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Distinguishing attentional gain and tuning in young and older adults

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ABSTRACT

Here we examined with functional magnetic resonance imaging (fMRI) whether advanced age affects 2 mechanisms of attention that are widely thought to enhance signal processing in the sensory neocortex: gain and tuning. Healthy young and older adults discriminated faces under varying levels of object competition while fMRI was acquired. In young adults, cortical response magnitude to attended faces was maintained despite increasing competition, consistent with gain. Cortical response selectivity, indexed from repetition suppression, also increased only for attended faces despite increasing competition, consistent with tuning. Older adults exhibited intact gain, but altered tuning, with extrastriate cortical tuning determined by object salience rather than attention. Moreover, the magnitude of this susceptibility to stimulus-driven processing was associated with a redistribution of attention-driven competitive processes to the frontal cortices. These data indicate that although both gain and tuning are modulated by increased perceptual competition, they are functionally dissociable in the extrastriate cortices, exhibit differential susceptibility to advanced aging, and spare the frontal cortices a considerable processing burden through early selection.

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1. Introduction

Attention is a distributed resource, embedded in distinct sub-systems specialized for different types of tasks, and operates in a manner that reflects the properties of those subsystems (Chun et al., 2011; Kastner and Pinsk, 2004). To date, however, most theories of cognitive aging focus on only one of these attentional subsystems, specifically the executive attention subsystem (Craik, 1986; Craik and Byrd, 1982; Demspter, 1992; Hasher and Zacks, 1988; Healey et al., 2008; Naveh-Benjamin, 2000; Park and Reuter-Lorenz, 2009; West, 1996). As such, age-related changes in attention are attributed to the well-established normative deterioration of frontal cortical micro-structure observed in older adults (Haug et al., 1981; Moscovitch and Winocur, 1992; Raz, 2000; Terry et al., 1987; West, 1996), which is hypothesized to gradually increase susceptibility to unwanted competition among encoded inputs, such as competition arising from

demand on working and long-term memory, task rules, and response selection (Hasher and Zacks, 1988).

There is growing evidence that age also affects attentional subsystems involved in reconciling perceptual competition among sensory inputs, such as competition arising from the physical dis-criminability of stimuli (Chee et al., 2006; Goh et al., 2010; Park et al., 2004, 2012; Payer et al., 2006; Schmitz et al., 2010; Schmolesky et al., 2000; Wang et al., 2005). These aging data are of critical interest because the attentional operations that reconcile perceptual competition differ from those that reconcile competi-tion at frontal executive stages of processing (de Haas et al., 2014; Rees et al., 1997, 1999; Xu, 2010; Yi et al., 2004), and, therefore, are suggestive of a distinct age-related change in perceptual attention. Indeed, age-related impairments in selection have been detected in visual cortex when attended and unattended visual stimuli are presented simultaneously, for example, through spatial overlap (Quigley et al., 2010; Schmitz et al., 2010). In young adults, unattended input was gated at early stages of this competition before encoding in the extrastriate cortex, consistent with the prior evidence (de Haas et al., 2014; Rees et al., 1997, 1999; Xu, 2010; Yi and Chun, 2005; Yi et al., 2004, 2006). Older adults, by contrast, were more susceptible to unattended input at later stages of competition, as indexed from task-incidental processing in visual cortex (Quigley et al., 2010; Schmitz et al., 2010) and from a

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recognition memory probe of task-incidental encoding (Schmitz et al., 2010). To date, however, little is known about how age affects the capacity to direct attention to one of multiple competing sensory inputs.

Here, we examined with functional magnetic resonance imaging (fMRI) whether advanced age affects 2 neural mechanisms that are widely thought to bias sensory input in accordance with perceptual attention: gain and tuning (David et al., 2008; Hayden and Gallant, 2009; Ling et al., 2009; Martinez-Trujillo and Treue, 2002; McAdams and Maunsell, 1999; Reynolds and Chelazzi, 2004). Psychophysical research suggests that when resource demands are imposed on perceptual attention, for instance, when a participant must discriminate a target from an increasingly salient unattended distractor, attention alters both gain and tuning in the extrastriate cortex (Ling et al., 2009). Gain is hypothesized to increase the overall sensitivity of sensory neurons to both attended and unattended input, without altering the signal-to-noise ratio of the population response. As such, gain is more beneficial to selection under conditions when attended input is physically more salient than the unattended input but less so when unattended input is more salient. Tuning is hypothesized to increase the selectivity of sensory neurons for attended input, by altering the signal-to-noise ratio of the population response. Tuning is, therefore, more beneficial to selection under conditions when unattended input is physically more salient than attended input, compared with conditions when unattended input is less salient. In sum, when competition from unattended information increases demand for perceptual attention, gain is expected to elicit nonselective cortical amplification, whereas tuning is expected to yield selective cortical filtering.

To differentially engage demand on perceptual attention, our experimental task induced varying levels of nonspatial competition (opacity) from unattended information (places) while participants directed attention to a superimposed face stimulus, yielding low object (LO) and high object (HO) competition conditions (Fig. 1A). To differentiate neural changes in gain and tuning induced by increased object competition (HO) from those induced by low-level changes in luminance and contrast (opacity) of the unattended layer (Avidan et al., 2002a) or an age decline in ocular contrast sensitivity (Owsley et al., 1981), we also included a separate control condition in which the phase structure of unattended object was randomized 100% to produce visual scramble (high scramble [HS]). Given that gender information has been found to evoke conscious perception without the requirement for attention (Koch and Tsuchiya, 2007; Reddy et al., 2004), a male/female judgment task was employed to ensure (and index) sustained perceptual attention with minimal demand on executive decision making, maintenance, or retrieval resources (Schmitz et al., 2010).

Attention is expected to influence competitive interactions across both object layers of the compound stimulus (the signal and noise). To index face- and place-selective processing in each participant, we, therefore, obtained anatomically dissociated a priori regions of interest (ROIs) in the fusiform face area (FFA) and parahippocampal place area (PPA) from an independent functional localizer task (Fig. 1B).

Under LO competition, demand for gain and tuning was expected to be minimal because the attended face is physically more salient than the unattended place. Under HO competition, however, when the attended face is less physically salient than the unattended place, demand for gain and tuning was expected to yield distinct effects on object-selective processing in the FFA and PPA (Fig. 1C). Cortical amplification by gain was expected to increase visual cortical sensitivity to both object layers of the compound stimulus (Ling et al., 2009). As such, blood oxygenation level–dependent (BOLD) response amplitudes were expected not only
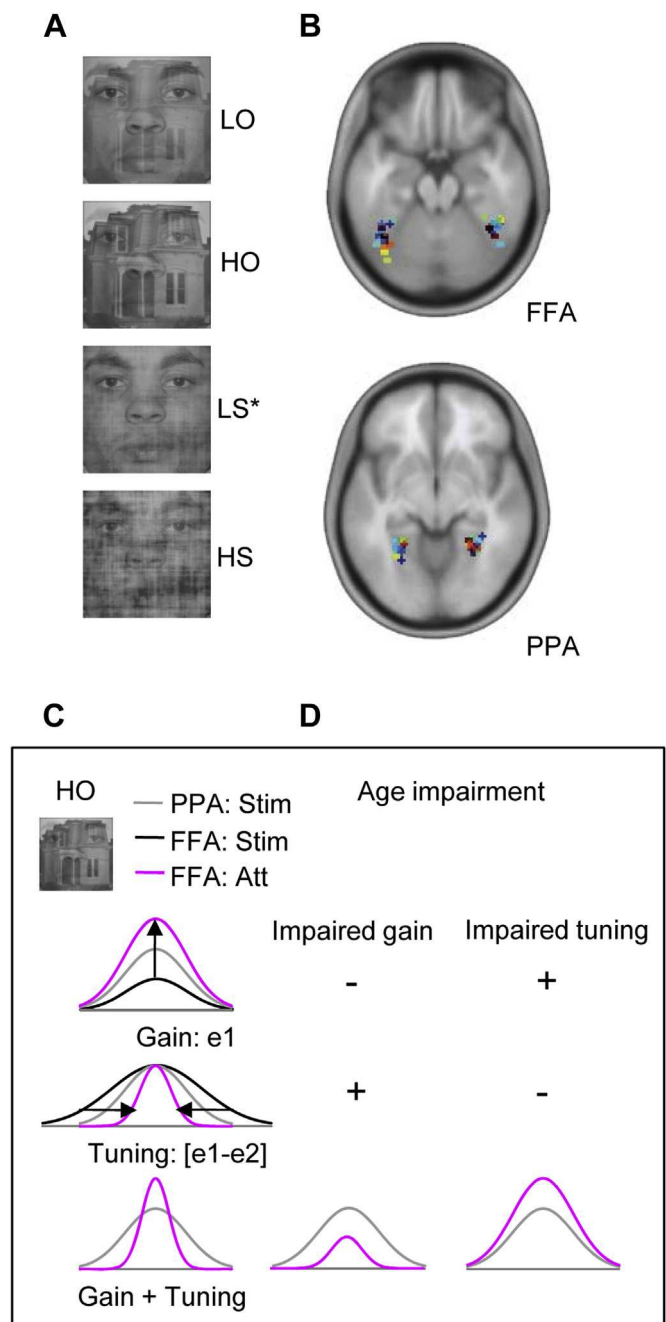
Fig. 1. Experimental design and hypotheses. (A) Participants decided whether attended faces were male or female. The strength of perceptual competition was manipulated by varying the opacity of unattended backgrounds at 35% (low) or 65% (high). Neural changes in gain and tuning induced by low and high object (LO vs. HO) competition were differentiated from those induced by LS versus HS competition to control for changes in background luminance and contrast. *Not used in experiment 2 (functional magnetic resonance imaging). (B) Fusiform face area (FFA) and parahippocampal place area (PPA) regions of interest were separately localized in each participant. (C) The HO condition was expected to increase attentional demand for gain and tuning because stimulus-driven input favored the unattended place. Gray line: stimulus-driven PPA response to places. Black line: stimulus-driven FFA response to faces. Magenta line: attention-driven modulation of FFA. Gain was indexed from blood oxygen level–dependent response amplitude to novel exposures (e1). Higher amplitude indicates higher face amplification. Tuning was indexed from repetition suppression to repeated exposures (e1 − e2). Narrower distribution indicates increasingly face-selective response. (D) Hypothesized age impairments to either gain or tuning.

to remain higher in the FFA relative to the PPA under HO competition (despite the attended face being less physically salient) but also to elevate substantially in the PPA (because of the unattended

place being more physically salient). Increases in the selectivity of population neural response at the level of the receptive field can be indexed from the magnitude of decrease in BOLD response amplitude to repeated objects, that is, repetition suppression (RS) (Desimone, 1996; Wiggs and Martin, 1998). Indeed, magnitudes of extrastriate cortical RS have been found to increase with the degree of physical similarity between repeated stimuli because of increased selectivity of population response in the visual receptive fields (Goh et al., 2010; Murray and Wojciulik, 2004). We, therefore, indexed tuning independently from gain in the FFA and PPA as a function RS to second exposures of the compound stimulus (Avidan et al., 2002b). Cortical filtering by tuning was expected to increase selectivity for the attended face to the exclusion of the unattended place (Ling et al., 2009). As such, we expected BOLD RS to increase in FFA under HO competition (despite the repeated attended face being less physically salient) and abolish in PPA (despite the repeated unattended place being more physically salient).

If a competition-dependent age impairment is isolated to either gain or tuning, such a finding would further indicate that these neural mechanisms are distinct (David et al., 2008; Ling et al., 2009) and, critically, provide insight as to how object-selective attention is altered across the lifespan (see Fig. 1D). If older age confers a selective impairment in gain, then cortical amplification would not be expected under HO competition, when demand for object-selective attention is high. Assuming this scenario, the FFA and PPA BOLD response amplitudes should reflect solely the physical properties of the stimulus, effectively inverting relative to LO competition, with higher response amplitude to the more salient unattended place in PPA relative to the FFA. If older age confers a selective decline in tuning, then attention-driven cortical filtering for the attended face would not be expected under HO competition. Assuming this scenario, FFA and PPA RS should reflect less selective tuning across the object layers of the compound stimulus, with a reduction of FFA RS to the less salient attended face, and an increase in PPA RS to the more salient unattended place. Finally, we also considered the possibility that an age-related change in tuning might not originate in the neural feedback signals that entrain filtering for the attended face in the FFA but rather in the inherent selectivity of FFA population coding for specific features (Schmolesky et al., 2000) or object categories (Park et al., 2004). Assuming this scenario, we would expect older adults to exhibit reduced FFA and PPA selectivity to object categories in the functional localizer task and reduced FFA RS to attended faces under low competition.

2. Methods

2.1. Participants

2.1.1. Experiments 1 and 2

For all participants, written informed consent was obtained before experimental procedures in this institutional review board–approved study. Young and older adults' medical histories were screened for incidence of prior head injury, mental health issues, chemotherapy or cranial radiation therapy, and neurologic disorders. All participants had normal or corrected-to-normal visual acuity.

2.1.2. Experiment 1

Twenty healthy right-handed young (11 females; mean age = 20.0 [standard deviation {SD} = 1.7] years) and 20 healthy right-handed older adults (13 females; mean age = 77.0 [SD = 5.0] years) participated. Older adults performed within the normal range on both the Mini-Mental State Examination (mean = 28.8, SD = 1.5; scores of 27–30 indicate normal cognitive function) and

the Short Blessed Test (mean = 0.9, SD = 2.0; scores of 0–4 indicate normal cognitive function).

2.1.3. Experiment 2

Fifteen healthy right-handed young (9 females; mean age = 22 [SD = 1.3] years) and 15 healthy right-handed older adults (7 females; mean age = 77.2 [SD = 5.2] years) participated. The 2 groups performed equivalently on the Mini-Mental State Examination (young: mean = 29.3, SD = 0.9; older: mean = 29.1, SD = 1.18) and the Short Blessed Test (young: mean = 0.8, SD = 1.33; older: mean = 0.6, SD = 1.05). Three participants were excluded from data analyses, 1 young adult and 2 older adults, because of self-reported drowsiness and excessive head motion in the scanner.

2.2. Experimental designs

2.2.1. Experiment 1

To limit demands on working memory and associated cognitive resources (Schmitz et al., 2010), participants performed a simple object-selective attention task under perceptual competition from unattended background information. In the attend face condition, participants decided whether faces were male or female under competition from unattended places. In the attend place condition, participants decided whether places were interior or exterior under competition from unattended faces. For the purposes of this study, these 2 attention conditions were collapsed together. Unattended objects were presented at 2 levels of opacity (35% and 65%), inducing LO and HO object competition, respectively. To differentiate the effects of object competition from those induced by low-level changes in luminance and contrast (opacity) of the unattended layer (Avidan et al., 2002a) or an age decline in ocular contrast sensitivity (Owsley et al., 1981), we also included conditions in which the phase structure of unattended object was randomized 100% to produce visual scramble. Unattended scrambles, which preserve low-level features of the original object (contrast, luminance, and spatial frequency), were presented at 2 levels of opacity (35% and 65%), inducing low scramble (LS) and HS competition. Forty unique compound stimuli (superimposed object pairs) were presented for each condition: load (35% and 65%), background (object, scramble), and object attention (face, place). Stimulus durations were 2000 ms, with an interstimulus interval ranging between 2–4 seconds. Each unique stimulus was presented 4 times (exposures e1–e4) in a pseudorandomized sequence to obviate confounds such as habituation and anticipation of forthcoming stimulus repetitions (Liu et al., 2001). Because the order of stimulus presentation was pseudorandomized, repetitions of a given compound stimulus occurred at variable intervals of intervening stimuli or lag. Although age differences in lag have not been found at intervals >15 (Schmitz et al., 2010), we constrained lag to a maximum of 10 trials to prevent possible age differences in implicit visual memory (Fleischman and Gabrieli, 1998), for example, greater interference from intervening trials, from influencing our neural measures of object-selective adaptation. The stimulus lags for each condition (LO, HO, LS, HS) were, therefore, drawn from a uniform distribution ranging from 1 to 10 intervening stimuli.

2.2.2. Experiment 2

An fMRI-optimized version of the discrimination task in experiment 1 was used for neuroimaging. Before scanning, participants were provided with instruction and practice on the task. To reduce fatigue in the scanner, we removed the attend place and the LS conditions and reduced the number of repetitions to one. In all conditions of the face-selective attention task, participants decided whether faces were male or female, rendering backgrounds

perceptible but task irrelevant. Forty unique compound stimuli (superimposed object pairs) were presented for each condition: competition (LO, HO) and the 100% phase scrambled 65% opacity background control condition (HS). Stimulus durations were 1000 ms, with a variable stimulus onset asynchrony ranging from 2 to 6 seconds (mean of 4 seconds) (Birn et al., 2002). Each unique stimulus was presented 2 times (e1–e2) in a pseudorandomized sequence. The stimulus lags for each perceptual load condition (LO, HO, HS) were drawn from a uniform distribution ranging from 1 to 10 intervening stimuli.

2.3. fMRI setup

The experiments were designed and implemented using the software package Presentation (version 9.81; Neurobehavioral Systems, Albany, CA, USA). Slice acquisition and stimulus delivery were synchronized via a parallel port cable that monitored low-amplitude transistor–transistor logic pulses. Stimuli were presented on a rear-mounted projection screen, set at a (native) 1024 × 768 resolution. The order and timing of stimuli presentation sequences for the experimental task were determined using Optseq (http://surfer.nmr.mgh.harvard.edu/optseq/).

Imaging data were collected with a Siemens Tim Trio 3.0-T scanner and a 12-channel asymmetric gradient head coil. Parameters for high-resolution T1-weighted structural volumes were as follows: 3-dimensional magnetization-prepared rapid gradient-echo pulse sequence, repetition time 2000 ms, echo time 2.63 ms, matrix 256 × 160, 256 × 256 mm field of view (FOV), slice thickness 1 mm, and 160 axial oblique slices. Parameters for T2*-weighted gradient-echo echo-planar image pulse sequences were as follows: echo time = 30 ms, repetition time = 2000 ms, flip angle = 70°, acquisition matrix 64 × 64, and 200 mm FOV. Thirty axial oblique slices of the brain were acquired at each time point, with a voxel resolution of 3.1 × 3.1 × 5 mm and no skip between slices.

2.4. fMRI analyses

Functional activation was determined from the BOLD signal using the software Statistical Parametric Mapping (SPM5; University College, London, UK, http://www.fil.ion.ucl.ac.uk/spm/software/spm5). Preprocessing steps for T1 and T2*-weighted volumes were identical to those reported in Schmitz et al. (2010). In each of the 4 task runs of the task, the first 3 volumes were discarded to allow for BOLD equilibration. The time-series data were high-pass filtered (128-second period cutoff) and corrected for temporal autocorrelation using AR1 model.

2.5. FFA/PPA functional localizer task

The FFA and PPA ROIs within each participant were localized using a separate task in which alternating epochs of faces and places were fully attended in the absence of competition (Schmitz et al., 2010). Block regressors coding for onsets and durations of face and place blocks were convolved with the hemodynamic response function and estimated using the general linear model. To determine individual FFA ROIs, in each participant, we contrasted activity associated with face blocks with that associated with place blocks. For the PPA ROI, we contrasted activity associated with place blocks with that associated with face blocks. Thresholds were adjusted starting from the most conservative threshold $p < 0.00001$ to $p < 0.01$. The final threshold was determined by the appearance of clusters $k \geq 10$ voxels within FFA and PPA. We used a fixed 3-mm radius spherical ROI centered on the peak voxel to ensure that the sampling volume was uniform

across participants. Bilateral fusiform activation clusters were detected in 25 out of 27 participants. Bilateral parahippocampal activation clusters were also detected in 25 out of 27 participants. Individual ROI coordinates derived from the extrastriate functional localizer were entered into MarsBar to create spherical 3-mm radius ROIs (http://marsbar.sourceforge.net/). To produce extrastriate indices of categorical selectivity for preferred and non-preferred stimuli, measures of percent signal change for the face and place conditions (β coefficients) were determined relative to the implicit baseline within each ROI (i.e., β coefficient of the session constants).

2.6. Face-selective attention task

The FFA and PPA ROIs defined by the independent localizer were entered into MarsBar to estimate a finite impulse response (FIR) model for the attention task. The experimental conditions (LO exposure 1, LO exposure 2, HO e1, HO e2, HS e1, HS e2) were separately modeled using 12 FIR basis functions, 1 for each peri-stimulus time point (trial window = 24 seconds). The 6 motion parameters produced at image realignment were included as covariates of no interest. To determine which time points should be entered for comparison in our random-effects analyses of variance (ANOVAs), we averaged the time courses across groups, conditions, and exposures e1 and e2. The numerical peak was statistically compared with each of the other time points. As in Schmitz et al. (2010), the peak BOLD response amplitude in both the FFA and PPA occurred 4–6 seconds after trial onset; this time point was significantly greater than all others (t tests, $p < 0.001$). For all tests of condition × hemisphere interactions, $F < 1$. We, therefore, averaged FFA and PPA ROIs between hemispheres, where applicable. Individuals' FFA and PPA response amplitudes obtained in the face-selective attention task were estimated as a proportion relative to their corresponding FFA and PPA response amplitudes obtained during the independent functional localizer (loc). This provided an ROI-specific baseline for stimulus-driven activation in the FFA and PPA, that is, face and place processing in the absence of perceptual competition. Formally, this was calculated for the FFA and PPA, respectively, as follows: ($FFA_{e1}/FFA_{loc:faces}$), ($FFA_{e2}/FFA_{loc:faces}$), ($PPA_{e1}/PPA_{loc:places}$), and ($PPA_{e2}/PPA_{loc:places}$). These baseline-corrected indices were used for our analysis of gain and tuning. Gain was inferred from FFA and PPA response amplitudes to novel (e1) exposures across conditions, whereas tuning was inferred from the magnitude of FFA and PPA RS (e1 − e2) across conditions.

2.7. Frontal ROI analysis

We also examined whether age-related changes in perceptual attention were present in anatomically defined lateral frontal areas. To do so, the experimental conditions (LO e1, LO e2, HO e1, HO e2, HS e1, HS e2) were also convolved with the canonical hemodynamic response function at the first level. The 6 motion parameters produced at image realignment were included as covariates of no interest. Contrast images modeling the effect of repetition (e1 − e2) for each condition were submitted to an *N*-way mixed (between and within subjects) ANOVA (Henson and Pennny, 2003) with age and competition (LO, HO, HS) as factors. We used the Automated Anatomic Labeling atlas of the Monteal Neurologic Institute template brain (Tzourio-Mazoyer et al., 2002) to explore possible age differences in the frontal cortices. The "Frontal_Mid" volume of the Automated Anatomic Labeling was imported to MarsBar, separately for the left and right hemispheres, to create anatomically defined ROIs of the middle frontal gyrus (MFG). Activations surviving a small volume

corrected $p < 0.05$, cluster size >10 voxels were deemed statistically significant.

3. Results

3.1. Experiment 1: effects of object competition on behavior

We first conducted a separate behavioral study (see "Methods" section) to determine whether the effects of object competition (LO, HO) on perceptual discrimination could be differentiated from low-level changes in luminance and contrast (opacity) of the unattended layer. To do so, we compared measures of discrimination accuracy and response priming on LO/HO with those obtained on contrast and luminance-equated conditions of competition from phase-scrambled objects (LS, HS). We used a $2 \times 2 \times 2$ mixed ANOVA design including age (young, older), competition (low, high), and background (object, scramble) in 4 separate analyses of response accuracy (first exposure, e1 only), response accuracy priming (e1 − e4), response latency (first exposure, e1 only), and response latency priming (e1 − e4), respectively.

3.1.1. Discrimination accuracy

We first examined discrimination performance to novel exposures of the attended layer, that is, in the absence of repetition-related priming. We found a significant 3-way age × competition × background interaction ($F_{1,38} = 7.1$, $p = 0.01$), driven by a selective age difference in discrimination accuracy under HO competition ($t_{38,[HO − LO] − [HS − LS]} = 2.7$, $p = 0.01$) (see Fig. 2A).

Critically, this age difference induced by object competition occurred over and above low-level differences attributable to increased background luminance/contrast, which trended toward a slightly larger influence in older adults ($t_{38,[HS − LS]} = 1.9$, $p = 0.07$). We also observed a competition × background interaction ($F_{1,38} = 46.8$, $p < 0.001$), indicating that increased object competition under HO selectively impaired discrimination performance in young adults ($t_{19, [HO − LO] − [HS − LS]} = 2.8$, $p = 0.01$), albeit to a lesser extent.

3.1.2. Discrimination accuracy priming

We next examined whether age, competition, or background might differentiate repetition-related changes in accuracy. This analysis revealed a significant age × competition interaction ($F_{1,38} = 11.7$, $p = 0.002$): older adults exhibited repetition-related increases in discrimination accuracy under increased object competition ($t_{38,[HO − LO]} = 2.5$, $p = 0.02$) (see Fig. 2B). However, increases in background luminance/contrast failed to differentiate repetition-related changes in response accuracy between groups ($t_{38,[HS − LS]} < 1$). In young adults, we detected no repetition-related changes in response accuracy in any of the conditions (all t tests < 1).

3.1.3. Response latency

Limiting our analysis of response latency to correct trials, we found no evidence of a 3-way interaction ($F < 1$) selectively differentiating young and older adult's response times to novel exposures of HO stimuli (Fig. 2C). However, we found a significant competition × background interaction ($F_{1,38} = 46.8$, $p < 0.001$):
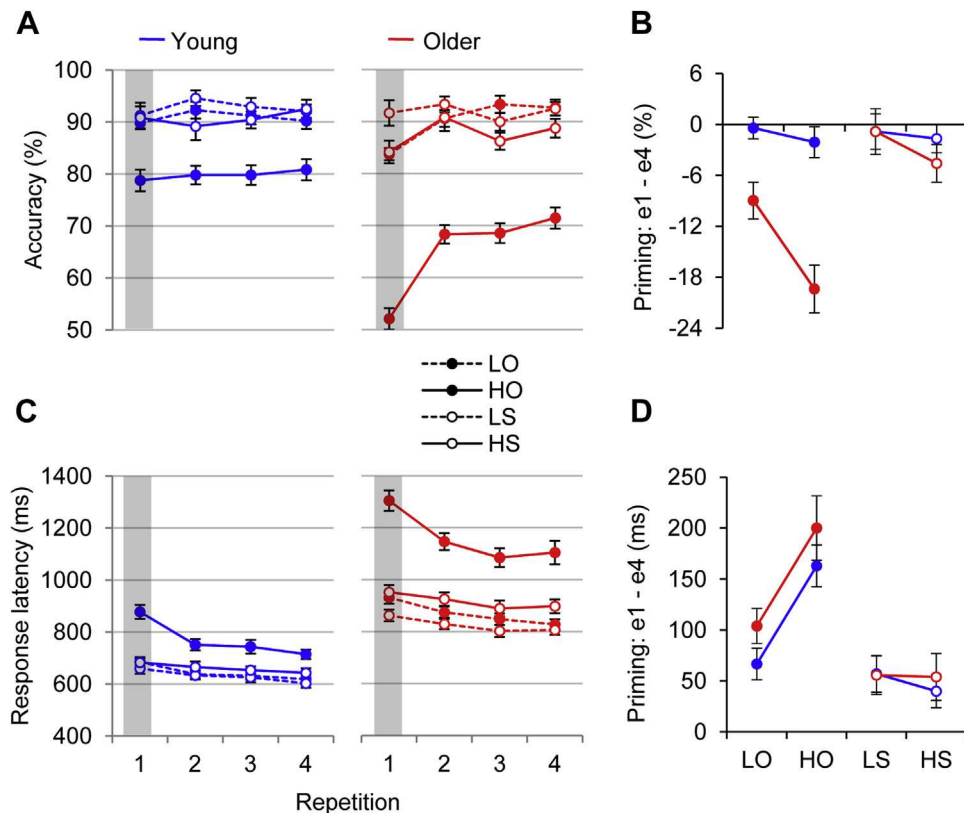
Fig. 2. Behavioral performance on experiment 1. (A) Discrimination accuracy to novel exposures (gray area) was significantly reduced under high object (HO) competition in both groups but significantly more so in older adults. This age difference is attributable to object competition, as opposed to increased luminance/contrast from the background (high scramble [HS] competition). (B) Discrimination accuracy priming: older adults exhibited repetition-related increases in discrimination accuracy under both object competition conditions (low object [LO] and HO) but significantly more so under HO. (C) Response latency to novel exposures (gray area) was significantly slowed under HO in both groups. The magnitude of slowing under HO failed to differentiate age groups. (D) The magnitude of response latency priming was selectively increased under HO in both young and older adults. The magnitude of priming under HO failed to differentiate age groups.

response slowing induced by HO was selectively increased in both young ($t_{19,[HO - LO] - [HS - LS]} = 5.8, p < 0.001$) and older adults ($t_{19,[HO - LO] - [HS - LS]} = 7.3, p < 0.001$). Post hoc comparisons further confirmed the absence of age differences in response latency arising from increased low-level background salience ($t_{38,[HS - LS]} < 1$) and increased object competition ($t_{38,[HO - LO] - [HS - LS]} < 1$). These latter findings indicate that under HO, age-related decreases in object discrimination accuracy are not attributable to concomitant increases in response uncertainty.

3.1.4. Response latency priming

Limiting our analysis of response latency priming to correct trials, we found no evidence of a 3-way interaction ($F < 1$) selectively differentiating the young and older adult's speeded responses to repeated exposures of HO stimuli (Fig. 2D). However, we found a significant competition × background interaction ($F_{1,19} = 18.2, p = 0.003$): magnitudes of response latency priming induced by HO were selectively increased in both young ($t_{19,[HO - LO] - [HS - LS]} = 3.4, p = 0.003$) and older adults ($t_{19,[HO - LO] - [HS - LS]} = 2.6, p = 0.02$). Post hoc comparisons further confirmed the absence of age differences in response latency priming arising from increased low-level background salience ($t_{38,[HS - LS]} < 1$) and increased object competition ($t_{38,[HO - LO] - [HS - LS]} < 1$). These latter findings indicate that under HO, although age was associated with decreased object discrimination accuracy, perceptual familiarity to repeated stimuli was unaltered, relative to young adults.

Taken together, the results of experiment 1 demonstrate that increased object competition (HO) impaired discrimination performance and elevated magnitudes of response latency priming across both age groups. Moreover, the control conditions (LS and HS) confirmed that these effects of object competition were not attributable simply to low-level increases in luminance and contrast (opacity) of the unattended layer. Critically, our experiment also isolated age differences in discrimination performance under HO. Unlike the relatively stable ∼80% discrimination performance achieved by younger adults, older adults exhibited near chance performance to novel exposures of HO but then improved dramatically (∼20%) on subsequent exposures.

3.2. Experiment 2: fMRI

We acquired fMRI data while a separate group of healthy young and older adults performed a perceptual task virtually identical to that described in experiment 1; the LS condition was not included in experiment 2 (see "Methods" section). We used a 2 × 3 mixed-ANOVA design including age (young, older) and competition (LO, HO, HS) in 4 separate analyses of response accuracy (first exposure, e1 only), response accuracy priming (e1 − e2), response latency (first exposure, e1 only), and response latency priming (e1 − e2), respectively. Behavioral performance on the fMRI task replicated the primary effects of experiment 1.

3.2.1. Response accuracy

Object discrimination to novel exposures elicited a significant age × competition interaction ($F_{2,50} = 4.0, p = 0.02$), driven by selectively larger decreases in accuracy in older adults under HO ($t_{25,[HO - LO]} = 2.9, p = 0.008$), which remained even when controlling directly for low-level effects of increased background salience ($t_{25,[HO - HS]} = 2.2, p = 0.04$). Mean young adult accuracy (±standard error): LO = 92.5% ± 1.0%, HO = 81.0% ± 1.2%, HS = 83.1% ± 1.3%. Mean older adult accuracy: LO = 88.0% ± 1.1%, HO = 70.3% ± 1.8%, HS = 77.0% ± 1.7%.

3.2.2. Response accuracy priming

We observed neither an age effect nor an age × competition interaction for changes in response accuracy to repeated exposures. However, consistent with experiment 1, a response accuracy priming effect was observed in older adults and only under HO ($t_{12} = 2.3, p = 0.04$).

3.2.3. Response latency

Novel stimulus exposures elicited a significant age × competition interaction ($F_{2,50} = 4.5, p = 0.02$), driven by selectively longer response times in older adults under HO ($t_{25,[HO - LO]} = 2.7, p = 0.01$). However, when controlling directly for low-level effects of increased background salience, this age difference disappeared ($t_{25,[HO - HS]} < 1$). Mean young adult latency (±standard error): LO = 743.6 ± 20.0 ms, HO = 810.1 ± 22.5 ms, and HS = 803.5 ± 24.7 ms. Mean older adult latency: LO = 878.4 ± 31.1 ms, HO = 1009.2 ± 36.6 ms, and HS = 978.1 ± 36.4 ms.

The accuracy and latency results for the ($HO_{e1} - HS_{e1}$) comparison, together with those obtained from the full factorial comparison ($HO_{e1} - LO_{e1}) - (HS_{e1} - LS_{e1}$) in experiment 1, further indicate that the interaction between age and competition on object discrimination is not attributable to age differences in response uncertainty.

3.2.4. Response latency priming

We next examined whether age or competition differentiated response time indices of perceptual familiarity to repeated exposures. The ANOVA revealed a significant main effect of competition ($F_{2,50} = 5.9, p = 0.005$), driven by larger magnitudes of priming under HO in both young ($t_{13,[HO - LO]} = 3.1, p = 0.04$) and older adults ($t_{12,[HO - LO]} = 2.1, p = 0.05$) but no age × competition interaction ($F_{2,50} < 1$). Post hoc comparisons confirmed that age differences were absent in all conditions (LO: $t_{25} < 1$, HO: $t_{25} < 1$, HS: $t_{25} < 1$). Hence, consistent with experiment 1, the interaction between age and competition on object discrimination also does not appear to arise from an age difference in perceptual familiarity to repeated exposures.

3.3. Extrastriate cortical ROI analysis

Our behavioral results thus far indicate that when competition from an unattended object is increased (HO), the percept of the attended object becomes relatively more diminished in older adults. We next turn to our extrastriate cortical ROI analyses to determine whether encoding of the attended object by population neural responses in the visual cortex is also diminished.

We first examined whether extrastriate categorical selectivity for face and place objects differentiated young and older adults. To do so, we measured extrastriate cortical response to the preferred and nonpreferred object categories from the FFA and PPA ROIs defined in the separate functional localizer task (Fig. 3A). Indices of categorical selectivity (preferred object − nonpreferred object) were entered into a 2 (age) × 2 (FFA, PPA) mixed-ANOVA model. Here, we found a main effect of age ($F_{1,25} = 25.9, p < 0.001$) and ROI ($F_{1,25} = 7.4, p = 0.01$) but no evidence of an age × ROI interaction ($F_{1,25} = 1.7, p > 0.1$). Between groups, younger adults exhibited higher overall magnitudes of modulation to the preferred object category in both ROIs compared with older adults, and magnitudes of BOLD response were stronger overall in the FFA than the PPA. Critically, direct between-group comparisons of ROI response to the nonpreferred object category were nonsignificant (FFA: $t_{25} = 1.3$, $p > 0.1$; PPA: $t_{25} = 1.1, p > 0.1$). Together, these results indicate that our young and older adult samples did not differ in extrastriate categorical selectivity for face and place objects. Moreover, these results suggest that task-independent influences arising from age
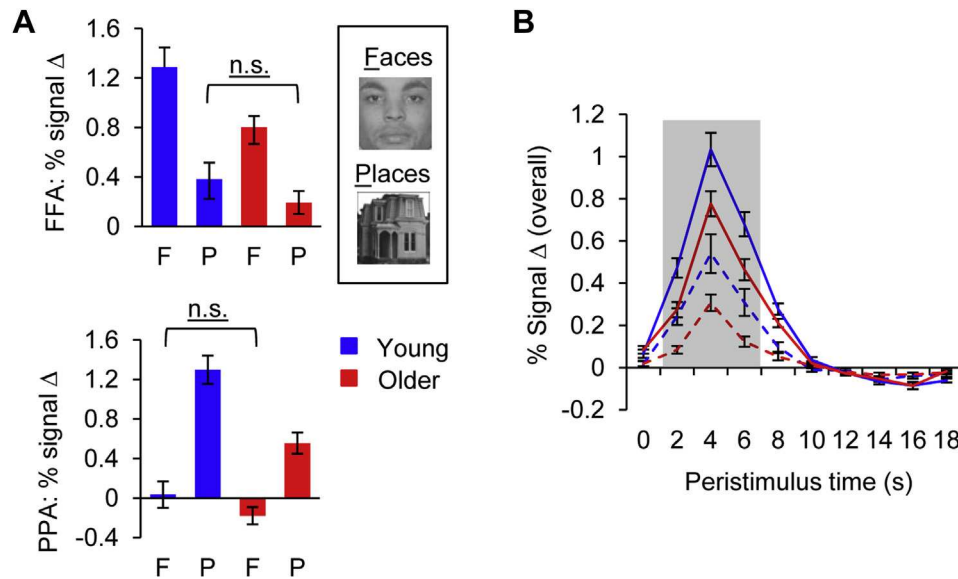
Fig. 3. Aging analysis of extrastriate categorical selectivity and hemodynamics. (A) Indices of categorical selectivity in each region of interest (ROI) (preferred object − nonpreferred object) were entered into a 2 (age) × 2 (fusiform face area [FFA], parahippocampal place area [PPA]) mixed analysis of variance (ANOVA). We found main effects of age and ROI, whereby younger adults exhibited stronger modulation to the preferred category in both ROIs and FFA exhibited stronger blood oxygenation level–dependent (BOLD) response modulation overall. There was no interaction between age and ROI. Critically, direct between-group comparisons of ROI response to the nonpreferred object category were nonsignificant in both the FFA and PPA, indicating that the young and older adult samples did not differ in extrastriate categorical selectivity for faces and places. (B) Mean estimates of task-related activation (collapsed across conditions low object [LO], high object [HO], high scramble [HS], and repetitions e1, e2) into a 2 (age) × 2 (FFA, PPA) × 3 (FIR) mixed ANOVA modeling a 6-second window centered on the peak hemodynamic response (shaded area). Peak latency and dispersion of extrastriate hemodynamic response was similar across both age and ROI. However, we found a main effect of age driven by higher overall amplitudes of blood oxygenation level–dependent (BOLD) response in young adults in both ROIs, indicating that age introduced a task-independent scaling effect on BOLD response amplitude. Abbreviation: n.s., not significant.

differences in neurovascular function (D'Esposito et al., 2003) and regional differences in extrastriate BOLD responsivity (Spiridon et al., 2006) may represent important confounds to consider in aging analyses of extrastriate categorical selectivity.

We next examined whether age-induced changes in the mean peak, latency, or dispersion of the FIR profile in the extrastriate cortical ROIs during the face-selective attention task. To do so, we entered mean estimates of task-related BOLD activation (collapsed across conditions LO, HO, HS, and repetitions e1, e2) into a 2 (age) × 2 (FFA, PPA) × 3 (FIR) mixed ANOVA modeling a 6-second window centered on the peak hemodynamic response (Fig. 3B, shaded area). We found interaction of age neither with ROI ($F_{1,25} < 1$) nor with FIR ($F_{1,25} < 1$) nor among all 3 factors ($F_{1,25} < 1$), indicating that the hemodynamic peak latency and dispersion were similar across both age and ROI. Limiting our post hoc analyses to the hemodynamic peak values (6 seconds), we found a main effect of age ($F_{1,25} = 10.3$, $p = 0.004$), driven by higher overall amplitudes of BOLD response in young adults (averaged across FFA and PPA, Fig. 3B).

Together, these findings indicate task-independent scaling effects on the BOLD response amplitude, both between the ROIs (FFA > PPA) and between age groups (young > old). For each individual, we, therefore, estimated our ROI indices of gain and tuning in the face-selective attention task relative to their corresponding baseline of stimulus-driven activity in the separate functional localizer task (see "Methods" section). These normalized indices of gain and tuning remove the effect of both task-independent scaling effects (ROI and age) from our subsequent analysis of the interaction among age, ROI, and competition.
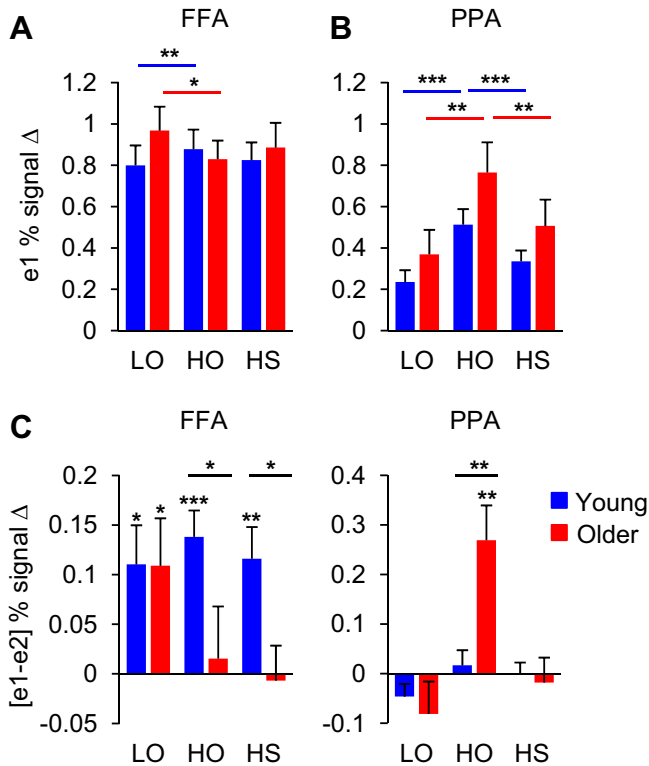
Extrastriate cortical indices of gain (first exposures, e1) were entered into a 2 × 2 × 3 mixed-ANOVA design including age (young, older), ROI (FFA, PPA), and competition (LO, HO, HS) to determine whether age differentiates cortical amplification of the compound stimulus as a function of object competition. Specifically, under HO, cortical amplification by gain was expected to increase FFA and PPA response to both object layers of the compound stimulus. We found

a significant 3-way interaction ($F_{2,50} = 7.3$, $p = 0.002$). There was no main effect of age ($F_{1,25} = 1.6$, $p > 0.1$). To interrogate the nature of this interaction, the ANOVA was decomposed into separate 2 (age) × 3 (competition) models for the FFA and PPA.

The age × competition interaction was significant in the FFA ($F_{2,50} = 7.5$, $p = 0.002$) (see Fig. 4A). FFA BOLD response amplitude to the attended face was significantly increased by HO in young adults ($t_{13,[HO − LO]} = 3.4$, $p = 0.004$) but significantly decreased by HO in older adults ($t_{12,[HO − LO]} = 2.5$, $p = 0.03$). No differences were detected between HO and the HS competition control condition (young: $t_{13,[HO − HS]} = 1.7$, $p > 0.1$; old: $t_{12,[HO − HS]} = 1.1$, $p > 0.1$). In older adults, the decrease in FFA response amplitude from LO to HO appears to originate from an unanticipated elevation of FFA response amplitudes under LO (relative to young adults), suggesting that modulation of gain was slightly stronger in older adults under LO. This difference was nonsignificant (LO: $t_{25} = 1.1$). Critically, FFA BOLD response amplitude did not differentiate young and older adults in the high competition conditions (HO: $t_{25} < 1$, HS: $t_{25} < 1$).

There was no age × competition interaction in the PPA ($F_{2,50} = 1.3$, $p > 0.1$) (see Fig. 4B). PPA BOLD response amplitude to the unattended place was significantly increased by HO in both young ($t_{13,[HO − LO]} = 6.7$, $p < 0.001$) and older adults ($t_{12,[HO − LO]} = 4.6$, $p = 0.001$). Moreover, PPA response remained significantly elevated in both groups comparing HO with the HS competition control condition (young: $t_{13,[HO − HS]} = 6.0$, $p < 0.001$; old: $t_{12,[HO − HS]} = 4.5$, $p = 0.001$). As with the FFA, BOLD response amplitudes in the PPA did not differentiate young and older adults in any of the conditions (LO: $t_{25} = 1.1$, $p > 0.1$; HO: $t_{25} = 1.6$, $p > 0.1$; HS: $t_{25} = 1.3$, $p > 0.1$).

Consistent with our hypotheses of gain, cortical amplification for the attended but physically less salient face was observed when demand for object-selective attention increased under HO. Moreover, we did not observe differences in the strength of cortical amplification under HO between young and older adults, suggesting that gain is relatively preserved with aging.

Fig. 4. Extrastriate region of interest analysis of gain and tuning. (A–B) Gain: indices of blood oxygenation level–dependent (BOLD) response amplitude to first exposures (e1). (A) Fusiform face area (FFA) BOLD response amplitude to the attended face was significantly increased by high object (HO) competition in young adults but significantly decreased by HO in older adults because of an unanticipated elevation of FFA response under low object (LO) competition (relative to young adults). Critically, no age differences were detected between HO and the high scramble (HS) competition control condition. (B) In both young and older adults, parahippocampal place area (PPA) BOLD response amplitude to the unattended place was significantly increased by HO relative to LO and to HS, consistent with the physical salience of the compound stimulus (face < place). (C) Tuning: indices of BOLD repetition-related suppression (RS) to repeated exposures (e1 − e2). Under LO, FFA RS to attended faces was significant in both young and older adults. PPA RS was not detected in either group. Under HS, FFA RS to attended faces was significant in young but not older adults, suggesting that HS competition also impaired face-selective tuning in older adults. Under HO, FFA RS was significant in young but not in older adults. By contrast, PPA RS was significant in older but not in younger adults. Consistent with attentional modulation of tuning, young adults filtered the attended face to the exclusion of the unattended place under HO. Consistent with impaired tuning, cortical filtering for the attended face was abolished in older adults, yielding stimulus-driven pattern of encoding for the unattended place. ***$p < 0.001$; **$p < 0.01$; *$p < 0.05$.

Extrastriate cortical RS indices of tuning (e1 − e2) were entered into a 2 × 2 × 3 mixed-ANOVA design including age (young, older) and ROI (FFA, PPA) and competition (LO, HO, HS) to determine whether age differentiates cortical filtering of the compound stimulus as a function of object competition. Specifically, under HO, cortical filtering by tuning was expected to yield increased selectivity for attended faces to the exclusion of unattended places. We found a significant 3-way interaction ($F_{2,50} = 6.8$, $p = 0.002$) (see Fig. 4D). There was no main effect of age ($F_{1,50} < 1$). Because our tuning hypotheses concern the interaction between face and place-selective RS, the ANOVA was decomposed into 3 separate 2 (age) × 2 (ROI) models, 1 for each condition, to isolate the locus of this interaction effect.

Under LO, we found only a significant main effect of ROI ($F_{1,25} = 16.8$, $p < 0.001$) but no age × ROI interaction ($F_{1,25} < 1$). Here, FFA RS to attended faces was significant in both young ($t_{13} = 2.8$, $p = 0.02$) and older adults ($t_{12} = 2.3$, $p = 0.04$), indicating that the selectivity of FFA population coding for face exemplars did not differentiate

young and older adults even in the presence of LO competition. Repetition-related changes in the PPA failed to reach significance in either group.

Under HS, we found a trend toward a main effect of age ($F_{1,25} = 3.7$, $p = 0.07$) but no age × ROI interaction ($F_{1,25} = 2.3$, $p > 0.1$). The main effect of age was driven by a significant pattern of FFA RS detected in young ($t_{13} = 3.6$, $p = 0.003$) but not older adults ($t_{12} < 1$), suggesting that HS competition backgrounds impaired face-selective tuning in older adults (between-group t test: $t_{25} = 2.6$, $p = 0.02$). Critically, however, place-selective PPA RS was absent in both young ($t_{13} < 1$) and older adults ($t_{12} < 1$). Our control scramble condition, therefore, confirms that the PPA did not exhibit task-independent cortical adaptation, for example, adaptation to noise, fatigue, or other low-level physiological changes over time.

Under HO, we found a significant age × ROI interaction ($F_{1,25} = 26.0$, $p < 0.001$) but neither main effect of age ($F_{1,25} = 1.4$, $p > 0.1$) nor main effect of ROI ($F_{1,25} = 3.2$, $p = 0.08$), indicating the principal locus of the 3-way interaction was induced by increased object competition from unattended places. Here, FFA RS was significant in young ($t_{13}=5.2$, $p < 0.001$) but not in older adults ($t_{12} < 1$), between-group t test ($t_{25} = 2.4$, $p = 0.04$). By contrast, young adults exhibited no repetition-related changes in the PPA ($t_{13} < 1$), whereas older adults exhibited significant PPA RS ($t_{12} = 3.8$, $p = 0.002$), between-group t test ($t_{25} = 5.3$, $p = 0.002$). Consistent with intact tuning, young adults exhibited cortical filtering for the attended face to the exclusion of the unattended place under HO, despite the face being less physically salient than the unattended place. Consistent with impaired tuning, cortical filtering for the attended face was abolished in older adults during HO, whereas unattended places elicited robust repetition-related encoding. Hence, our findings indicate that age alters the neural feedback that entrains tuning of a selected sensory input.

Gain and tuning mechanisms are thought to be highly integrated in the receptive field (David et al., 2008; Ling et al., 2009). To more directly explore this functional integration, we examined whether magnitudes of nonselective cortical amplification by gain predict the scaling of selective cortical filtering by tuning across individuals. For the correlations, we used indices of the competition-dependent change in gain ($HO_{e1} − LO_{e1}$) and the competition-dependent change in tuning ($HO_{e1 − e2}) − (LO_{e1 − e2}$). We examined this relationship separately in the FFA and PPA to differentiate patterns in the attended and unattended streams of object processing.

In young adults, we found that gain and tuning for the attended face were highly positively correlated (FFA: $r = 0.79$, $p = 0.001$) (see Fig. 5A). Across individuals, cortical amplification for novel attended faces was tightly coupled with cortical selectivity for repeated faces. Gain and tuning were uncorrelated for the unattended place (PPA: $r = −0.16$, $p > 0.1$) (see Fig. 5B). That is, cortical amplification for novel places did not predict changes in cortical selectivity for repeated places. These data suggest that gain and tuning are integrated across young adult individuals to bias competition among face and place inputs for the attended face.

Across older adult individuals, we again found a positive correlation between gain and tuning for the attended face (FFA: $r = 0.64$, $p = 0.02$). However, unlike young adults, we also found a significant positive correlation between gain and tuning for the unattended place (PPA: $r = 0.82$, $p = 0.001$) (see Fig. 5C and D). A direct between-group comparison of PPA coupling strength (r' values) revealed that this pattern of stimulus-driven coupling was stronger in older than younger adults ($z = 2.97$, $p = 0.001$). Taken together, the FFA and PPA correlations in older adults demonstrate that although magnitudes of gain and tuning were tightly integrated across individuals, this integration did not bias competition toward the attended face.
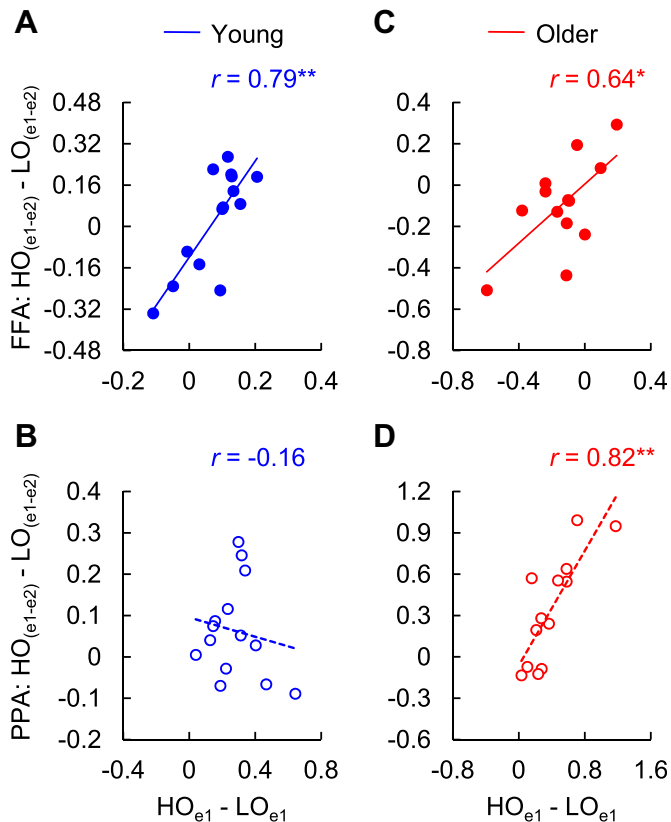
Fig. 5. Attentional integration of gain and tuning across individuals. We examined the relationship between competition-dependent changes in gain (high object [HO_{e1}] − low object [LO_{e1}]) competition and tuning ($HO_{e1 − e2}$) − ($LO_{e1 − e2}$), separately in the fusiform face area (FFA) and parahippocampal place area (PPA). (A and B) Across young adult individuals, cortical amplification for novel attended faces was tightly coupled with cortical selectivity for repeated faces. Gain and tuning were uncorrelated for the unattended place. These data suggest that gain and tuning are integrated across young adult individuals to bias the attended face. (C and D) Across older adult individuals, we again found a positive correlation between gain and tuning for the attended face. However, unlike young adults, we also found a significant positive correlation between gain and tuning for the unattended place. Taken together, these twin correlations demonstrate that although magnitudes of gain and tuning were tightly integrated across older adult individuals, this integration did not yield a bias toward the attended face. $**p < 0.01$; $*p < 0.05$.

3.4. Frontal ROI analysis

Thus far our extrastriate cortical ROI data indicate intact attention-driven modulation of gain in both young and older adults and intact attention-driven modulation of tuning in young but not older adults. In prior work, age-related decreases in posterior cortical function have been linked with "compensatory" effects in MFG, for example, concomitant age-related increases in MFG involvement during divided visual selective attention (Madden et al., 1997), visual multitasking (Clapp et al., 2011), perceptual discrimination of similar objects (Goh et al., 2010), and perceptual discrimination between competing objects (Schmitz et al., 2010). Extending on this prior work, we examined whether age-compensatory redistribution of resources to frontal cortex conforms to the competition-dependent predictions of a tuning model. Specifically, we expected to observe stronger MFG RS in older adults exclusively under HO, when extrastriate cortical tuning mechanisms failed to tune the correct object stream.

To interrogate this hypothesis, we examined indices of RS (e1 − e2) in a 2 (age) × 3 (competition) mixed ANOVA and constrained our search region to bilateral MFG ROIs (see "Methods" section). We

found a significant age × competition interaction in the right MFG extending into superior frontal sulcus, consistent with Brodmann area 8 ($F_{1,25} = 8.9$, $p = 0.001$). The interaction was driven by selectively larger magnitudes of RS under HO in older compared with young adults ($t_{25} = 4.1$, small volume corrected $p = 0.05$; Monteal Neurologic Institute coordinates: $x = 24$, $y = 30$, $z = 45$) (see Fig. 6A). These data support the prediction that stronger MFG RS in older adults would arise exclusively under HO.

To further determine whether this frontal correlate of compensatory late selection (increased MFG RS) was related with impaired extrastriate cortical tuning (decreased FFA RS), we examined the correlations between frontal and posterior indices of RS (e1 − e2) across older adults individuals. We found that decreased magnitudes of FFA RS correlated with increased MFG RS in older ($r = −0.56$, $p = 0.05$) but not younger adults ($r = −0.08$, $p = 0.7$), similar to results found previously (Schmitz et al., 2010). Critically, however, we demonstrate here that this pattern was exclusive to HO (see Fig. 6B and C). No significant MFG-FFA relationships were detected for LO or HS, in either group. There were also no significant MFG-PPA relationships detected in either group. Hence, in older adults, we observed a frontoposterior relationship under HO, when attentional modulation of FFA RS was impaired, but not LO, when attentional modulation of FFA RS was preserved. These collective brain-brain correlations suggest that impaired tuning of attended input at early stages of selection yields an increased compensatory reliance on competitive processing in MFG.

4. Discussion

The present study provides evidence that directed perceptual attention modulates both gain and tuning mechanisms embedded in the extrastriate cortical receptive fields. In young adults, increased attentional demand on gain and tuning induced the complementary but dissociable functions of cortical amplification and filtering, respectively. Across young adult individuals, these 2 mechanisms were strongly coupled in the FFA, but not the PPA, indicating that the integration of gain and tuning biased competing face and place inputs to favor the attended face. In older adults, we found that attention-driven modulation of gain was intact, whereas attention-driven modulation of tuning was abolished, with tuning driven instead by the physical salience of the stimulus. Moreover, gain and tuning were strongly coupled in both the FFA and PPA across older adult individuals, indicating that the integration of gain and tuning did not bias the attended face. Our results, therefore, indicate that age selectively diminishes the neural feedback signals that entrain tuning of selected sensory input.

Age-related impairments in attentional modulation of tuning may also arise at stages before object-selective extrastriate cortex. Indeed, scalp electroencephalography work examining age-related changes in feature-selective attention (Quigley et al., 2010) has also provided indirect evidence for an age impairment in perceptual tuning. In this study, healthy young and older adults directed attention to 1 of 2 superimposed color arrays. Whereas young adults exhibited robust modulation of occipital steady visual-evoked potential (SSVEP) amplitude to the attended color, older adults exhibited no difference in SSVEP amplitude to attended and unattended colors, indicative of impaired early feature selection. As with the present study, the age deficit in early selection observed by Quigley et al. (2010) does not appear to arise from an impairment of visual discrimination: older adults exhibited discriminate SSVEP responses to each feature. Nor does it appear to be driven by age differences in cortical modulation of gain: aside from the isolated post-cue deficit in feature-selective modulation, the overall topographic distribution and amplitude of the SSVEP were identical
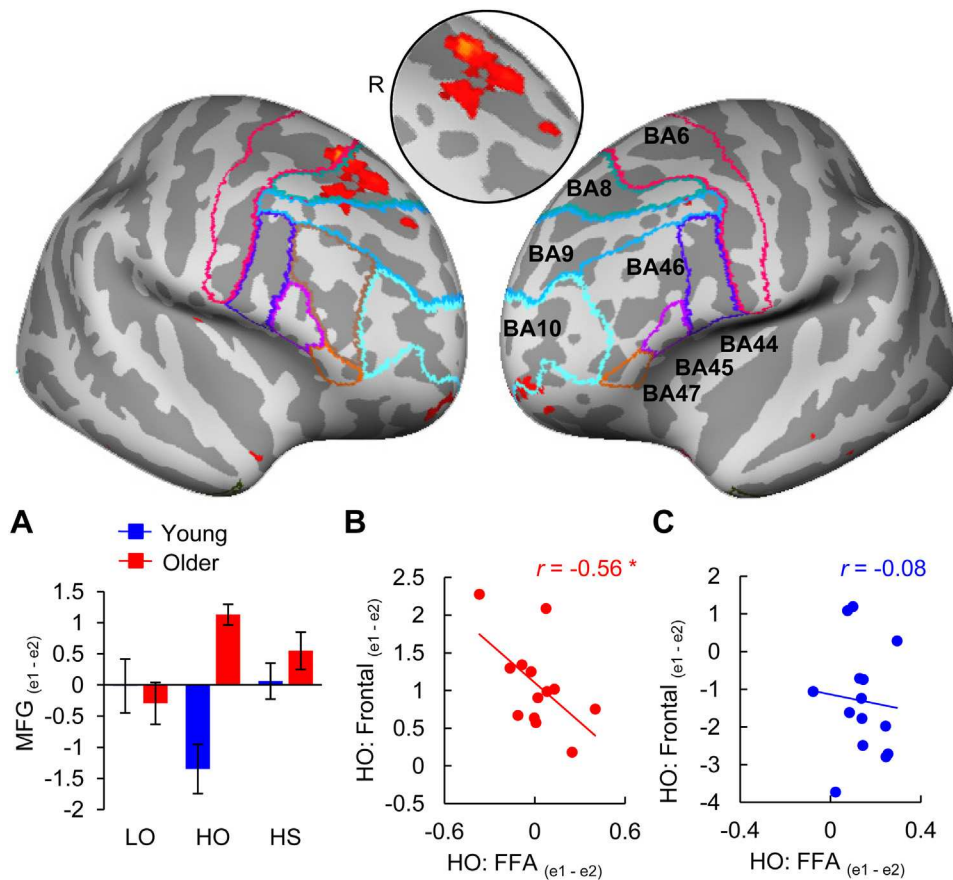
Fig. 6. Frontal region of interest analysis. (A) Age interacted with repetition suppression (RS) indices of tuning (exposures e1 − e2) at later stages of selection in the right middle frontal gyrus (MFG). High object (HO) competition isolated larger magnitudes of MFG RS in older compared with young adults. Activations were overlayed on an inflated cortical surface (fsaverage) registered to MNI atlas space using Freesurfer (http://surfer.nmr.mgh.harvard.edu/). Brodmann area labels included in the Freesurfer distribution are projected onto the surface for anatomic reference. (B) In older adults, decreased magnitudes of fusiform face area (FFA) RS correlated with increased MFG RS only under HO, indicating that impaired tuning of attended input at early stages of selection yields an increased compensatory reliance on competitive processing in MFG. (C) In young adults, this selective FFA-MFG relationship was not observed neither in HO (plotted) nor in any other condition. *$p < 0.05$.

between young and older adults. Under HO competition, our finding of an age impairment in early selection for attended faces, demonstrated by the absence of repetition-dependent changes in FFA selectivity, may, therefore, originate from earlier stages of impaired feature selection, in which the unattended input was afforded a competitive advantage. In older adults, the absence of FFA RS under HS competition supports this interpretation.

It is well established that the selectivity of visual cortical neurons to both features and objects is diminished in older adults. For instance, visual cortical neurons in senescent monkeys exhibit decreased orientation- and direction-selective response a increased spontaneous activity, both of which adversely affect the signal-to-noise ratio of sensory input (Schmolesky et al., 2000; Wang et al., 2005). Similarly, healthy older human adults have been found to exhibit decreased discriminatory neural response in extrastriate cortex to different object categories, for example, faces and places (Park et al., 2004, 2006, 2012), to different faces morphed to appear similar (Goh et al., 2010) and to repetitions of objects (Ballesteros et al., 2013). Extending on these collective results, we provide evidence that this age-related decline in discriminatory visual cortical response originates in the neural feedback signals that entrain tuning of an attended sensory input, rather than the inherent capacity for neurons in FFA and PPA to discriminate object categories, or repetitions of intracategory exemplars. In the latter 2 cases, we would expect to observe age differences in FFA and PPA selectivity for face and place stimuli, respectively, and age differences in the

magnitude of RS to repeated face exemplars under LO competition. Neither of these age differences were observed.

We next consider how attentional modulation of gain and tuning influenced behavioral measures of object discrimination. Taken together, the behavioral findings across experiment 1 and 2 demonstrate that increased object competition (HO) selectively decreased object discrimination in older adults. The control conditions (LS and HS) confirmed that this interaction between age and object competition was not attributable simply to low-level increases in luminance and contrast (opacity) of the unattended layer, that is, reduced perceptibility of the attended layer. Moreover, this effect does not appear to arise from age differences in response uncertainty: magnitudes of response slowing to novel exposures of HO competition stimuli (relative to the control conditions) were similar between groups. Nor does it appear to arise from age differences in perceptual familiarity to repeated exposures: magnitudes of response speeding to repetitions of HO competition stimuli (relative to control conditions) were also similar between groups.

Our behavioral results thus point to an age-related reduction in the encoding of the attended object by population neural responses in the visual cortex, which is related to the level of competition among sensory inputs. Our fMRI results confirm that this age-related reduction manifests, specifically, when competition from an unattended object is increased in older adults. This interpretation fits well with the observed impairment in attentional modulation of extrastriate cortical tuning. Together, our behavioral and

extrastriate cortical ROI findings suggest that with increasing competition among sensory inputs, perceptual encoding in the older adult population is characterized by cortical amplification at the expense of cortical selectivity, akin to boosting the volume on a radio without the capacity to tune the correct frequency.

The stimulus-driven pattern of extrastriate cortical tuning observed in older adulthood may, therefore, account for a wide array of observations typically attributed to age deficits in post-encoding executive function, specifically in the research domains of selective attention (Alain and Woods, 1999; Andres et al., 2006; Campbell et al., 2010; Chee et al., 2006; Rowe et al., 2006) and memory (Campbell et al., 2010; Gazzaley et al., 2005; Rowe et al., 2006; Stevens et al., 2008; Wais et al., 2012). We propose that these collective data may in part reflect a common age-related alteration in the neural basis of tuning at early stages of selection in the sensory cortices, perhaps because of loss of modulatory feedback from posterior parietal cortices (Mevorach et al., 2010; Vandenberghe et al., 2005; Xu and Chun, 2009) or cholinergic basal forebrain nuclei (Bartus et al., 1982; Mesulam, 1996). More work is needed to examine whether and how age potentially alters the feedback architecture of these posterior sites.

The influence of age was not limited to tuning in the extrastriate cortex, where older adults exhibited impaired early selection. We also observed age differences in the frontal cortex, where older adults exhibited a pattern of increased late selection. Critically, both observations of age-altered early and late selection were limited to the perceptually demanding HO competition condition, suggesting that these 2 patterns might be related. Consistent with this interpretation, we found an age- and competition-dependent relationship between weaker early selection for attended faces and increased late selection in frontal cortex. Our data, therefore, indicate that age-related changes in posterior attention subsystems, for example, those selectively engaged by visual selection (Jovicich et al., 2001; Mevorach et al., 2010; Wojciulik and Kanwisher, 1999) and those which influence the tuning profiles of population response in the extrastriate cortex (Goard and Dan, 2009), may represent an important functional antecedent to age-related changes at later stages of processing.

Age-related hyperactivation of the frontal cortex during cognitive tasks is typically attributed to neural compensation because of fewer available processing resources or to changes in cognitive effort when age-compensatory resources are exhausted (Grady, 2012; Reuter-Lorenz and Cappell, 2008; Reuter-Lorenz and Mikels, 2006). In particular, increased right MFG/IFG activity has been found in older compared with younger adults under low (but not high) working memory load (Cappell et al., 2010) and under low (but not high) perceptual demand (Goh et al., 2010), suggesting that this area represents a flexible but capacity-limited compensatory resource in advanced age. Our data suggest that the MFG may also represent an age-compensatory resource for impaired early selection, when competition among perceptual representations cannot be reconciled at downstream processing stages before encoding. Thus, in the context of perceptual attention, the compensatory but computationally inefficient nature of this frontoposterior cortical circuit may have afforded older adults the repetition-dependent improvements in male/female discrimination accuracy and priming observed under HO competition, accomplished by greater reliance on competitive processes in frontal executive systems rather than posterior perceptual systems. Future neuroimaging work examining age-related changes in selective attention would benefit from a more precise characterization of the temporal dynamics of competitive processing across the frontal and posterior cortical subsystems.

In older adulthood, as sensory cortical receptive fields yield increasingly to stimulus-driven tuning, directed attention may in turn come to rely increasingly on selection resources in the frontal cortices to preserve behavioral performance. With increasing age, this may represent 1 avenue for developing executive dysfunction, as frontal cortical resources become increasingly encumbered with compensatory redistribution of function from the perceptual cortices. Many well-described age-related deficits of executive function may, therefore, represent a consequence of impaired early selection, rather than its cause.

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