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Repetition Suppression in Low- and High-Order Regions of the Primate Visual Cortex

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Abstract

Stimulus recency has a strong effect on both behavior and neural responses. Its effects on neural responses have been most closely studied in the visual system in inferotemporal cortex (IT) in which recency gives rise to suppressed responses by a phenomenon known as *repetition suppression*. This observation has led to many possible explanations of how repetition suppression arises in the visual system. Here, we explore three of them: (1) top-down, (2) bottom-up and (3) independently in each brain region. Each of these accounts makes different predictions about the pattern of effects at different stages in visual processing for cases in which the stimulus either is or is not a match for the location or the identity of the preceding stimulus. We tested these predictions by recording from neurons in IT and V2, two separate stages of processing, while monkeys viewed displays of repeated and non-repeated image sequences.

Keywords: monkey; repetition suppression; IT; V2; visual; neuron; object; representation; top-down; bottom-up

INTRODUCTION

Our visual environment is populated with objects that are relatively stable: Objects rarely suddenly disappear, jump to new locations, or change identities. Extensive evidence suggests that our brains are sensitive to this stability. Specifically, regions of the brain that encode object identity – in particular, inferotemporal cortex (IT) - respond primarily to objects when they are initially seen, and subsequently respond less as the same objects continue to be observed. This robust phenomenon, known as *repetition suppression*, is consistently observed in neural responses measured from both the hemodynamic response using fMRI (Kourtzi & Kanwisher, 2001) and at the level of single neurons (Baylis & Rolls, 1987). Moreover, repetition suppression is associated with behavioral improvements. For example, judgments about object properties such as ‘moves’ vs ‘does not move’ (e.g. bicycle vs statue) are faster for repeated versus non-repeated objects (Buckner et al., 1998; McMahon & Olson, 2007).

Despite its prevalence and possible link to behavioral priming, we know little about how repetition suppression arises within the visual system. To illuminate how repetition suppression arises at different levels of visual processing, the current study investigated repetition suppression to objects in IT and V2, one of its input regions, at the level of individual neurons in a non-human primate model – the macaque monkey. Our recordings from multiple brain regions at different levels of sensory processing under the same stimulus conditions could begin to arbitrate between different candidate network-level accounts of repetition suppression. This research could therefore inform how connections within the visual system shape object representations in response to recent visual experience.

The goal of the present research was to investigate the dynamics of how the visual system generates repetition suppression to objects. Specifically, this research investigated how repetition suppression may arise in IT and V2 by: (1) bottom-up transmission, in which suppression effects are passed from lower-order to higher-order regions, (2) top-down transmission, in which suppression effects are passed from higher-order regions to lower-order regions, and/or (3) independent effects occurring in higher-order and lower-order regions.

Repetition Suppression in IT

Our current understanding of repetition suppression for objects consists primarily of extensive evidence that it is a robust phenomenon in IT. IT is a high-order region of the visual system with neurons that have large receptive fields and respond with high selectivity to complex natural objects (Desimone, Albright, Gross, & Bruce, 1984; Kobatake & Tanaka, 1994). Consistent with these characteristics, electrophysiological responses in IT are reduced when the same object is presented at the same location compared to when a different object is presented (Sawamura, Orban & Vogels, 2006). This is evidence that repetition suppression in IT is highly sensitive to object identity.

Critically however, we know little about how this representation of object repetition is constructed by the visual system, in which IT is only one high-order region. IT builds representations from the input it receives from lower-order regions in the visual hierarchy including V2, a region with neurons that have smaller receptive fields typically restricted to within a single quadrant of the visual field (Gattas, Sousa, Mishkin & Ungerleider, 1997). In addition to its smaller receptive fields, V2 is thought to primarily represent visual features such as orientation, color and other low-level stimulus properties without particular selectivity to the unique object identities resulting from combinations of these features (Burkhalter & Van Essen, 1986). In what follows, we describe three ways in which repetition suppression may emerge in both a higher-order region (IT) and a lower-order afferent region (V2).

Bottom-Up Transmission of Repetition Suppression

IT receives much of its input from lower-order regions in the ventral stream hierarchy such as V2 (Baizer, Ungerleider & Desimone, 1991; Nakamura, Gattass, Desimone, & Ungerleider, 1993). These afferent pathways have led some (Grill-Spector, 2006; Kohn, 2007) to speculate that repetition suppression observed in IT is inherited from earlier visual regions by a primarily bottom-up process. If this were the case, then IT would inherit from V2 its pattern of suppression effects, including its dependence on object identity and location.

Top-Down Transmission of Repetition Suppression

It is known from anatomical studies that there are top-down projections from IT to V2 in the macaque brain (Baizer, Ungerleider & Desimone, 1991). However, we know little about the function of these projections, let alone regarding repetition suppression. A top-down account suggests that effects observed in IT will also manifest in V2 (Garrido et al., 2009; Grotheer & Kovacs, 2016). If this were the case, then V2 would inherit from IT its pattern of suppression effects, including its dependence on object identity and location.

Independent Repetition Suppression in IT and V2

A third possibility is that repetition suppression occurs independently in IT and V2. This possibility allows for contrasting effects in V2 and IT. Due to the small receptive field sizes of V2 neurons and the fact that they are selective for simple features rather than complex images (Gattas, Sousa, Mishkin & Ungerleider, 1997), suppression in V2 might occur primarily when objects appear at the same location, regardless of object identity. By the same token, repetition suppression in IT might occur primarily when objects share the same identity, and not the same location.

Interaction of Identity and Location in Repetition Suppression

It is worth noting that repetition suppression could be synergistically modulated by location and identity, such that the magnitude of suppression could be greater for the same object repeated in the same versus different locations above and beyond the sum of each independent effect. These types of interaction effects can be predicted based on the architecture of correlation-based models of repetition suppression (Kohn, 2007; Solomon & Kohn, 2014; Barlow & Foldiak, 1989; see also De Meyer & Spratling, 2009) in which lateral connections are the most plausible biological substrate for these computations, for which there is some experimental evidence (Hosoya, Baccus & Meister, 2005). These models suggest that repetition suppression can show enhanced selectivity above and beyond the sum of repetition effects associated with a single stimulus feature such as identity or location.

The Current Study

The overall goal of the current study was to cast light on the issue of how repetition suppression is constructed from representations at multiple levels of the visual system. To accomplish this goal, we measured the degree to which neural responses in IT and V2 were suppressed when an initial image (the Prime) of an object was followed by an image of the same or a different object (the Probe) at either the same or a different location. We used this approach to distinguish between bottom-up, top-down and independent accounts of repetition suppression. From each account we can make specific predictions about the patterns of repetition suppression that would be observed in V2 and IT.

Based on previous studies of repetition suppression, we know two things about the response properties of neurons in IT: (1) they are only suppressed for repetitions of the same object, and not for different objects in the same location (Sawamura, Orban & Vogels, 2006) and (2) responses to repeated presentations are suppressed even when they appear in different locations (De Baene & Vogels, 2010). We also know that V2 has small receptive fields restricted to a single quadrant of visual space. These observations constrain our interpretations of what effects observed in V2 might mean for each account.

A bottom-up account predicts that the selectivity of repetition suppression to object identity in IT might be transmitted from V2. Specifically, this predicts that responses in V2 will likewise not be suppressed when different objects appear in the same location. On the other hand, if we do see repetition suppression to different objects in the same location in V2, this would suggest against a purely bottom-up account. Due to the small receptive field sizes of V2 neurons, a purely bottom-up account of the location-generalization observed in IT seems implausible and therefore we rule out this interpretation.

In contrast, a purely top-down account predicts that lower-order regions such as V2, which have small receptive fields, may inherit some location-generalization via top-down influence of neurons in IT with larger receptive fields. In other words, top-down influence from IT may cause V2 neurons that do not respond to an initial object that is outside their receptive field to nonetheless show suppressed responding to a repetition of the same object when it then appears within their receptive field. If, on the other hand, we do not see repetition suppression to objects initially presented outside the receptive field in V2, this would suggest against a purely top-down account.

Finally, the possibility that repetition suppression occurs independently in V2 and IT makes the prediction that we would see different patterns of repetition suppression in each area. The most plausible pattern would be that suppression in V2 (but not IT) will occur for repeated locations even when objects are not repeated and that suppression in IT (but not V2) will occur for repeated objects even at different locations.

METHODS

Experimental Subjects

Three adult male rhesus macaques (*Macaca mulatta*) were used in the course of these studies. Monkey O was used for both IT and V2 recording experiments. Monkey S was used for IT recording experiments and monkey R was used for V2 recording experiments. Surgeries were performed to implant subjects with a headpost and craniotomies to access recording sites. All surgical procedures were carried out under gas anesthesia using aseptic technique. Vital signs were monitored continuously during surgery. All experimental procedures complied with local and national guidelines for the care and use of laboratory animals.

Apparatus

Neurophysiological Recording. On each recording day, a cylindrical grid was placed in the recording chamber over either IT or V2 and a single varnish coated tungsten microelectrode was advanced through a stainless steel transdural guide tube using a hydraulic micromanipulator until phasic visual responses were obtained. The analog electrical signal was digitally recorded and stored using a Plexon system.

Eye Tracking. The monkey's gaze was monitored continuously via an infrared eye tracking system (ISCAN).

Experiment Presentation. The experiment was presented on a PC running NIMH Cortex. All images were presented on an LCD monitor at a viewing distance of 32 cm and a refresh rate of 60 Hz.

Stimuli

We used a set of 1,000 photographs of objects on a blank background that each subtended 5° of visual angle as a stimulus bank.

Design

Two subsets (A and B) of 2 images each were used to generate pairs of Prime and Probe presentations in one of four match conditions, generated from the combination of two factors: identity (same versus different) and location (same versus different). Specifically, the match conditions were: (1) BothMatch, in which the same image appeared twice in the same location; (2) IDMatch, in which the same image appeared twice in different locations, (3) LocMatch, in which the two different images in a subset were presented in the same location, and (4) NoMatch, in which the two images in a subset were presented in different locations (see Figure 1). In each condition, the first image was the Prime, and the second was the Probe. All images in subsets were used as Primes and Probes in all 4 conditions.

Procedure

Identifying Preferred Stimulus Sets. From a panel of 16 daily novel images the 4 that elicited the highest firing rates at the recording site were selected as the stimulus set for the recording session. These 4 images were then each arbitrarily assigned to one of two subsets of 2 images each. See Figure 1 for examples of stimuli used.

Behavioral Task. Monkeys completed a passive fixation task. In each trial of this task, monkeys were required to maintain gaze within 1-2° visual angle of a central fixation point while images were displayed in the periphery.

The fixation point was presented throughout each trial. During each trial, the fixation point first appeared alone for

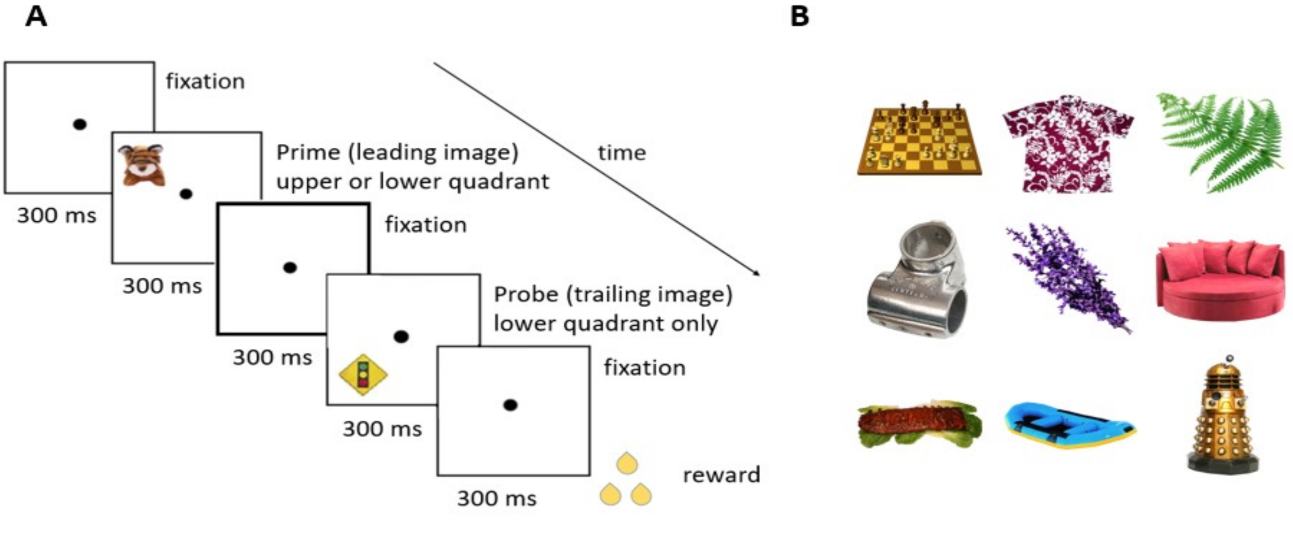

Figure 1: A: Schematic of events within a single trial. An example NoMatch trial is shown. B: A representative subset of example stimuli chosen from the image bank used for IT and V2 recordings.

300ms. Subsequently, one image was presented as a Prime for 300 ms at a location above or below the fixation point at 6° eccentricity. After 300 ms following the offset of the Prime, another image was presented as a Probe for 300 ms at a location below the fixation point at 6° eccentricity. Finally, the monkey received a juice reward (see Figure 1). If the monkey diverted its gaze from the fixation window the trial was aborted, no juice was delivered, and a brief checkerboard mask was displayed.

Trial Conditions. In each trial, the pair of Prime and Probe images came from either subset A or subset B, and were presented in one of four conditions: BothMatch (same image at the same location), IDMatch (same image in different location), LocMatch (different image at the same location), or NoMatch (different image in different location). Each Subset was used to generate eight unique trials in these four conditions by using each image in a subset as the Prime and/or Probe across trials, for a total of 16 unique trials across subsets. Consecutive trials always alternated between subsets A and B. Consequently, no image was presented in two consecutive trials. This design prevented cross-trial carryover of image-specific repetition effects. A session consisted of four repetitions of the 16 unique trials, for a total of 64 trials recorded for each neuron.

RESULTS AND DISCUSSION

We analyzed the data with the goal of testing predictions about the network-level effects which give rise to repetition suppression in regions at different levels of the visual hierarchy. Each of these network-level accounts gave us predictions about the patterns of suppression effects we would expect to see both within and between regions. We conducted analyses to test these predictions separately for the responses of neurons in IT and V2. The main outcome measures were the 2 main effects of location and image identity and the interaction term from a 2-way ANOVA. We also conducted two planned pairwise comparisons designed to test the predictions of each of the network-level accounts. A purely bottom-up account would predict that location-based effects in V2 should transfer to IT. We planned to test for a pure location effect (NoMatch > LocMatch) in V2 and IT. The presence of a significant effect in both would constitute evidence in favor of a bottom-up account. We also planned to test for a pure identity effect (NoMatch > IDMatch) in IT and V2. A significant effect in both would constitute evidence in favor of a top-down account. A significant effect in one region but the absence of an effect in the other would suggest a lack of direct transfer via either bottom-up or top-down input, and would instead be compatible with an independent account. The observation of a significant interaction would also be compatible with an account whereby the synergistic component of repetition suppression arises independently in each region.

Preliminary Analysis

We recorded from 108 neurons in IT and 55 neurons in V2. The raw data consisted of neuronal voltage waveforms. For analyses, we performed waveform sorting using Plexon Offline Sorter on these raw data to manually separate clusters of waveforms in PCA space into single units.

The Prime responses served as an internal control for the effectiveness of image identity and presentation sequence counterbalancing. They also served as a baseline for the unsuppressed response, to which we would compare the Probe responses to assess the level of repetition suppression. We took as our basic unit of analysis the total spike count between 100-250 ms post stimulus onset, both to the Prime, and to the Probe, for each neuron, for each condition. The matched-location Prime was used as a pre-repetition baseline because V2 neurons did not respond to the Prime presentation on IDMatch and NoMatch trials, as it was presented outside of their receptive fields and this lack of response in these conditions was expected. Only Prime presentations that occurred at the same location as the Probe were thus appropriate to use for both IT and V2.

The response of the neurons to the Prime in conditions in which it appeared at the same location as the subsequent Probe were not significantly different from each other (2-sample t-test, p = .9461 in V2, p = .9225 in IT) and so we collapsed across them for subsequent analysis. We next generated a suppression score for each neuron for each condition by taking the response to the Prime (when it appeared at the Probe location) and subtracting the response

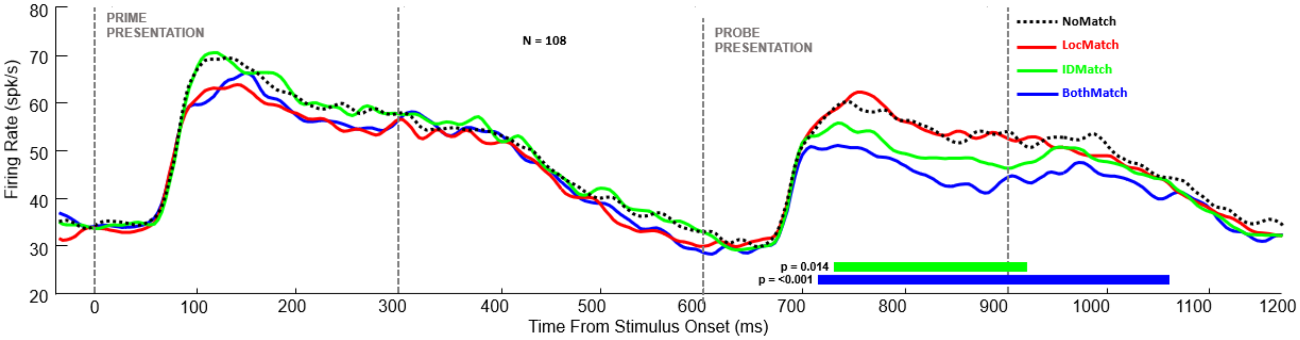

Figure 2: PSTH of the response of IT neurons to Prime and Probe image sequences. Vertical axis: firing rate in spikes per second, horizontal axis: time from stimulus onset in milliseconds. Colored bars indicate the largest significant cluster for the corresponding condition using a cluster-based permutation test.

to the Probe. This gave us a suppression score in number of spikes for each match condition. Lastly, we mean-normalized the suppression scores across the 4 conditions to control for neuron-to-neuron variability in firing rate magnitude.

Repetition Suppression in IT

We first considered repetition suppression in IT. Fig. 2 shows a peristimulus time histogram (PSTH) of the average response of all the neurons recorded in IT to each of the 4 match conditions separately.

To investigate the separate contributions of stimulus location and identity to overall repetition suppression in IT, we submitted these data to a 2x2 ANOVA with two factors: (1) Identity (levels: Same versus Different), and (2) Location (levels: Same versus Different). This analysis revealed a significant main effect of Identity (greater suppression when identity was the same, $F(1,108) = 114.54$, $p < .001$). The main effect of Location (greater suppression when location was the same) did not reach our alpha level of $p < .01$ with a value of $p = .0223$. Importantly, these main effects were qualified by a significant interaction ($F(1,108) = 10.4$, $p = .0014$) whereby suppression when both identity and location were a match was greater than the sum of the independent identity and location effects.

We conducted two planned pairwise comparisons (2-sample t-tests at an alpha level of .01) based on the predictions of the different network-level accounts, designed to test the predictions of each: One comparing repetitions of the same image in a different location versus a different image in a different location, and one comparing presentations of different images in the same versus different locations. These comparisons revealed that repetition suppression was greater for the same image even when presented in different locations ($t(108) = 5.3883$, $p = 1.8702\text{e-}07$). In contrast, no such effect was observed for different images at the same location ($p = .5029$).

To analyze these patterns across match conditions without *a priori* selecting an arbitrary analysis window, we employed a nonparametric cluster-based permutation test for analysis of time series data as described by Maris and Oostenveld (2007). This analysis tested whether the firing rates between a pair of match conditions continuously exhibited a consistent difference greater in strength than would be expected by chance during any period of the trial from Probe onset to the end of the trial. Each of the three match conditions was compared to the NoMatch condition from Probe onset to the end of the trial. The LocMatch comparison revealed no significant temporal clusters. The IDMatch comparison revealed the longest single significant cluster ($p = .014$) to occur from 130-317 ms post Probe onset and the BothMatch comparison revealed the longest single significant cluster ($p < .001$) to occur from 111-453 ms post Probe onset.

Repetition Suppression in V2

We next considered repetition suppression in V2. Fig. 3 shows a PSTH of the average response of all the neurons recorded in V2 to each of the 4 match conditions separately.

We carried out the same analyses on the V2 data that we submitted the IT data to. The 2x2 ANOVA with Identity and Location as factors revealed a significant main effect of Identity (greater suppression when identity was the same, ($F(1,55) = 62.89$, $p = 1.1627\text{e-}13$), and a significant main effect of Location (greater suppression when location was the same ($F(1,55) = 173.58$, $p = 1.7554\text{e-}29$). Importantly, these effects were qualified by a significant interaction ($F(1,55) = 29.94$, $p = 1.22997\text{e-}07$) whereby suppression when both identity and location were a match was greater than the sum of the independent identity and location effects.

In contrast to what was observed in IT, the planned comparisons revealed that repetition suppression was greater for the same location even when a different image was presented ($t(55) = 6.4063$, $p = 3.9894\text{e-}09$) and that no such effect was observed for the same image at a different location ($p = .0461$).

We also employed the same nonparametric cluster-based permutation test that we used for the IT data. The IDMatch comparison revealed no significant temporal clusters. The

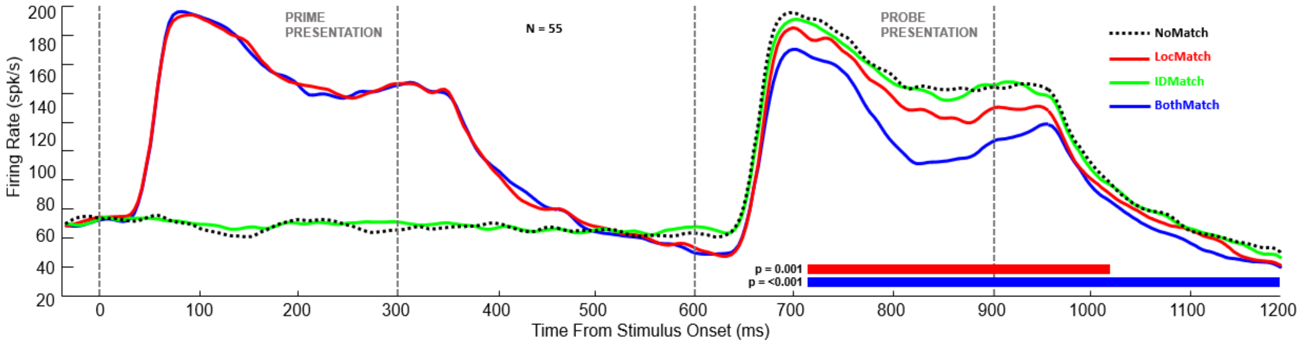

Figure 3: PSTH of the response of V2 neurons to Prime and Probe image sequences. Vertical axis: firing rate in spikes per second, horizontal axis: time from stimulus onset in milliseconds. Colored bars indicate the largest significant cluster for the corresponding condition using a cluster-based permutation test.

LocMatch comparison revealed the longest single significant cluster ($p = .001$) to occur from 111-412 ms post Probe onset and the BothMatch comparison revealed the longest single significant cluster ($p < .001$) to occur from 111-598 ms post Probe onset.

General Discussion

The purpose of the present experiment was to arbitrate between three possible ways in which repetition suppression may arise at two different levels of the visual hierarchy; at the level of IT, at the level of V2 or at both levels independently. Our pattern of results was most consistent with an independent account. IT responses were only suppressed for repetitions of the same object, whereas V2 responses were only suppressed for the same or different objects at the same location.

Synergistic Effects of Identity and Location

Our results replicate in a single experiment several previously independent observations of image-specificity and location-generalization of repetition suppression in IT. We added to these findings by observing a synergistic interaction whereby when both location and image identity are a match to the Prime, suppression is enhanced beyond a simple linear sum of the location component and identity component, as evidenced by the significant interaction effect. Interestingly, in V2, we also observed a synergistic interaction whereby when both location and image identity are a match to the Prime, suppression is enhanced more than the linear sum of location-based and identity-based effects, as evidenced by the significant interaction effect. These observations are in line with an independent account.

Implications for Bottom-Up and Top-Down Accounts

The fact that there is a component of repetition suppression that is specific for location even when the image is not a match in V2 but that we do not see evidence of this same effect being present in IT suggests against a purely bottom-up account of repetition suppression in IT. That is not to say that stimulus information is not being passed from V2 to IT, as this is almost certainly the case, but that the stimulus specific effects of repetition suppression in IT do not arise solely due to bottom-up signals from V2. Conversely, the fact that we do see suppression in IT when the same image is presented at a different location, but this effect is absent in V2 suggests against a strong top-down influence of IT on repetition suppression in V2. Again, that is not to say that there are not top-down connections from IT to V2, but that there is no evidence in this paradigm for their having an influence on repetition suppression, at least with respect to generalization across spatial locations in V2.

Repetition Suppression Effects in V2

It is interesting on its own that we observed such robust repetition suppression effects in V2 under these stimulus conditions, which have previously been used to induce repetition suppression in IT and therefore were tailored to the properties of IT neurons i.e. preference for complex naturalistic images and large receptive fields, and not specifically tailored to the response properties of V2 neurons. We had some reason to believe that we might see repetition suppression under these conditions in V2, as suppressive effects due to stimulus adaptation have been observed in V2, albeit under very different experimental conditions. It was, however, unclear what form these effects might have taken.

The images used for this study were not quantified based on their physical properties, and so it is not possible to determine to what extent specific suppression effects are due to how well the stimuli were tailored to the response properties of the neurons. This is an interesting question and could be explored in more detail in a future study.

Conclusions

While inferential and not directly causal, given the predictions made by each network-level account considered, when taken together, these results highlight the role of independent processing and downplay the roles of bottom-up and top-down influences giving rise to repetition suppression effects seen in different brain regions at different levels within the visual hierarchy. These results have implications for understanding the general flow of information within the visual system and specifically how stimulus recency changes object representations.

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