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Research Report

Category expectation modulates baseline and stimulus-evoked activity in human inferotemporal cortex

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ABSTRACT

Expectation of locations and low-level features increases activity in extrastriate visual areas even in the absence of a stimulus, but it is unclear whether or how expectation of higher-level stimulus properties affects visual responses. Here, we used event-related functional magnetic resonance imaging (fMRI) to test whether category expectation affects baseline and stimulus-evoked activity in higher-level, category-selective inferotemporal (IT) visual areas. Word cues indicating an image category (FACE or HOUSE) were followed by a delay, then a briefly presented image of a face or a house. On most trials, the cue correctly predicted the upcoming stimulus. Baseline activity in regions within the fusiform face area (FFA) and parahippocampal place area (PPA) was modulated such that activity was higher during expectation of the preferred (e.g., FACE for FFA) vs. non-preferred category. Stimulus-evoked responses reflected an initial bias (higher overall activity) followed by increased selectivity (greater difference between activity to a preferred vs. non-preferred stimulus) after expectation of the preferred vs. non-preferred category. Consistent with the putative role of a frontoparietal network in top-down modulation of activity in sensory cortex, expectation-related activity in several frontal and parietal areas correlated with the magnitude of baseline shifts in the FFA and PPA across subjects. Furthermore, expectation-related activity in lateral prefrontal cortex also correlated with the magnitude of expectation-based increases in stimulus selectivity in IT areas. These findings demonstrate that category expectation influences both baseline and stimulus-evoked activity in category-selective inferotemporal visual areas, and that these modulations may be driven by a frontoparietal attentional control network.

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1. Introduction

The ability to anticipate some aspect of a stimulus can provide an advantage for subsequent visual processing of that stimulus. For instance, stimuli appearing within anticipated locations are processed more efficiently (Posner et al., 1980;

Yeshurun and Carrasco, 1999), and similarly, attention to, or expectation of, other low-level features (e.g., color, direction of motion) leads to facilitated processing of stimuli containing those features (e.g., Ball and Sekuler, 1981; Corbetta et al., 1990; Saenz et al., 2002). Moreover, violations of expectation regarding simple stimulus attributes such as spatial location

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or low-level features can also incur perceptual costs in the form of increased reaction times for detection or discrimination (Posner et al., 1980).

In the real world, however, our expectations range from simple estimates of the potential locations of upcoming events, higher-level predictions related to the types of objects or scenes we will encounter, and even expectations regarding the identity of objects or individuals we will come into contact with. Recent studies have shown that the efficiency of perceptual processing of complex visual stimuli (e.g., faces, scenes) can be influenced by expectation of their category (Puri and Wojciulik, 2008) or identity (Faulkner et al., 2002; Puri and Wojciulik, 2008), leading to benefits for discrimination after valid expectation, and costs after invalid expectation. Thus, expectation of higher-level attributes (e.g. category) of complex stimuli can also enhance and/or interfere with perception.

What are the neural bases for expectation-based facilitation and interference? Results from studies of spatial and feature attention in monkeys and humans suggest that this may occur through modulation of pre-stimulus activity in relevant cortical regions after an attentional cue (baseline shifts), as well as attention-dependent changes in stimulus-evoked responses. Baseline shifts in visual cortex have been observed following cues to locations or low-level stimulus features (e.g., color, direction of motion) (Chawla et al., 1999; Fannon et al., 2008; Giesbrecht et al., 2003, 2006; Haenny et al., 1988; Hopf and Mangun, 2000; Hopfinger et al., 2000; Kastner et al., 1999; Luck et al., 1997; Luks and Simpson, 2004; Ress et al., 2000; Reynolds et al., 1999), and attention to particular locations or features is typically associated with increased firing rate or population response to an effective stimulus when it appears in that location and/or contains the expected feature (Anllo-Vento and Hillyard, 1996; Gandhi et al., 1999; McAdams and Maunsell, 2000; Moran and Desimone, 1985; O'Craven et al., 1997; Saenz et al., 2002; Spitzer et al., 1988; Treue and Martinez-Trujillo, 1999).

At the level of more complex stimuli, however, it is less clear how anticipatory attention affects related cortical activity. Although it has been demonstrated that attention to objects or object categories can modulate responses in monkey and human object processing areas during stimulus presentation (Chelazzi et al., 1998, 1993; Corbetta et al., 2005; Murray and Wojciulik, 2004; O'Craven et al., 1999; Serences et al., 2004; Wojciulik et al., 1998; Yi et al., 2006), the few studies that have investigated expectation-related, stimulus-independent baseline shifts in human object processing areas have been inconclusive (e.g., Corbetta et al., 2005). Moreover, the influence of pre-stimulus expectation on subsequent stimulus-evoked activity in human category-selective visual cortex has never been explored in the absence of competing stimuli; previous studies have not distinguished between effects induced by expectation per se and modulation due to selective attention to a subset of stimuli present in a display. Available evidence regarding cortical mechanisms of selective attention and how competitive interactions between stimulus representations arise, whether consistent with the predominant neural gain model (e.g., McAdams and Maunsell, 1999; Treue and Martinez-Trujillo, 1999) or (less commonly) demonstrating changes in tuning at the individual neuron level

(Haenny et al., 1988; Spitzer et al., 1988), suggests at least two ways in which expectation of a particular stimulus or category of stimuli could influence activity in neural populations selectively involved in processing that stimulus when it appears (Desimone and Duncan, 1995; Duncan, 1998).

First, expectation of a region's preferred stimulus may result in increased activity to any stimulus, reflecting an overall bias in neural populations selectively involved in processing the expected stimulus. Second, expectation of a particular stimulus could have the effect of increasing selectivity of population responses in relevant regions. That is, a greater difference between activity to a preferred vs. non-preferred stimulus after expectation of the preferred vs. non-preferred category could reflect enhancement/suppression of differentially tuned subpopulations within a region, regardless of the population's overall preference for a particular category, consistent with previous findings at the feature and early object-processing levels (Martinez-Trujillo and Treue, 2004; Murray and Wojciulik, 2004) and evidence for distributed representation of object categories in human inferotemporal cortex (Haxby et al., 2001; Ishai et al., 1999). Thus, effects of category expectation on stimulus-evoked activity in a category-selective region could include an overall bias (increased response to any stimulus), a relative increase in selectivity for the preferred stimulus, or a combination of both.

To distinguish between these possibilities, we used event-related functional magnetic resonance imaging (fMRI) to examine effects of category expectation on baseline and stimulus-evoked activity in extrastriate regions thought to be selectively involved in processing particular categories of complex objects, specifically, faces (fusiform face area [FFA]; Kanwisher et al., 1997; Puce et al., 1995) and scenes (parahippocampal place area [PPA]; Aguirre et al., 1998; Epstein and Kanwisher, 1998). During scanning, participants were cued on each trial to expect an image belonging to one of two object categories (faces and houses). After several seconds of expectation, on most trials an image from the expected category would appear; however, occasionally, an image from the other category would be presented instead (Fig. 1). This design enabled us to assess effects of category expectation on baseline activity in the FFA and PPA as well as to characterize stimulus-evoked activity as a function of both expectation and stimulus category. Additionally, we explored the relationship between activity in frontal and parietal regions and our observed effects of expectation in FFA and PPA, as effects of attention on baseline and stimulus-evoked activity in sensory cortex are generally considered to be driven by top-down signals generated in frontal and parietal cortex (Corbetta and Shulman, 2002; Kastner and Ungerleider, 2000; Miller and Cohen, 2001).

2. Results

2.1. Behavior

Reaction times (RTs) and accuracy (percent correct) for the behavioral task were recorded during the scanning runs in order to identify trials on which participants were not engaged in the task. Trials with incorrect responses were excluded

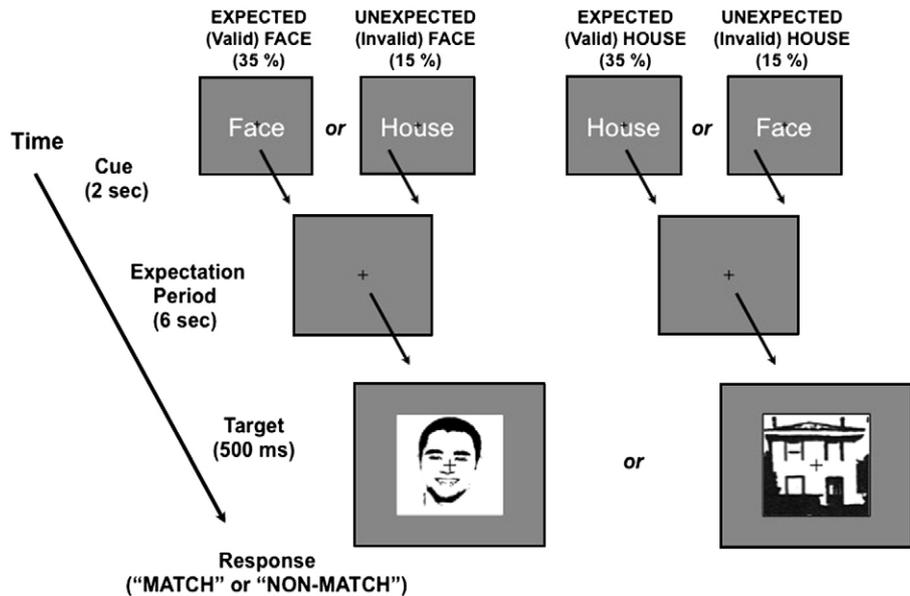


Fig. 1 – Task design. Trials began with a cue indicating the category of an upcoming stimulus (face or house). Cues correctly indicated the category on 70% of trials. Participants responded with a button press indicating whether the stimulus category matched the cue.

from the fMRI data analysis. Correct RT and accuracy data were entered into ANOVAs with expectation condition (valid/invalid) and stimulus category (faces/houses) as factors. RTs were faster for valid compared to invalid trials ($p < .0001$, $F(1,16) = 55.48$), with no main effect of stimulus category ($p = .21$, $F(1,16) = 1.74$). The expectation effect was greater for faces than for houses (expectation by stimulus category interaction: $p < .05$, $F(1,16) = 6.85$). Accuracy was close to ceiling (~98%), with marginally higher accuracy for valid vs. invalid trials ($p = .08$, $F(1,16) = 3.49$), no difference between faces and houses ($F(1,16) = .15$), and no interaction between expectation and stimulus category ($F(1,16) = .01$). The presence of effects of expectation on performance provides assurance that participants were attending to the cues, and may to some degree reflect facilitated perceptual processing of the target after expectation of the appropriate category (and/or costs incurred by invalid expectation). Because participants were informed of the greater proportion of valid trials, preparation for a “match” response may have contributed substantially to the observed effect that RTs were overall faster for valid than invalid trials. Importantly, however, RTs were faster for valid compared to invalid trials for both faces and houses. Therefore any motor bias to respond “match” will not affect cross-category comparisons in the imaging results below.

2.2. Effects of category expectation on delay period activity in category-selective regions

We first identified category-selective regions in IT cortex by contrasting activation during the localizer task between blocks of viewing faces vs. houses. These results were then masked using an anatomically defined region of interest that included anterior portions of the fusiform and parahippocampal gyri. Results from this analysis yielded large, bilateral clusters in

the fusiform (faces > houses; 206 voxels, $p < .005$), and parahippocampal (houses > faces; 418 voxels; $p < .005$) gyri (Fig. 2, black regions), consistent with previous reports of category selectivity in ventral extrastriate cortex in humans (Aguirre et al., 1998; Epstein and Kanwisher, 1998; Kanwisher et al., 1997; Puce et al., 1995).

To determine whether category expectation elicits shifts in baseline activity in category-selective regions, we looked for voxels within these ROIs that were more active during

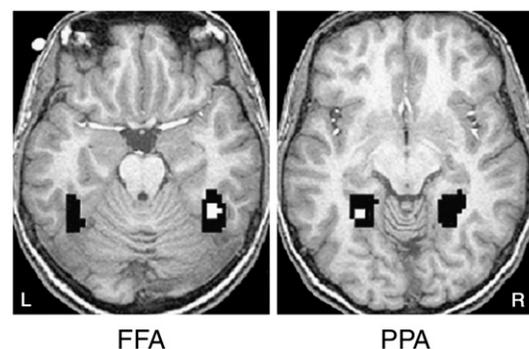


Fig. 2 – Baseline shifts in the fusiform face area (FFA) and parahippocampal place area (PPA). Left panel: Bilateral regions of inferotemporal cortex (in black) showing greater activity for passive viewing of faces compared to houses. A cluster in the right hemisphere within the face-selective ROI showed greater activity during face expectation compared to house expectation (in white). Right panel: House viewing vs. face viewing produced greater activity in bilateral regions of parahippocampal cortex (in black). Greater activity for house vs. face expectation was observed within the left hemisphere place-selective region (in white).

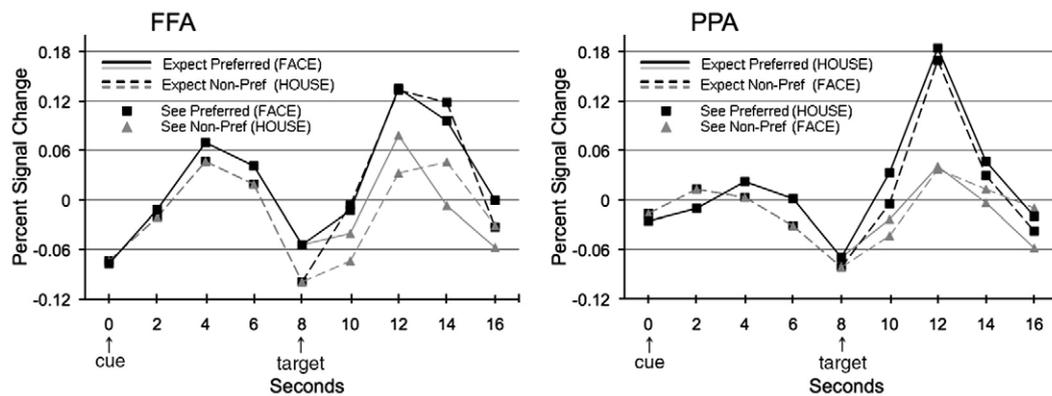


Fig. 3 – Time course of activity in expectation-sensitive regions of interest (ROI)s: Trial-averaged time courses extracted from expectation-sensitive regions in the FFA (left panel) and PPA (right panel) show greater activity during expectation of the preferred (solid) compared to the non-preferred category (dashed) 4–6 s after cue onset. Traces after target onset represent each of the four target conditions: preferred target after expectation of the preferred (black squares, solid) or non-preferred category (black squares, dashed), and non-preferred target after expectation of the preferred (gray triangles, solid) or non-preferred category (gray triangles, dashed).

expectation of a face compared to expectation of a house, and vice versa. We predicted that baseline activity would be higher during expectation of a region's preferred category than during expectation of its non-preferred category. Consistent with this prediction, activity in a cluster of 9 voxels within the right FFA showed increased activity during expectation of a face as compared to expectation of a house, whereas 10 contiguous voxels in the left PPA showed increased activity during house expectation as compared to face expectation ($p < .05$ for both, small volume corrected) (Fig. 2, white regions). Thus, activity in category-selective regions of extrastriate cortex is higher during expectation of a stimulus from the preferred vs. non-preferred category.

2.3. Effects of category expectation on stimulus-evoked activity in expectation-sensitive ROIs

Our next analyses assessed effects of expectation on activity related to stimulus processing. We examined target-evoked activity within the FFA and PPA clusters identified in the previous analysis as a function of expected category and subsequent stimulus category. Specifically, we sought to determine whether expectation of a region's preferred vs. non-preferred category (1) leads to a greater response to any stimulus (overall bias), and/or (2) increases stimulus selectivity (a greater difference between the response to stimuli from the preferred vs. non-preferred category after expectation of the preferred category). Trial-averaged time courses extracted from each of these clusters showed higher activity during expectation of their preferred category (Fig. 3), consistent with the criterion used for defining them (i.e., greater parameter estimates averaged across cue and delay for expectation of the preferred vs. non-preferred category). Critical for our question regarding bias and selectivity, however, is the effect of expectation on activity in these ROIs evoked by viewing of the target image.

Analysis of BOLD responses following presentation of the target revealed two temporally distinct expectation-related

effects. A four-way repeated measures ANOVA with ROI (FFA/PPA), expectation category (preferred/non-preferred), target category (preferred/non-preferred), and time (2/4/6/8 s after target presentation) showed main effects of target category (preferred > non-preferred; $p < .0001$, $F(1,16) = 32.53$) and time ($p < .0001$, $F(3,48) = 37.39$), but not expectation category or ROI. A three-way interaction between ROI, target category, and time ($p < .001$, $F(3,48) = 13.59$) was due to an earlier peak of stimulus selectivity (difference between activity to a preferred vs. non-preferred target) in PPA vs. FFA (Fig. 3). Furthermore, a three-way interaction between expectation category, target category, and time ($p < .02$, $F(3,48) = 11.56$) reflected different effects of expectation on early vs. later target-evoked activity. Initially upon target presentation, activity was greater overall (i.e., regardless of target category) after expectation of the region's preferred vs. non-preferred category (Fig. 4). In contrast, the later time points revealed a greater difference

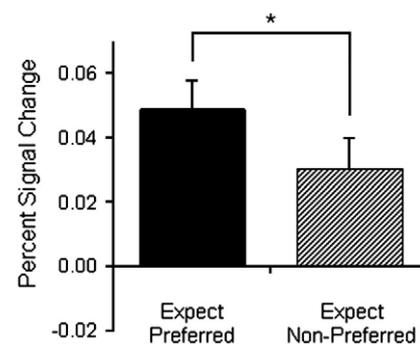


Fig. 4 – Initial bias in stimulus-evoked response: Activity averaged across 2 and 4 s after target presentation after expectation of the preferred (solid) or non-preferred (hatched) category (collapsed across target category and ROI). Responses were greater after expectation of the preferred category than after expectation of the non-preferred category. Error bars represent standard error of the mean.

between responses to preferred and non-preferred stimuli after expectation of the preferred category, consistent with an increase in selectivity of the region (Fig. 5).

These observations were quantified by separately analyzing percent signal change during the early (averaged across 2 and 4 s post-target) and late (averaged across 6 and 8 s post-target) phases of the stimulus-evoked response using ANOVA with expectation category (preferred/non-preferred), target category (preferred/non-preferred), and ROI (FFA/PPA) as factors. A main effect of expectation category during the early phase ($p < .02$, $F(1,16) = 7.57$) reflected larger responses (in general) after expectation of a region's preferred vs. non-preferred category (Fig. 4). This effect could be due, at least in part, to baseline shifts carried over from the expectation period; however, given that stimulus selectivity is already evident during the early post-target time points (main effect of target category; $p < .0001$, $F(1,16) = 34.97$), it is feasible that these expectation-based pre-stimulus modulations indeed influence activity evoked by target onset. Additional effects during the early phase included higher overall activity in PPA (main effect of ROI; $p < .03$, $F(1,16) = 6.13$), and a three-way interaction between expectation condition, target category, and ROI revealing that this expectation-induced "bias" was independent of target category in the PPA, but carried by responses to the non-preferred category in the FFA ($p < .005$, $F(1,16) = 11.61$).

Examination of activity during the later phase of the stimulus-evoked response (averaged across 6 and 8 s post-target) yielded a strikingly different result. A main effect of target category (greater activity for preferred vs. non-preferred stimuli; $p < .005$, $F(1,16) = 14.08$) confirmed that general category selectivity of the target-evoked responses continued into this phase of the time course. However, rather than the main effect of expectation (overall bias) observed in the early phase, a significant interaction between expectation condition and target category ($p < .03$, $F(1,16) = 6.27$) reflected a greater differ-

ence between the response to a preferred and non-preferred stimulus (stimulus selectivity) after expectation of the preferred vs. non-preferred category (Fig. 5). This increase in selectivity was consistent across face and place-selective regions (no significant main effect of or interaction with ROI).

To assess the degree to which a behavioral, or motor, bias toward a "match" response could account for the effects on stimulus-evoked activity, we performed an alternative analysis with validity instead of expectation category as a factor (along with ROI, stimulus category, and time) and found no main effect of validity. A three-way interaction between validity, stimulus category and time ($p < .02$, $F(3,48) = 12.48$) was due to higher activity for valid trials than for invalid trials during the late phase of the response, but this effect was only significant for non-preferred targets ($p < .01$, $F(1,16) = 9.29$). Moreover, there was no evidence of a "match" bias during the early phase of the response; instead, expectation of the preferred category, regardless of validity, led to greater activity. Thus it is unlikely that a general motor bias could alone account for the observed modulations.

2.4. Source of expectation-related modulations in inferotemporal cortex

Several findings suggest that frontal and parietal regions may be critical for the allocation of attentional resources across a variety of spatial and object-based tasks (Corbetta and Shulman, 2002; Kanwisher and Wojciulik, 2000; Pessoa et al., 2003, for review). Accordingly, we predicted that such areas might serve as the sources of top-down input that give rise to response modulation in category-selective extrastriate regions. If this is the case, we reasoned that category expectation should be associated with increased activity in frontal and parietal cortices and that expectation-related activity in these regions should be correlated with the category-specific expectation effects observed in FFA and PPA.

To test this prediction, we first generated an "expectation selectivity" index for each participant by computing the mean difference in parameter estimates extracted from the previously described expectation-sensitive clusters in the FFA and PPA during expectation of a preferred stimulus, as compared with expectation of a non-preferred stimulus (i.e., the "expect face" – "expect house" difference was computed for the FFA ROI and averaged with the "expect house – expect face" difference for the PPA ROI). This index reflected the degree to which category expectation elicited category-selective pre-stimulus activity for each participant. We next performed a group-level analysis to identify areas throughout the brain exhibiting general expectation-related baseline shifts (higher activity during the cue and delay periods of the task relative to fixation) and searched within the resulting map for voxels within which the magnitude of these baseline shifts correlated with expectation selectivity index values (see [Experimental Procedures](#) for details). This analysis revealed clusters in the left dorsolateral prefrontal cortex (DLPFC), right ventrolateral prefrontal cortex (VLPFC), left frontal eye fields (FEF), and right superior parietal lobule (SPL) (Fig. 6), possibly suggesting that recruitment of these regions during the expectation period influenced the degree of category-selective modulation

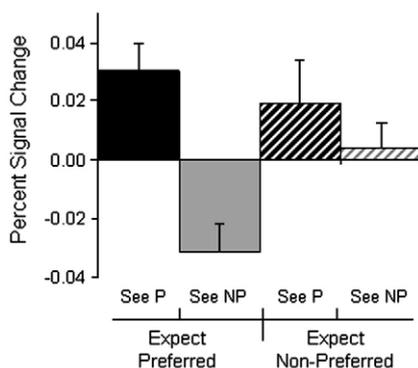


Fig. 5 – Change in selectivity of stimulus-evoked response: Activity averaged across 6 and 8 s post-target to preferred (See P, black) and non-preferred (See NP, gray) stimuli after expectation of the preferred (solid) or non-preferred (hatched) category (collapsed across ROI). The difference between responses to preferred vs. non-preferred stimuli was greater after expectation of the preferred (solid) vs. non-preferred (hatched) category. Error bars represent standard error of the mean.

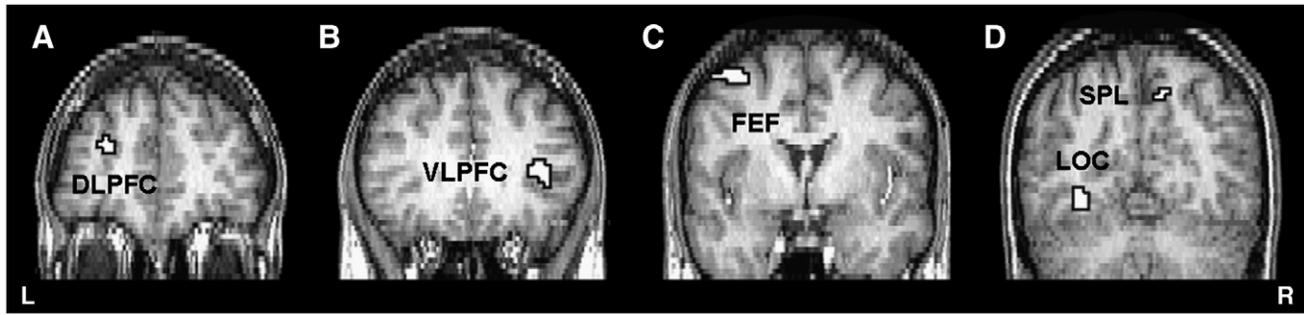


Fig. 6 – Correlations with baseline effects: Frontal and parietal regions in which activity during expectation (in general) correlated with the degree to which delay activity in face- and place-selective areas was selectively modulated by expectation of the preferred category. (A) Dorsolateral prefrontal cortex (DLPFC). (B) Ventrolateral prefrontal cortex (VLPFC). (C) Frontal eye fields (FEF). (D) Superior parietal lobule (SPL) and lateral occipital complex (LOC).

observed in object processing areas. In addition to these frontal and parietal regions, expectation-related activity in several intermediate visual processing areas, including MT (not shown) and regions within the lateral occipital complex (LOC) (Fig. 6D) was also correlated with the category-selective expectation effects in FFA and PPA.

We further hypothesized that if delay activity within these putative sources of category-selective expectation-based modulation in IT has consequences for subsequent stimulus processing, it should also correlate with the expectation-dependent changes in the stimulus-evoked response observed in the FFA and PPA ROIs. For this analysis, we defined “bias” as the difference between activity to any target following expectation of the preferred category vs. non-preferred category 2–4 s following onset of the target (e.g., the difference between the stimulus-evoked FFA response after expectation of a face vs. expectation of a house, independent of the target

stimulus). The index for “change in selectivity” was computed as the difference between activity to a preferred vs. non-preferred target as a function of category expectation 6–8 s following onset of the target stimulus (e.g., in FFA, the difference between the response to a face and response to a house after expectation of a house, subtracted from the difference after expectation of a face). For each participant, the bias and change in selectivity indices were averaged across the FFA and PPA ROIs. Correlational analyses revealed that whereas there were no significant correlations between delay activity in the frontal and parietal ROIs and the bias effects, activity in the left DLPFC cluster during the expectation period correlated significantly with the magnitude of the expectation-dependent changes in selectivity of the IT ROIs ($r(15) = .53, p < .03$; Fig. 7, left panel). A trend in the same direction was observed in the right VLPFC ($r(15) = .39, p = .12$; Fig. 7, right panel), but not in the FEF or SPL.

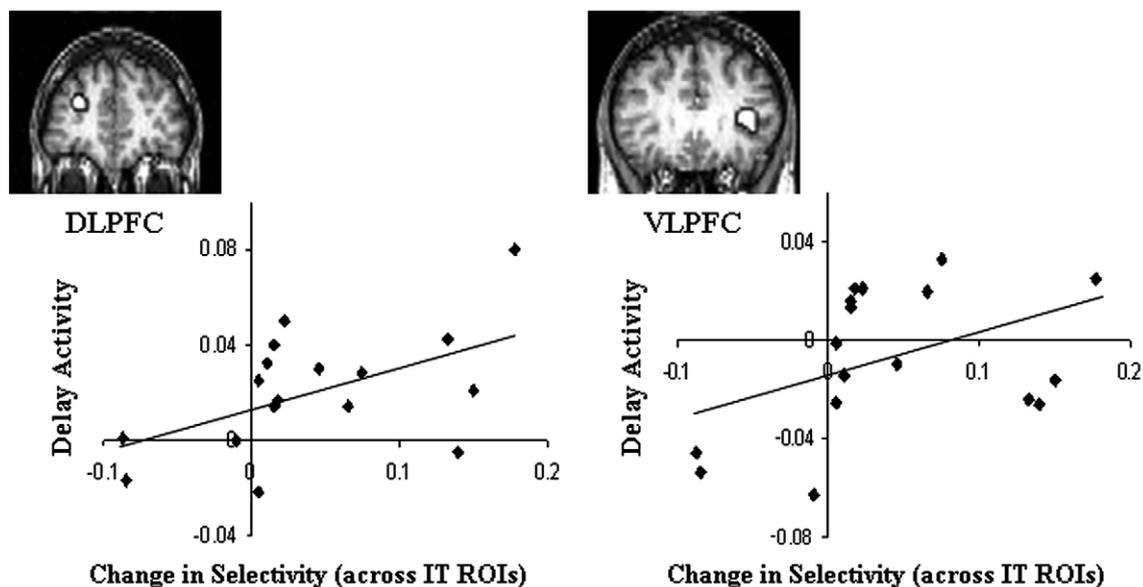


Fig. 7 – Correlations with selectivity effects. Left panel: Positive correlation ($r = .53$) between expectation-related activity in the DLPFC ROI and the subsequent change in selectivity observed in the expectation-sensitive, category-selective inferotemporal regions. Right panel: Similar trend in the VLPFC ($r = .39$).

3. Discussion

We used fMRI to determine whether category expectation selectively influences pre-stimulus (baseline) and stimulus-evoked activity in category-selective object processing regions of human IT cortex. We found that expectation of faces and houses resulted in category-selective increases in pre-stimulus activity within the FFA and PPA, respectively, and that across participants, these modulations were correlated with expectation-related activity in the DLPFC, VLPFC, FEF, and SPL. Furthermore, the initial response to a face or house target within these expectation-sensitive, category-selective regions was greater after expectation of the region's preferred category, possibly reflecting an expectation-induced biasing of the response to the target. In contrast, subsequent activity was characterized by an increase in the category selectivity of these regions. The increase in selectivity of stimulus-evoked responses was correlated with the magnitude of prefrontal activity during the expectation period. These findings demonstrate that category expectation indeed influences neural activity in a category-selective manner, both prior to and during subsequent stimulus processing. In addition, our results provide evidence that top-down modulation of sensory activity at the object processing level may be driven by components of a general attentional control network.

3.1. Category-selective baseline shifts in inferotemporal cortex

Our finding of category-based expectation-related baseline shifts in FFA and PPA is perhaps not surprising given previous evidence of increased activity in retinotopic areas during expectation of stimuli within particular locations (Kastner et al., 1999; Ress et al., 2000). However, such stimulus-independent attention-related baseline shifts have not yet been consistently demonstrated in category-selective visual processing areas (Corbetta et al., 2005). Nonetheless, based on recent behavioral studies showing effects of exemplar and category expectation on perceptual processing of faces and places (Faulkner et al., 2002; Puri and Wojciulik, 2008), we predicted that expectation of an object from a particular category should result in modulation of the BOLD signal in cortical regions selectively involved in processing objects from that category, prior to stimulus presentation.

Furthermore, although previous fMRI studies have shown increased activity in FFA and PPA in the absence of a stimulus during imagery and working memory tasks (Ishai et al., 2002; Johnson et al., 2007; O'Craven and Kanwisher, 2000; Ranganath et al., 2004; Lepsien and Nobre, 2007), in those studies participants were required to generate representations of *specific exemplars* from the region's preferred category. Here, we demonstrated that *category* expectation can also influence baseline activity in object-selective regions. These data not only are consistent with reports of baseline shifts in earlier visual areas due to attention to locations or low-level features (Chawla et al., 1999; Kastner et al., 1999) and previous reports of weak modulations in IT cortex induced by exemplar expectation at the object level (Corbetta et al., 2005) but also provide new evidence demonstrating stimulus-independent

effects of category expectation on activity in visual processing areas.

3.2. Modulation of stimulus-evoked activity in FFA and PPA

Activity evoked by faces or houses in expectation-sensitive FFA and PPA clusters reflected an initial bias (higher overall stimulus-evoked response) after expectation of the preferred category, as well as a later increase in the selectivity of responses (greater difference between activity to a preferred versus non-preferred stimulus after expectation of the preferred category). The feature-similarity gain model (Maunsell and Treue, 2006; Treue and Martinez-Trujillo, 1999), if applied at the object level, would suggest that category expectation may serve to increase activity in neurons selective for relevant object classes, while inhibiting others, leading to an increase in population selectivity as previously proposed regarding features (Martinez-Trujillo and Treue, 2004).

Accordingly, baseline activity would increase in cortical regions dominated by neurons selective for an expected category. Critically, because the region may also include neurons selective for different categories (Haxby et al., 2001; Ishai et al., 1999) whose activity would be simultaneously suppressed, the difference in activity for a preferred vs. non-preferred target should be greater after preparation for the preferred target. For example, after face expectation, FFA neurons preferring faces would respond more to a face, whereas those few preferring houses would respond less to a house. The reverse would be true after expectation of a house, leading to a greater difference between responses to the two classes of stimuli after expectation of the region's preferred category. However, as seen in our data, such an increase in population selectivity may be initially masked by an expectation-based bias, as the onset of any stimulus may elicit a higher response from neurons primed for their preferred category.

This pattern of expectation-based modulation of stimulus-evoked activity can be interpreted in the context of previously reported behavioral benefits and costs for processing of complex object stimuli. Specifically, valid expectation of the preferred stimulus category may serve to enhance processing of the subsequent preferred stimulus, both by increasing overall activity and by improving the stimulus selectivity at the population level. The same expectation, when invalid, may result in a misallocation of resources such that the efficiency of processing stimuli from the different category is reduced, and in cases of ambiguous or noisy stimuli, could even lead to "misperception" (Summerfield et al., 2006).

3.3. Correlations with delay activity in frontal and parietal areas

Activity in frontal and parietal regions during the expectation period was significantly correlated with the magnitude of category-selective baseline shifts in IT cortex. Furthermore, for the subset of these regions located within prefrontal cortex (PFC), this activity was also correlated with expectation-based increases in selectivity of the stimulus-evoked response in FFA and PPA. Involvement of the lateral PFC both in attentional selection and in visual working memory maintenance has

been well documented (D'Esposito et al., 1999; Egner and Hirsch, 2005; Ranganath et al., 2000; Funahashi et al., 1989; Shulman et al., 2002). In the current study, to the extent that "category expectation" likely consists of both attentional (selection of the relevant category based on the cue) and working memory (maintenance of the relevant category over the delay) components, either or both may have contributed to the observed expectation-based modulations. Although dissociating the role of PFC in attention and working memory remains an area of active investigation, one interpretation of the available evidence suggests a shared selection mechanism underlying both processes (Awh and Jonides, 2001; Awh et al., 1998; Barnes et al., 2001; Deco and Rolls, 2005; Lebedev et al., 2004; Rutman et al., 2009).

Thus, our findings are consistent with the view that prefrontal regions may form part of the network that provides top-down signals to sensory cortex (e.g., Miller and D'Esposito, 2005), in this case modulating activity at the object processing level. Moreover, our data indicate that the strength of sensory modulation is likely to depend on the degree to which participants engage in expectation. It has been shown previously that activity in left DLPFC covaries with the degree of category selectivity in IT regions during a perceptual decision task (Heekeren et al., 2004). The present data go beyond these findings by demonstrating that the magnitude of expectation-dependent increase in selectivity is related to activity in this region during expectation itself.

4. Experimental procedures

4.1. Participants

Nineteen individuals from within the UC Davis community (9 females) participated in the study and were financially compensated for their participation. All participants had normal or corrected-to-normal vision, and gave written informed consent under a protocol approved by the University of California, Davis, Institutional Review Board on Human Subjects Research. Data from two participants were excluded from analysis: one due to excessive head motion, and another due to a technical problem with acquisition of behavioral responses.

4.2. fMRI data acquisition and pre-processing

Scanning was performed using a 1.5 T GE Signa scanner at the University of California, Davis Imaging Research Center in Sacramento, California. A gradient echo-planar imaging sequence was used for the functional scans (TR=2, TE=40 ms; FOV=220 mm; 64×64 matrix). Each volume consisted of 18 6-mm (5-skip-1) axial slices, acquired in an interleaved fashion, starting with the bottom slice. Coplanar images for each participant were acquired within the same session. High-resolution T1-weighted images were acquired within the same session for a subset of the participants. Pre-processing of functional data was performed using statistical parametric mapping (SPM5) software (<http://www.fil.ion.ucl.ac.uk/spm>) and included slice timing correction, motion correction, spatial normalization to the Montreal Neurological

Institute (MNI) template, reslicing into 3 mm isotropic voxels, and smoothing with an 8 mm Gaussian kernel.

4.3. Design and procedure

Each scanning session began with two localizer runs, during which participants passively viewed sequences of centrally presented black-and-white face and house photographs. Each of these runs consisted of six 28-s stimulus epochs, alternating between faces and houses, with 20-s periods of fixation in between. Each stimulus epoch contained 32 different face or house images presented for 700 ms each, for a total duration of just over 5 minutes per run. These passive viewing epochs were used to localize regions in the fusiform and parahippocampal gyri that responded more to faces than houses, and vice versa (respectively).

Following the localizers, each participant completed five runs of the expectation task. As shown in Fig. 1, trials began with a centrally presented word cue, either "Face" or "House," for 2 s. Following a 6-s delay, an image of either a face or a house appeared for 500 ms. Participants responded with a button press indicating whether the image matched their expectation based on the cue. Responses were made using the first two fingers of the right hand, and the specific finger used to indicate a "match" vs. "non-match" was counterbalanced across participants. Each face and house image was trial-unique. All stimuli were presented on a gray background, and participants were instructed to maintain fixation on a cross that was present in the center of the display throughout the experiment. Each experimental run consisted of an initial fixation period, followed by 18 valid (9 face trials and 9 house trials) and 8 invalid (4 face trials and 4 house trials) trials presented in random order within each run, for a total of 130 trials across all five runs. Participants were informed that on the majority of trials (~70%), the cue would correctly predict the category of the upcoming image. Each participant completed between five and ten practice trials outside of the scanner prior to the scanning session. The stimuli for the localizer and expectation tasks were displayed using Presentation® software (www.neuro-bs.com), and rear-projected onto a screen positioned at the foot of the scanner bed.

4.4. Data analysis

Functional data were analyzed by applying a general linear model (GLM) using VoxBo (www.voxbo.org); covariates modeling the blood oxygenation level-dependent (BOLD) signal associated with conditions or events of interest were convolved with a hemodynamic response function (HRF). High and low temporal frequencies were removed, and trends in global signal as well as the 1/f noise component were accounted for in the model (Aguirre et al., 1997; Zarahn et al., 1997). Maps of group-level t-contrasts "face viewing>house viewing," and vice versa, were generated from the localizer runs in order to identify clusters of category-selective voxels within an anatomically defined region of inferotemporal (IT) cortex. Based on Monte Carlo simulations using the AlphaSim program (Ward, 2000), it was determined that a voxel-wise threshold of $p < .005$ along with a cluster size threshold of 41 would result in a corrected family-wise error rate of $p < .05$.

For the experimental runs, we treated the cue (“Face” or “House”) and face or house expectation (modeled as occurring at the time point halfway between cue and target onset) as covariates of interest in the GLM for those trials for which participants responded correctly. Trials with incorrect responses were modeled with separate covariates. Parameter estimates corresponding to each contrast of interest for individual subjects were entered into second-level analyses with which significant areas of expectation-related activation were identified for the group. We searched within the localizer-defined category-selective IT regions of interest (ROIs) for clusters of voxels for which activity related to face- or house-specific expectation exceeded a voxel-wise threshold of $p < .005$, and a cluster size threshold of 8 voxels (Fig. 2). Again, simulations using AlphaSim indicated that, with these thresholds, the corrected family-wise error rate was $p < .05$.

To identify regions in frontal and parietal cortex that showed expectation-related activity correlated with category-selective expectation effects in IT cortex, we generated an index of expectation selectivity for each participant by calculating the difference between parameter estimates extracted from each face and house expectation-selective region during expectation of the preferred vs. non-preferred category, and averaging these differences across expectation-selective ROIs. These individual participants’ expectation selectivity indices were then entered into a group-level correlation analysis in SPM5, identifying clusters for which activity during the cue and expectation periods correlated with the expectation selectivity indices at a threshold of $p < .01$, within a map of regions showing greater activity during the cue and expectation periods in general (thresholded at $p < .01$). Under the assumption of no effects in either condition, this would correspond to a $p < .0001$ threshold for the conjunction analysis.

Time courses were extracted from the two expectation-sensitive face- and house-selective IT ROIs and averaged across each of the expectation conditions (expectation of a face or house) prior to target presentation, and across the four target conditions (expect preferred/see preferred, expect preferred/see non-preferred, expect non-preferred/see preferred and expect non-preferred/see non-preferred) at target onset (Fig. 3). Stimulus-evoked activity was divided into an “early” phase (average of 2 and 4 s after target onset) and late phase (average of 6 and 8 s after target onset), and percent signal change during each stage was entered into separate 3-way ANOVAs with expectation category (preferred/non-preferred), target category (preferred/non-preferred), and ROI (FFA/PPA) and as factors in order to explore temporally distinct patterns of expectation-based modulation apparent in the time courses (Figs. 4 and 5). Frontal and parietal regions for which expectation-related activity correlated with the IT expectation selectivity indices described above (Fig. 6) were also tested for correlations with expectation-based modulations of stimulus-evoked activity (Fig. 7).

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