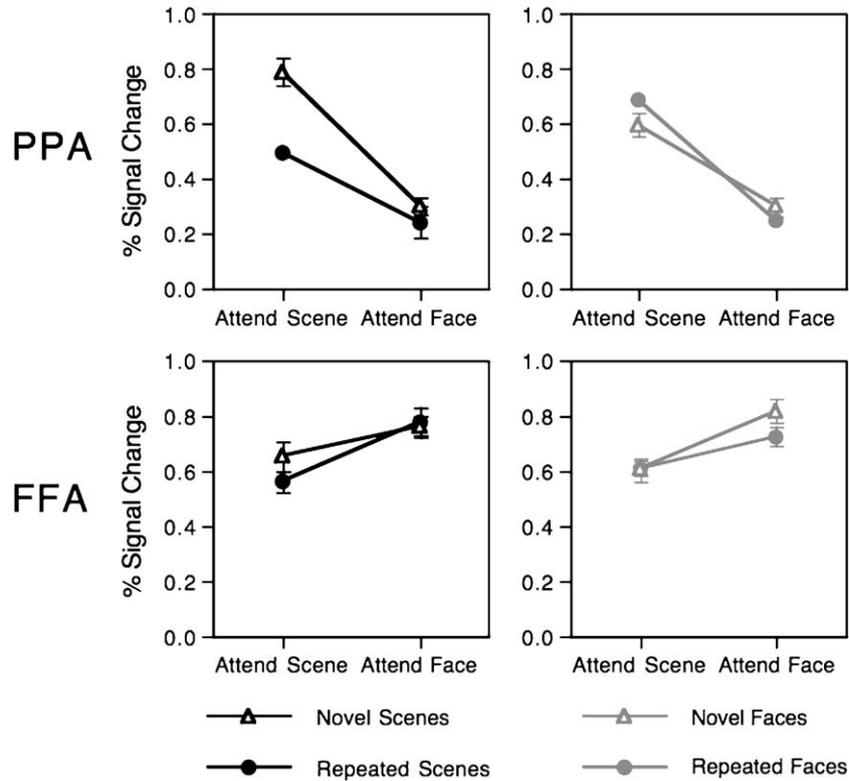
Fig. 3 – Percent signal change BOLD responses to novel or repeated scene and face stimuli in the PPA and FFA ROIs as a function of attention (scenes or faces). There was attenuation mainly for attended repeated scenes in the PPA and for attended repeated faces in the FFA. Error bars indicate within-subject standard error of the mean.

other main effects or interactions, not to mention repetition-related pair-wise differences (including the *t* test between novel and repeated scenes in the attend face condition), were not significant, all P's > 0.1.

2.2.3. Control experiment

As noted in the introduction, we conducted a control experiment to rule out the possibility that the lack of adaptation for unattended stimuli simply reflects a scaling effect where the lower BOLD signal levels prevented us from observing attenuated activity. For example, activation levels in the right hemisphere PPA dropped from 0.79% signal change for attended new scenes to 0.30% signal change for unattended new scenes. Although activation was significantly above baseline in the unattended condition, one must convincingly rule out potential floor effects (Avidan et al., 2002). To address this issue here, we measured adaptation for scene images that varied in contrast while matched for mean luminance. Reducing stimulus contrast weakens the overall level of neural activity and BOLD signal in relevant cortical areas (Boynton et al., 1996; Avidan et al., 2002). Thus, we presented new or cycling scene stimuli at high, medium, or low contrast. The low contrast condition provides a critical control for our attention manipulation. If overall signal strength is important, adaptation should be reduced. However, if attention is important, then adaptation should be observed because the low contrast images were fully attended.

Fig. 4 shows the results from 9 subjects. The PPA data were submitted to a 2 × 3 ANOVA with scene repetition (novel or repeated) and scene contrast (high, medium, or low) as factors. First, reducing contrast reduced the overall level of activity in the PPA. The main effect of scene contrast was significant $F(2,16) = 3.98$, $P < 0.05$, and its linear trend was also marginally significant, $F(1,8) = 5.00$, $P = 0.06$. Second, the adaptation effect was even across all levels of contrast. There was no interaction between the contrast and repetition factors, $F < 1$, and there was a significant main effect of repetition, $F(1,8) = 14.70$, $P < 0.005$. Most critically, attenuation was significant in the low contrast condition, $t(8) = 2.78$, $P < 0.05$, where the level of activity was comparable to the unattended condition in the PPA in the primary experiment above (0.33% vs. 0.30%, $P > 0.8$). Thus, reducing overall level of activity per se did not weaken
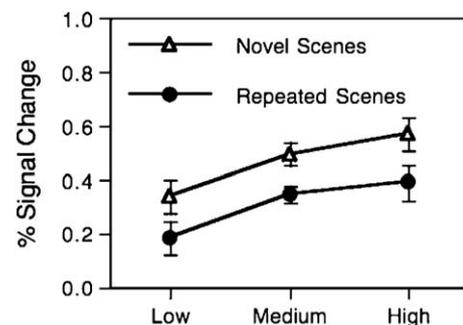

Fig. 4 – BOLD signal attenuation to repeated scenes in the PPA was robust across decreasing stimulus contrast levels. Error bars indicate within-subject standard error of the mean.

the learning effect, suggesting that we had sufficient sensitivity to detect learning even when the BOLD signal level was relatively low. These results strengthen our claim that adaptation is modulated by attention, rather than the overall level of neural activity *per se*.

2.2.4. Left hemisphere data

The data in the left PPA closely resembled those in the right PPA. In Experiment 1, a three-way ANOVA with attention, scene repetition, and face repetition as factors revealed main effects of attention, $F(1,12) = 110.67$, $P < 0.00001$, scene repetition, $F(1,12) = 7.71$, $P < 0.05$, and their two-way interaction, $F(1,12) = 18.14$, $P < 0.005$. Repetition attenuation was only significant for repeated scenes relative to novel scenes when the scenes were attended, $t(12) = 6.79$, $P < 0.0001$. Other main effects or interactions did not reach significance, all P's > 0.1. In the control experiment, a two-way ANOVA with scene repetition and scene contrast revealed both a main effect of scene contrast, $F(2,16) = 7.35$, $P < 0.01$, and a main effect of scene repetition, $F(1,8) = 13.64$, $P < 0.01$, but no interaction between contrast and repetition factors, $P > 0.3$. The repetition attenuation to low contrast scenes was also significant, $t(8) = 3.21$, $P < 0.05$.

The left FFA showed a pattern of activity different from the other ROI's in the main experiment. The same three-way ANOVA employed for its right hemisphere counterpart revealed a significant main effect of attention, $F(1,8) = 25.38$, $P < 0.005$, a significant interaction between attention and scene repetition, $F(1,8) = 9.24$, $P < 0.05$, and a marginal interaction between attention and face repetition, $F(1,8) = 3.95$, $P = 0.08$. These two interactions further support the commonly accepted notion that the left fusiform gyrus is less specialized for face processing than the right fusiform gyrus (Puce et al., 1996; De Renzi, 1997; Kanwisher et al., 1997). In fact, repetition attenuation was observed for attended scenes, $t(8) = 2.86$, $P < 0.05$, but not for attended faces, $P > 0.2$.

3. Discussion

We demonstrated that attention modulates learning-related attenuation of activity in the PPA and FFA for scenes and faces respectively. In the PPA, neural attenuation occurred for attended repeated scenes, but not for ignored repeated scenes or attended repeated faces. The right FFA revealed neural attenuation for attended repeated faces, but not for ignored repeated faces or attended repeated scenes. These results confirm prior work demonstrating that the neural attenuation effect is dependent on task and attention (Eger et al., 2004; Yi and Chun, 2005; Murray and Wojciulik, 2004; Ishai et al., 2004; Henson et al., 2002; Dobbins et al., 2004). However, the present study makes two novel points that extend previous work. First, it shows that attentional modulation of neural attenuation is robust, such that there was no evidence of attenuation in the unattended conditions even when stimuli were repeated up to 16 times every 2 s within a block. Previous studies that manipulated task or attention had typically only tested attenuation over one or two repetitions. The present results demonstrate the crucial role of attention on repetition attenuation across a wide range of stimulus repetitions.

Second, this study reveals that repetition attenuation and the attentional modulation of repetition attenuation occurred in an anatomically specific manner, at least for the face and house stimuli used here, which are known to have fairly distinct neural substrates (Epstein and Kanwisher, 1998; Kanwisher et al., 1997; Puce et al., 1996; McCarthy et al., 1997; Aguirre et al., 1996). The PPA bilaterally exhibited attenuation mainly to attended scene repetitions, while the right FFA mainly differentiated attended face repetitions. This dissociation is important because it shows that each of these cortical regions is primarily sensitive to attended repetitions of stimuli that it is specialized for, rather than responding to any perceptual repetition that is attended. These are useful constraints to identify because of the broader functions that these cortical regions play in perception and cognition. For example, parahippocampal cortex is involved in a wide variety of memory encoding tasks (Wagner et al., 1998; Brewer et al., 1998), while the fusiform gyrus has been implicated in perceptual expertise for non-face stimuli (Gauthier et al., 2000).

There were some interesting limitations in the selectivity of PPA and FFA responses to feature repetitions, however. There was a marginal effect of face repetition on PPA responses when scenes were attended (but not when faces were attended). This suggests intrusion of low-level face feature repetitions that overlapped the attended scene stimuli. Because the scene responses were enhanced by the unattended face repetitions, this result suggests that it was easier to suppress the repeated faces versus novel faces in the background, although this pattern was not present in the FFA for ignored scene repetitions. A different type of pattern emerged in the left hemisphere FFA, showing attenuation to repeated scene features when scenes were attended. This latter result is not surprising, however, given that left FFA exhibits less selectivity for face processing (Puce et al., 1996; De Renzi, 1997; Kanwisher et al., 1997).

Furthermore, it should be clearly noted that repetition attenuation effects are not restricted to the FFA or PPA, even for faces and scenes. The present study focused on selectivity between the FFA and PPA in order to test concrete hypotheses within cortical regions whose extensively studied responses are generally viewed as category-specific. However, across a variety of stimuli and tasks, repetition attenuation is routinely observed throughout a broader network of cortical regions, ranging from posterior occipital regions to prefrontal areas (Grill-Spector et al., 1999; Schacter and Buckner, 1998; Wig et al., 2005; Wagner et al., 2000). For example, in addition to fusiform gyrus, repeated faces yielded attenuation in the amygdala and insula (Ishai et al., 2004).

Thus, although attention modulates neural attenuation to repeated visual features in an anatomically dissociable manner for visual categories such as faces and scenes, selectivity was not perfect, in that repetition in the unattended or nonoptimal category mildly influenced activity. In this sense, the results may be compatible with prior demonstrations of attenuation in specialized cortical regions to nonoptimal stimuli, that is repeated house stimuli in the FFA or repeated face stimuli in the PPA (Avidan et al., 2002). The demonstration of stronger selectivity in our study may be attributed to several factors. Our use of overlapping stimuli

introduced more feature changes across repetition than Avidan et al. Moreover, our task had a different, intervening stimulus between repetitions, while Avidan et al. repeated stimuli consecutively. Finally, differences in how the ROIs were defined may lead to more or less selective responses.

Our control experiment showed that attentional modulation of learning is not simply an effect of reduced neural activity within a cortical area, replicating prior empirical and computational demonstrations (Yi and Chun, 2005; Murray and Wojciulik, 2004). This is not to say that it is not important to consider the overall level of neural activity within a region; for example, one of the primary effects of attention is to regulate the magnitude of activity within a cortical region (O'Craven et al., 1999; Wojciulik et al., 1998; O'Craven et al., 1997). The main point is simply that the lack of attenuation in the ignored stimuli conditions cannot be attributed to lack of sensitivity in fMRI to detect learning-related changes at lower signal strengths. It is also worth noting that the scenes were psychophysically discernible at the low contrasts used in this study. This is an important point because attenuation effects dissipate at even lower contrasts, where visibility is close to threshold (Avidan et al., 2002).

A final point we wish to make about our attentional manipulations is that these should not be interpreted as all-or-none effects. Attention to or away from a stimulus should be characterized along a continuum. Thus, under certain task conditions repeated stimuli may lead to learning and detectable attenuation effects even when task-irrelevant and ignored (Watanabe et al., 2001, Jiang and Chun, 2001; Jiang and Leung, 2005; Yi et al., 2004; Miller and Desimone, 1994). Learning of unattended stimuli will typically be observed when the primary task is easy or when it recruits attentional resources not required for processing the unattended events (Lavie, 1995; Rees et al., 1997; Yi et al., 2004). What is clear is that attentional modulation of learning-related attenuation effects are observed when the perceptual demands on attention are sufficiently taxing to minimize residual processing of ignored stimuli (Eger et al., 2004; Yi et al., 2004; Jiang and Chun, 2001).

3.1. Future directions

In closing, it is now uncontroversial that repetition attenuation effects can be modulated by task and attention. An important question for future research is to characterize the top-down control mechanisms that govern whether a stimulus will be encoded or not. One plausible mechanism, working memory, does not appear to be essential for repetition attenuation. Working memory maintains templates of attended stimuli within the frontal and parietal cortex (Desimone and Duncan, 1995), and so it would be reasonable to hypothesize that these template representations provide top-down signals to perceptual regions, gating whether attenuation effects occur or not. If so, attenuation effects should occur primarily for stimuli that were maintained in working memory, even momentarily. However, electrophysiological and fMRI evidence indicates that attenuation effects occur robustly even when working memory is occupied by other visual stimuli irrelevant to the repeating stimuli (Miller and Desimone, 1994; Yi et al., 2004). In other words, working memory maintenance does not appear necessary for repetition attenuation.

Thus, an alternative attentional mechanism may focus on selection processes within perceptual cortex itself. For example, if one considers multiple visual stimuli to be in competition with each other for limited cortical processing resources, then an attentional mechanism that biases this competition in favor of attended stimuli may allow these stimuli to be learned at the expense of unattended stimuli (Desimone and Duncan, 1995). Such biasing mechanisms may not require active maintenance of attended events in working memory. One clear example of such competitive bias may be spatial attention, which can be directed to objects in one location, filtering out objects in other locations. Accordingly, it is likely that modulation of repetition attenuation effects in prior studies benefited from mechanisms of spatial selection (Eger et al., 2004; Yi et al., 2004; Murray and Wojciulik, 2004). The neural mechanisms of object-based attention, necessary for the present task, are not clear yet, but the present findings indicate that object-based mechanisms must operate to modulate neural activity to attended stimuli within perceptual processing stages within or prior to cortical regions such as the PPA and FFA. The role of the fronto-parietal network in biasing competition in perceptual cortex represents an interesting agenda for future research.

Another issue for future research is to clarify how repetition attenuation effects relate to memory performance. In the present study, we employed recognition judgments, and subjects found attended stimuli to be more familiar than unattended stimuli, which were as unfamiliar as novel images that subjects had never viewed. These measures correspond to what memory researchers term explicit or declarative memory, the ability to consciously recognize or recollect past events (Squire et al., 1993; Tulving and Schacter, 1990). Explicit memory is distinguished from implicit memory, in which prior experience with a stimulus influences behavioral performance on future encounters with that stimulus even when the repeated stimulus cannot be consciously recognized as old or familiar. An example of implicit memory is behavioral priming (Squire et al., 1993; Tulving and Schacter, 1990). Repetition attenuation has typically been associated with behavioral priming rather than recognition judgments (Schacter and Buckner, 1998; Schacter et al., 2004; Wiggs and Martin, 1998). Thus, one observes repetition attenuation in frontal regions and perceptual cortex (e.g., fusiform gyrus) for stimuli that also support repetition priming in behavioral performance (Buckner et al., 1998; Koutstaal et al., 2001). In fact, one can even observe significant correlations between priming measures and neural attenuation effects (Maccotta and Buckner, 2004). The question is whether neural attenuation effects exclusively underlie implicit memory or whether they provide signals for explicit memory as well. Evidence from our lab suggests that neural attenuation effects can be linked to both explicit and implicit measures of memory, suggesting that the perceptual representations that support different forms of memory may have considerable overlap (Turk-Browne et al., in press). Thus, there is good reason to believe that attention may influence not just explicit memory, as is well-known to be the case, but also implicit memory (Jiang and Chun, 2001; Jiménez and Méndez, 1999; Turk-

Browne et al., 2005; Bentin et al., 1998; Mulligan, 1998). The present demonstration of attentional modulation of repetition suppression effects further bolsters the likelihood that implicit memory is not as automatic as has been proposed in the literature.

4. Experimental procedures

4.1. Participants

Twenty-four healthy volunteers gave written consent to participate in the two experiments. This project was conducted in compliance with the Institutional Review Board of Vanderbilt University.

4.2. Experimental design: main experiment

Thirteen subjects participated in six 394-s runs. The first four runs presented the primary task. The second two runs were localizer scans.

The primary task was to monitor a stream of composite grayscale scene-face stimuli, each presented for 800 ms, followed by a 200-ms blank, yielding a presentation rate of one composite image per second. The scene stimuli consisted of outdoor and indoor scenes, and the face stimuli included both male and female faces. Composite images were generated by presenting one scene and one face stimulus in rapid alternative flicker, each presented for a single 12 ms screen refresh. Because the alternation rate exceeds the temporal resolution of the visual system, the two alternating images appear simultaneous, overlapping in space. Scene and face stimuli were roughly matched in average luminance to minimize masking effects. This presentation method undoubtedly reduced the visibility of the stimuli, but this had the desired effect of increasing the demands of selective attention in our task. Selective attention is most effective when task perceptual load is high (Lavie et al., 2004; Yi et al., 2004).

The design manipulated attention and repetition. To vary attention, subjects attended to either scenes or faces in different blocks of trials. To study neural attenuation, we varied whether images were all novel or repeated within a block in a factorial design for both face attend and scene attend conditions (See Fig. 1). In the novel image condition, 29 to 30 of the 32 images presented in each block were different, with the remaining 2 or 3 images repeated once in succession for the 1-back task (see below). The majority of images appeared only once during the entire fMRI session; the 1-back task images were also novel in that they were only repeated once for the 1-back task during the entire session. In the repeating image condition, two different images repeatedly alternated 16 times across trials within each block, except on 2 or 3 occasions per block when one of the 2 images was immediately repeated for the 1-back task.

Each run contained 11 blocks of trials: four scene attention, four face attention, and three blank fixation blocks. The fixation blocks appeared at the beginning, middle, and the end of each run. The first fixation block was 34 s in duration; the rest were 36 s long. The scene and face attention blocks alternated in a counterbalanced manner. The four scene attention blocks and the four face attention blocks consisted of the following four types of image combinations (illustrated in Fig. 1): (a) novel scenes superimposed with novel faces, (b) novel scenes superimposed with 2 cycling faces, (c) 2 cycling scenes superimposed with novel faces, and (d) 2 cycling scenes superimposed with 2 cycling faces. Combining conditions (a) and (b) yielded the *novel scenes* condition, combining (c) and (d) formed the *repeated scenes* condition, combining (a) and (c) formed the *novel faces* condition, and combining (b) and (d) formed the *repeated faces* condition. Thus, an important feature of our experimental design is that the stimuli sequences were constructed in an identical manner for both attend face and attend scene blocks.

Each 36 s block began with a 4-s instruction period, during which the cue "Attend SCENES" or "Attend FACES was presented at fixation." This was followed by a series of 32 composite images, each lasting 1 s, as described above. To ensure that subjects attended to the correct stimuli class, they were asked to determine whether the present target was identical to the one immediately preceding it. In this 1-back task, subjects pressed a button upon detection of the consecutive repetition within the 1-s duration of each image frame. The consecutive repetitions only occurred about 2 or 3 times per block, independent of the cycling image manipulation. It is important to note that the attenuation response at focus here was primarily driven by the cycling image manipulation, not by the occasional back-to-back repetitions that occurred equally for both novel and cycling image conditions. Accuracy in the 1-back task was 93% correct for the novel image conditions and 92% correct for the cycling image conditions; the difference was not significant, indicating that the two conditions were matched for difficulty.

4.3. Experimental design: memory test

To confirm that attention enhanced learning, subjects participated in a surprise behavioral memory test at the end of the scanning session. We presented subjects with 80 scenes that were either previously attended (16 from novel scene blocks and 16 from repeated scene blocks), ignored (16 from novel scene blocks and 16 from repeated scene blocks), or not seen at all (16 completely novel). Subjects rated whether each image was presented earlier during the main experiment using a three-option scale, where 1 was yes, 2 was maybe, and 3 was no.

4.4. Experimental design: control experiment

Eleven subjects participated; two subjects were removed due to technical problems during scanning. Each subject participated in a total of five 394-s runs. Each run contained twelve 26-s blocks of 20 trials. Each trial lasted 1.3 s, with 1000 ms image presentation and a 300-ms blank fixation interval between trials. There were six types of experimental blocks, obtained by presenting novel or cycling scenes at each of the three levels of contrast (high, medium, low) in a counterbalanced manner. In addition, there were three fixation blocks: a 30-s fixation block at the beginning, and a 26-s fixation block in the middle and the end of the run. Subjects performed the 1-back task while viewing the stimuli, pressing

a key whenever a consecutive repetition was detected. Scene contrast was manipulated using Matlab. The contrast of each scene was first enhanced using histogram equalization. To reduce the contrast of scenes in the medium contrast condition, the intensity values of individual scenes were mapped to the values in a new intensity range, determined as a half standard deviation around the mean intensity. The same procedure was applied to scenes in the low contrast conditions, but with a narrower intensity range that was 1/6 standard deviation around the mean.

4.5. Experimental design: localizer task

Each subject performed two 394-s localizer runs prior to the main or control experiments. Each run contained 11 blocks of trials: two intact scene, two intact face, two scrambled scene, two scrambled face, and three blank fixation blocks. The fixation blocks appeared at the beginning, middle, and end of each run. The other blocks alternated in a counterbalanced manner. The first fixation block was 34 s in duration; the remaining blocks lasted 36 s each. The image blocks presented 36 images, each lasting 1 s (800 ms presentation, 200 ms blank). Subjects were asked to determine whether the present target was identical to the one immediately preceding it. In this 1-back task, subjects pressed a button upon detection of the consecutive repetition within the 1-s duration of each image frame. The consecutive repetitions occurred 3 times per block. Scrambled images were included in a pilot attempt to examine activity in the lateral occipital cortex (LOC) region, important for object recognition (Grill-Spector et al., 1998a,b; 1999). However, the use of scenes and faces to localize the LOC made the ROI difficult to define and interpret, and so these data will not be discussed in this paper.

4.6. fMRI design

Subjects were scanned with a 3T GE MRI system with resonant gradients for echoplanar imaging. T1-weighted structure images were first acquired using conventional parameters. T2* scan parameters for the primary experiment were as follows: repetition time (TR), 2 s; echo time (TE), 25 ms; flip angle (FA), 60°; 197 images per slice, with 28 slices (6 mm thick, 0 mm skip) acquired perpendicular to the anterior commissure–posterior commissure (AC–PC) line. T2* scan parameters were identical for the control experiment except that nineteen slices (7 mm, no skip) were acquired parallel to the AC–PC line. All experiments were controlled using Matlab equipped with Psychophysics toolbox extensions (Brainard, 1997; Pelli, 1997).

4.7. Data analysis

Analyses were conducted using the Yale fMRI software package (http://mri.med.yale.edu/individual/pawel/fMRIpackage.html). The PPA and FFA were localized in each individual by contrasting the averaged brain activity in scene blocks with face blocks of the localizer task. Statistical parametric maps of BOLD activation for each subject were created using a skew-corrected signal difference. The PPA ROI was defined as the voxel with the peak difference to scenes over faces and its eight surrounding voxels in the parahippocampal gyrus/

collateral sulcus regions (Marois et al., 2004; Yi and Chun, 2005; Yi et al., 2004). Mean PPA Talairach coordinates were $x = 20$, $y = -38$, $z = -8$; $x = -23$, $y = -38$, $z = -9$. Similarly, the FFA ROI was defined as the voxel with the peak difference to faces over scenes and its eight surrounding voxels in the anterior fusiform gyrus (Mean Talairach coordinates: $x = 39$, $y = -48$, $z = -15$; $x = -39$, $y = -48$, $z = -15$). The mean percent signal change was then computed for each condition relative to fixation from each ROI of each subject.

R E F E R E N C E S

Aguirre, G.K., Detre, J.A., Alsop, D.C., D'Esposito, M., 1996. Cereb. Cortex 6, 823–829.

Avidan, G., Hasson, U., Hendler, T., Zohary, E., Malach, R., 2002. Curr. Biol. 12, 964–972.

Bentin, S., Moscovitch, M., Nirhod, O., 1998. Acta Psychol. (Amst.) 98, 311–341.

Boynton, G.M., Engel, S.A., Glover, G.H., Heeger, D.J., 1996. J. Neurosci. 16, 4207–4221.

Brainard, D.H., 1997. Spatial Vision 10, 433–436.

Brewer, J.B., Zhao, Z., Desmond, J.E., Glover, G.H., Gabrieli, J.D., 1998. Science 281, 1185–1187.

Buckner, R.L., Petersen, S.E., Ojemann, J.G., Miezin, F.M., Squire, L.R., Raichle, M.E., 1995. J. Neurosci. 15, 12–29.

Buckner, R.L., Goodman, J., Burock, M., Rotte, M., Koutstaal, W., Schacter, D., Rosen, B., Dale, A.M., 1998. Neuron 20, 285–296.

Chun, M.M., Marois, R., 2002. Curr. Opin. Neurobiol. 12, 184–189.

Desimone, R., 1996. Proc. Natl. Acad. Sci. U. S. A. 93, 13494–13499.

Desimone, R., Duncan, J., 1995. Annu. Rev. Neurosci. 18, 193–222.

De Renzi, E., 1997. In: Feinberg, T., Farah, M.J. (Eds.), Behavioral Neurology and Neuropsychology. McGraw-Hill, New York, pp. 245–255.

Dobbins, I.G., Schnyer, D.M., Verfaellie, M., Schacter, D.L., 2004. Nature 428, 316–319.

Eger, E., Henson, R.N., Driver, J., Dolan, R.J., 2004. J. Neurophysiol. 92, 1241–1247.

Epstein, R., Kanwisher, N., 1998. Nature 392, 598–601.

Epstein, R., Harris, A., Stanley, D., Kanwisher, N., 1999. Neuron 23, 115–125.

Epstein, R., Graham, K.S., Downing, P.E., 2003. Neuron 37, 865–876.

Gauthier, I., Skudlarski, P., Gore, J.C., Anderson, A.W., 2000. Nat. Neurosci. 3, 191–197.

Grill-Spector, K., Malach, R., 2001. Acta Psychol. (Amst.) 107, 293–321.

Grill-Spector, K., Kushnir, T., Edelman, S., Itzchak, Y., Malach, R., 1998a. Neuron 21, 191–202.

Grill-Spector, K., Kushnir, T., Hendler, T., Edelman, S., Itzchak, Y., Malach, R., 1998b. Hum. Brain Mapp. 6, 316–328.

Grill-Spector, K., Kushnir, T., Edelman, S., Avidan, G., Itzchak, Y., Malach, R., 1999. Neuron 24, 187–203.

Grossberg, S., 1980. Psychol. Rev. 87, 1–51.

Haxby, J.V., Gobbini, M.I., Furey, M.L., Ishai, A., Schouten, J.L., Pietrini, P., 2001. Science 293, 2425–2430.

Henson, R.N., Rugg, M.D., 2003. Neuropsychologia 41, 263–270.

Henson, R.N., Shallice, T., Gorno-Tempini, M.L., Dolan, R.J., 2002. Cereb. Cortex 12, 178–186.

Ishai, A., Pessoa, L., Bikle, P.C., Ungeleider, L.G., 2004. Proc. Natl. Acad. Sci. U. S. A. 101, 9827–9832.

Jiang, Y., Chun, M.M., 2001. Q. J. Exp. Psychol., A 54A, 1105–1124.

Jiang, Y., Leung, A.W., 2005. Psychon. Bull. Rev. 12, 100–106.

Jiménez, L., Méndez, C., 1999. J. Exper. Psychol., Learn., Mem., Cogn. 25, 236–259.

Kanwisher, N., Wojciulik, E., 2000. Nat. Rev., Neurosci. 1, 91–100.

Kanwisher, N., McDermott, J., Chun, M.M., 1997. J. Neurosci. 17, 4302–4311.

Kastner, S., Ungerleider, L.G., 2000. Annu. Rev. Neurosci. 23, 315–341.

Koutstaal, W., Wagner, A.D., Rotte, M., Maril, A., Buckner, R.L., Schacter, D.L., 2001. Neuropsychologia 39, 184–199.

Lavie, N., 1995. J. Exp. Psychol. Hum. Percept. Perform. 21, 451–468.

Lavie, N., Hirst, A., de Fockert, J., Viding, E., 2004. J. Exp. Psychol. Gen. 133, 339–354.

Maccotta, L., Buckner, R.L., 2004. J. Cogn. Neurosci. 16, 1625–1632.

Marois, R., Ivanoff, J., 2005. Trends Cogn. Sci. 9, 296–305.

Marois, R., Yi, D.-J., Chun, M.M., 2004. Neuron 41, 465–472.

McCarthy, G., Puce, A., Gore, J.C., Allison, T., 1997. J. Cogn. Neurosci. 9, 605–610.

Miller, E.K., Desimone, R., 1994. Science 263, 520–522.

Miller, E.K., Li, L., Desimone, R., 1991. Science 254, 1377–1379.

Miller, E.K., Li, L., Desimone, R., 1993. J. Neurosci. 13, 1460–1478.

Mulligan, N.W., 1998. J. Exper. Psychol. Learn, Mem., Cogn. 24, 27–47.

Murray, S.O., Wojciulik, E., 2004. Nat. Neurosci. 7, 70–74.

O'Craven, K.M., Rosen, B.R., Kwong, K.K., Treisman, A., Savoy, R.L., 1997. Neuron 18, 591–598.

O'Craven, K.M., Downing, P.E., Kanwisher, N., 1999. Nature 401, 584–587.

Pelli, D.G., 1997. Spatial Vision 10, 437–442.

Puce, A., Allison, T., Asgari, M., Gore, J.C., McCarthy, G., 1996. J. Neurosci. 16, 5205–5215.

Rees, G., Frith, C.D., Lavie, N., 1997. Science 278, 1616–1619.

Rock, I., Gutman, D., 1981. J. Exp. Psychol. Hum. Percept. Perform. 7, 275–285.

Schacter, D.L., Buckner, R.L., 1998. Neuron 20, 185–195.

Schacter, D.L., Dobbins, I.G., Schnyer, D.M., 2004. Nat. Rev., Neurosci. 5, 853–862.

Squire, L.R., 1992. J. Cogn. Neurosci. 99, 195–231.

Squire, L.R., Knowlton, B., Musen, G., 1993. Annu. Rev. Psychol. 44, 453–495.

Stern, C.E., Corkin, S., Gonzalez, R.G., Guimaraes, A.R., Baker, J.R., Jennings, P.J., Carr, C.A., Sugiura, R.M., Vedantham, V., Rosen, B. R., 1996. Proc. Natl. Acad. Sci. U. S. A. 93, 8660–8665.

Tarr, M.J., Gauthier, I., 2000. Nat. Neurosci. 3, 764–769.

Tulving, E., Schacter, D.L., 1990. Science 247, 301–306.

Turk-Browne, N.B., Junge, J.A., Scholl, B.J., 2005. J. Exp. Psychol. Gen. 134, 552–564.

Turke-Browne, N.B., Yi, D.-J., Chun, M.M., in press. Neuron.

Wagner, A.D., Schacter, D.L., Rotte, M., Koutstaal, W., Maril, A., Dale, A.M., Rosen, B.R., Buckner, R.L., 1998. Science 281, 1188–1191.

Wagner, A.D., Koutstaal, W., Maril, A., Schacter, D.L., Buckner, R.L., 2000. Cereb. Cortex 10, 1176–1184.

Watanabe, T., Nanez, J.E., Sasaki, Y., 2001. Nature 413, 844–848.

Wig, G.S., Grafton, S.T., Demos, K.E., Kelley, W.M., 2005. Nat. Neurosci. 8, 1228–1233.

Wiggs, C.L., Martin, A., 1998. Curr. Opin. Neurobiol. 8, 223–227.

Wojciulik, E., Kanwisher, N., Driver, J., 1998. J. Neurophysiol. 79, 1574–1578.

Yi, D.-J., Chun, M.M., 2005. J. Neurosci. 25, 3593–3600.

Yi, D.-J., Woodman, G.F., Widders, D., Marois, R., Chun, M.M., 2004. Nat. Neurosci. 7, 992–996.