

Impossible expectations: fMRI adaptation in the lateral occipital complex (LOC) is modulated by the statistical regularities of 3D structural information☆

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ABSTRACT

fMRI adaptation (fMRIa), the attenuation of fMRI signal which follows repeated presentation of a stimulus, is a well-documented phenomenon. Yet, the underlying neural mechanisms supporting this effect are not fully understood. Recently, short-term perceptual expectations, induced by specific experimental settings, were shown to play an important modulating role in fMRIa. Here we examined the role of long-term expectations, based on 3D structural statistical regularities, in the modulation of fMRIa. To this end, human participants underwent fMRI scanning while performing a same-different task on pairs of possible (regular, expected) objects and spatially impossible (irregular, unexpected) objects. We hypothesized that given the spatial irregularity of impossible objects in relation to real-world visual experience, the visual system would always generate a prediction which is biased to the possible version of the objects. Consistently, fMRIa effects in the lateral occipital cortex (LOC) were found for possible, but not for impossible objects. Additionally, in alternating trials the order of stimulus presentation modulated LOC activity. That is, reduced activation was observed in trials in which the impossible version of the object served as the prime object (i.e. first object) and was followed by the possible version compared to the reverse order. These results were also supported by the behavioral advantage observed for trials that were primed by possible objects. Together, these findings strongly emphasize the importance of perceptual expectations in object representation and provide novel evidence for the role of real-world statistical regularities in eliciting fMRIa.

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Introduction

fMRIa, the attenuation of blood oxygenation level-dependent (BOLD) signal which follows repeated presentation of a stimulus, is considered the neuroimaging equivalent of neuronal repetition suppression. Despite the popularity of this technique, its underlying neural mechanisms are still unclear (Grill-Spector et al., 2006; Malach, 2012).

Several theories view fMRIa as an outcome of bottom-up processing, thus attributing the signal reduction to more efficient processing of the repeated stimulus (Grill-Spector et al., 2006). In contrast, fMRIa has been associated with top-down processes related to perceptual expectations. Specifically, stimulus repetition leads to increased expectations and reduction of prediction errors (Rao and Ballard, 1999). This account is supported by studies demonstrating that fMRIa is modulated by the

likelihood of stimulus repetition, and that this effect is independent of bottom-up repetition effects (Summerfield et al., 2008; Larsson and Smith, 2012; Grotheer and Kovács, 2014a,b)

These latter studies induced expectations by increasing the probability of repeated versus alternating trials (i.e., short-term expectations). However, perceptual expectations may also be instantiated based on real-world statistical regularities (i.e., long-term expectations). Here we examine whether such regularities could modulate fMRIa by utilizing possible and impossible objects (Penrose and Penrose, 1958). These stimuli are visually similar, but the perceived 3D structure of impossible objects violates real-world statistical regularities (Fig. 1, Elber, 2011). Thus, the comparison between these object categories offers a unique test-case for examining the role of long-term expectations in fMRIa.

To examine the role of such expectations in fMRIa, we compared the activation profiles of the alternated trials that were composed of possible and their matched impossible objects, and manipulated the order of stimulus presentation (Fig. 2A). We assumed that in the context of an experimental trial, the visual system generates a representation based on the first object within a pair (prime) and this representation is then compared to the second object (probe). Importantly, the likelihood

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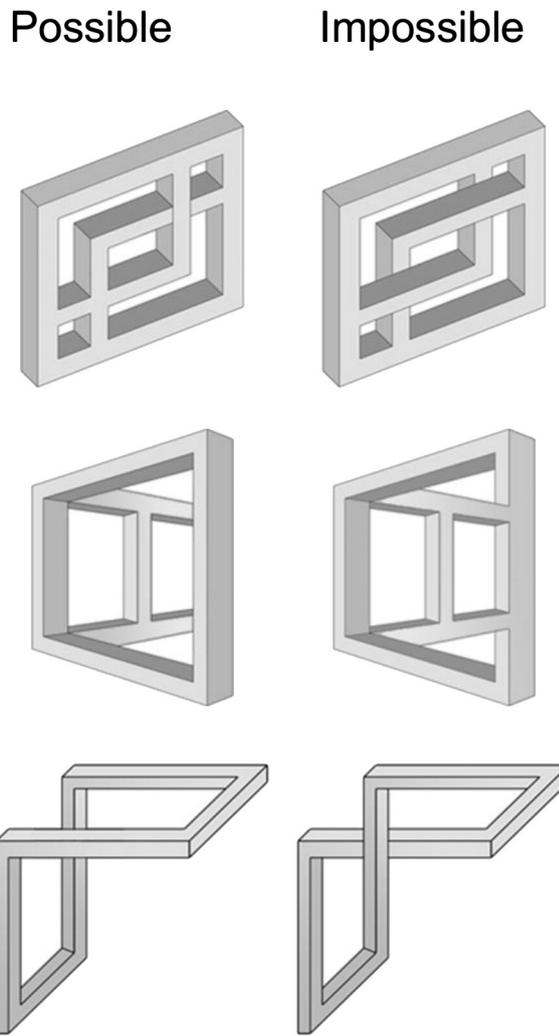


Fig. 1. Examples of possible (left panel), and their matched counterpart impossible objects (right panel). Note that there are minimal physical differences between object types, while the perceptual experience when viewing these two object categories can be substantially different.

of alternated and repeated trials was identical in order to avoid short-term expectation effects.

The manipulation of stimulus order could provide informative insights regarding the nature of stimulus representation. The bottom-up account predicts a similar activation profile in the LOC in alternated trials, regardless of stimulus presentation order, since the visual information in such trials is identical. This approach also predicts a similar fMRIa for possible and impossible objects (Fig. 2B).

However, one of the basic assumptions underlying the perceptual expectations account is that fMRI adaptation reflects the expectation of the visual system to repeated events. Specifically, according to Summerfield et al. (2008), the more probable event is that a previously seen object would be repeated rather than a novel object would be presented (i.e. alternation). Increasing the likelihood of repeated trials further augments this basic expectation and therefore, greater fMRIa effect is observed under such conditions (Summerfield et al., 2008). Hence, if long-term statistical regularities play an important role in the generation of perceptual expectations, the order of presentation would modulate LOC response. Specifically, when possible objects serve as the prime, the most likely prediction is that the probe would be the previously seen object. Thus, when the probe is impossible, it elicits an unexpected event. Contrary, when an impossible object serves as the prime, the visual system follows long-term statistical regularities and predicts that the next stimulus would be its possible counterpart

and this expectation is fulfilled. Hence, stronger LOC activation is predicted for alternated trials primed by possible objects. Intriguingly, this model also predicts an opposite pattern in the repeated trials with greater response to repeated impossible objects compared to possible ones. In particular, when both the prime and the probe are possible, the perceptual expectation is fulfilled. In contrast, when the prime is impossible, the visual system predicts that the next stimulus would be its possible counterpart and this prediction is violated. Taken together, these predictions suggest that fMRIa would be observed for possible, but not for impossible objects (Fig. 2C).

Methods

Participants

Eighteen healthy, right handed participants (8 males; aged 24–31) with normal or corrected to normal vision provided informed consent to participate in the experiment. Three participants were excluded from the study due to excessive head movements. The experiment was approved by the Helsinki committee of the Soroka Medical Center, Beer-Sheva, Israel.

Stimuli

Stimuli were sixty pairs of grayscale line-drawings of possible and matched impossible objects that were used in previous studies (Freud et al., 2013, 2015c). Matched objects were identical objects, except for one or a few features that modify the object's global 3D structure from possible to impossible or vice versa (Fig. 1).

Procedure

MRI setup

Participants were scanned in a 3 T Philips Ingenia scanner equipped with 32 channels head coil, located at the Soroka Medical Center, Beer Sheva, Israel. fMRI BOLD contrast was acquired using the gradient-echo echo-planar imaging sequence with parallel acquisition (SENSE: factor 2.8). Specific scanning parameters were as follows: whole brain coverage 35 slices, transverse orientation, voxel resolution $2.61 \text{ mm} \times 2.61 \text{ mm}$, 3 mm thickness, no gap, TR = 2000 ms, TE = 35 ms, flip angle = 90° , FOV = 256×256 and matrix size 96×96 . High-resolution anatomical volumes were acquired with a T1-weighted 3D pulse sequence ($1 \times 1 \times 1 \text{ mm}^3$, 170 slices).

Visual stimulation

Stimuli were projected to an LCD screen located at the back of the scanner bore behind the subject's head (distance 140 cm). Participants viewed the stimuli, which were presented at the center of the screen (visual angle $\sim 6^\circ \times 6^\circ$), through a tilted mirror mounted above their eyes on the head coil; prior to scanning they all completed a short training session to familiarize themselves with the experimental tasks and stimuli.

Localizer scan

Participants were presented with a standard blocked-design localizer experiment used for delineating object selective regions. Stimuli were presented in 10 s blocks comprised of 20 images. The stimuli in a given block were from a specific visual category (faces, houses, musical instruments, novel objects or scrambled objects). Participants performed a one-back task to maintain their attention throughout the experiment and there was one image repetition within each block.

Possible/impossible scans

Participants completed four fast event-related runs in which a total of 240 pairs of objects were presented and they were asked to make speeded same/different judgments for each stimulus pair. In each run,

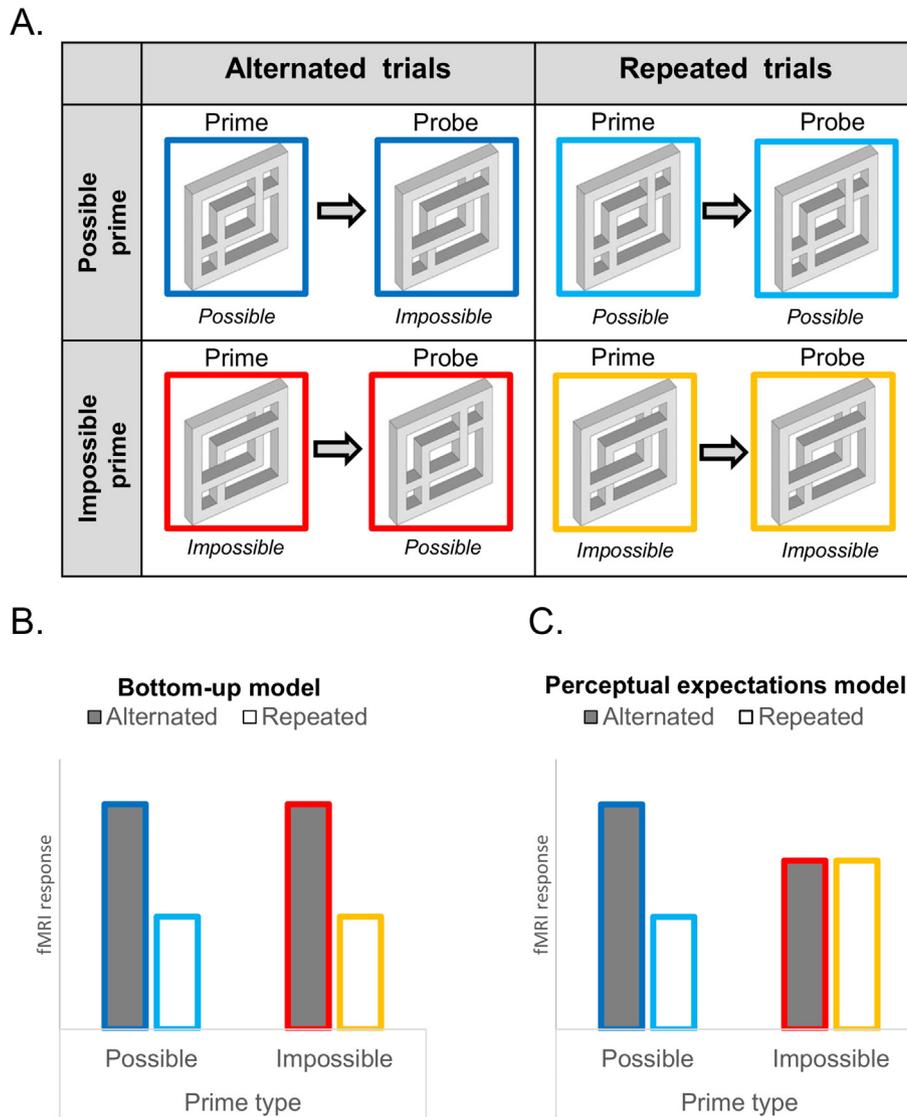


Fig. 2. A schematic illustrations of the experimental design and expected results. (A) Experimental design. Participants were asked to perform same/different classifications on pairs of possible and impossible objects. Each condition is delineated by a different colored frame which corresponds to the colors used in the graphs below and in Fig. 3. (B) According to a bottom-up model, fMRI adaptation relies solely on bottom-up process of visual features. Thus, for the alternating trials, a similar activation profile is expected regardless of stimulus order in addition to similar adaptation effect for the two object categories. (C) According to the perceptual expectations model—the visual system always predicts that the probe would be a possible object, regardless of the prime category. Hence, for alternating trials in which possible objects are the prime, the perceptual expectation is violated, while for repeated possible trials the expectation is fulfilled. In trials primed by impossible objects, the visual system still expects the occurrence of the possible version of the same objects. Hence, greater response is predicted for alternating trials in which the possible objects serve as the prime stimulus, compared to trials in which an impossible object precedes its possible counterpart. Additionally, stronger activation is predicted for repeated trials of impossible objects compared to repeated trials of possible objects. Subsequently, fMRI adaptation is predicted only for possible objects.

half of the pairs (30) were composed of the same object presented twice (repeated trials, possible or impossible) and half were composed of two different objects. These latter alternating trials were composed of possible and matched impossible objects that differed from each other by few features. The first object in half of these trials was of the possible version, while in the remaining trials the first object was of the impossible version (Fig. 2A). Each object was presented only once in each trial type along the experiment. The nature of object possibility/impossibility was not discussed with the participants prior to the experiments to avoid attentional confounds. Note that throughout the experiment stimuli were always presented in the exact same location and size in contrast to previous studies that investigated the role of perceptual expectations in fMRIa (e.g., Summerfield et al., 2008; Larsson and Smith, 2012; Grotheer and Kovács, 2014a,b). This means that in repeated trials the two consecutive images were not only visually identical, but also stimulated the exact same retinal locations, thus potentially leading to low level retinal adaptation. In contrast, in alternating trials

images differ in their identity as well as the exact elicited retinal stimulation. Importantly however, this design was used for both possible and impossible objects, and therefore could not account for the critical comparisons across these two object categories that were tested in the current study.

Experimental trials were 4 s long. The first object within a trial was presented for 800 ms, followed by a mask screen (400 ms) that was composed of scrambled (400 fragments) possible and impossible objects and then the second object that was presented for 800 ms. A 2000 ms fixation was presented at the beginning of each trial. The order of the trials and the inter-trial intervals were counterbalanced using optseq2 software (Dale, 1999).

Data analysis

fMRI data was processed using BrainVoyager 2.6 QX software (BrainInnovations, Maastricht, Netherlands. RRID: nif-0000-00274)

and complementary in-house software written in Matlab (The MathWorks, Inc, Natick, MA, USA. RRID: nlx_153890). Preprocessing included 3D-motion correction and filtering of low temporal frequencies (slow drift) and was followed by concatenation of the four experimental runs for each participant.

Rapid event-related experiment

Behavioral data (RT and accuracy) that were obtained during the imaging session were also analyzed. Object type (possible/impossible) and pair type (repeated/alternated) served as within subject independent variables.

The time-course for each trial was modeled including both the probe and prime (total trial duration 4 s) and was estimated using a deconvolution algorithm implemented in BrainVoyager. This algorithm produces estimates of the hemodynamic response at each TR (TR = 2 s) during a 20 s window following trial onset. Beta weights of each experimental condition were estimated for each subject.

Adaptation effects were calculated similarly to a previous study (Freud et al., 2013), comparing the mean peak response of the alternating trials to the mean peak response of the repeated trials separately for possible and impossible objects.

We initially measured the adaptation effect with hemisphere as an independent variable, however, since there were no significant hemispheric differences, we describe the results below after pooling the data across the two hemispheres while taking into account the

size of the ROI (in terms of the number of voxels) in each hemisphere similarly to our previous study (Freud et al., 2013):

$$\frac{((RH\text{ beta weight} \times RHROI\text{ size}) + (LH\text{ beta weight} \times LHROI\text{ size}))}{(RHROI\text{ size} + LHROI\text{ size})}$$

ROI selection

The localizer experiment was analyzed using the general linear model (GLM) and responses (percent signal change compared to baseline) were estimated for each condition. For each participant, the lateral occipital complex (LOC, Fig. 3A) was defined at a significance level of $q(\text{FDR}) < 0.05$ by the contrast of novel objects and musical instruments compared to scrambled objects (Malach et al., 1995).

Results

Effect of stimulus order on LOC activation

First we compared the activation profile for the alternating trials. Note that the visual information in these trials was completely identical and the only difference between them was the order of stimulus presentation. Specifically, in half of these trials the possible version was the prime, while in the other half the impossible version served as the prime object (Fig. 2A). In support of the perceptual expectations model, planned comparison revealed greater activation for trials in

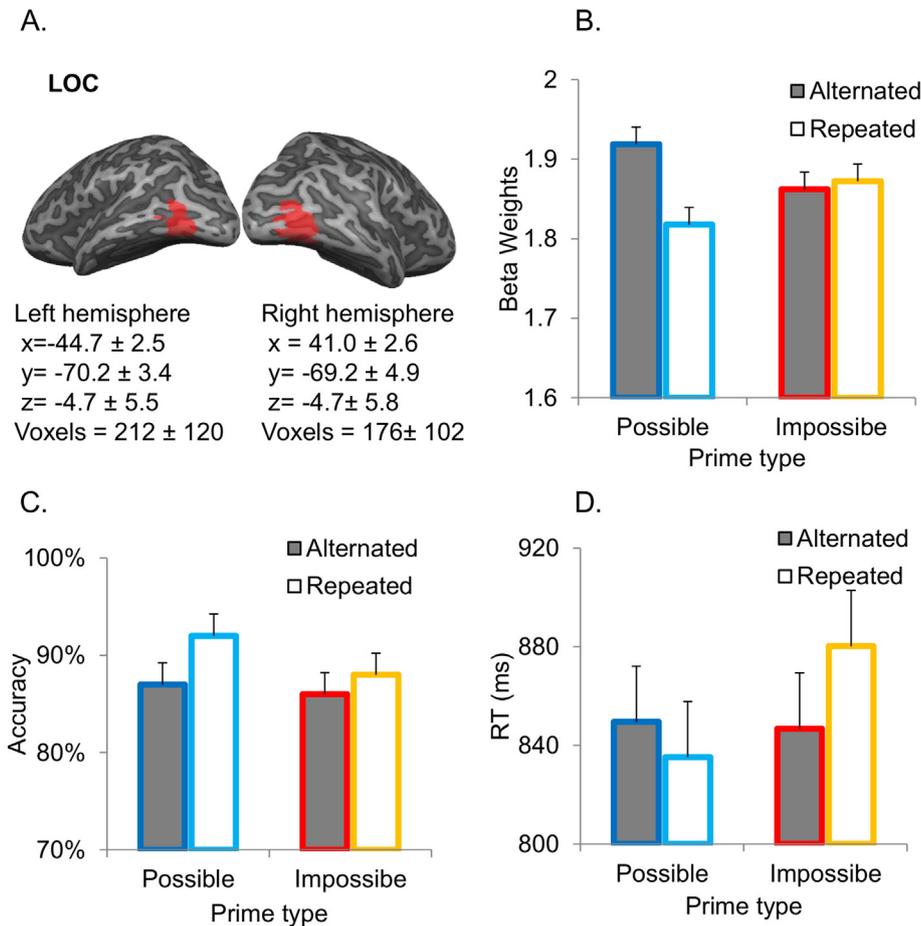


Fig. 3. fMRI and behavioral results (A) Center-of-mass locations for the average LOC are delineated in red on a representative inflated brain. LOC was independently defined using a localizer scan. (B) The average beta weights for the different conditions. Adaptation effect in LOC was found only for possible objects and not for impossible objects. Additionally, greater LOC activation was found for the alternated trials in which the possible version preceded the impossible versions compared to the reversed order. Greater activation was also found for repeated impossible objects compared to repeated possible ones. (C,D) Increased accuracy (C) as well as marginally faster reaction times (D), were found for trials primed by possible objects. Error bars in all figures represent confidence intervals for the main effect of pair-type as calculated from repeated measure ANOVAs (Jarmasz & Hollands, 2009).

which the possible object preceded the impossible one [$F_{(1,14)} = 6.98$, $p < .05$, $\eta_p^2 = 0.33$] (Fig. 3B). This finding supports the notion that perceptual expectations which are based on long-term statistical regularities may affect the fMRI activation profile.

Adaptation effects

Adaptation effects were tested in LOC. A repeated measures ANOVA revealed a significant interaction between object type and pair type [$F_{(1,14)} = 17.78$, $p < .01$, $\eta_p^2 = 0.55$]. Planned comparisons showed that for possible objects, alternating trials elicited greater activation compared to repeated trials (i.e. adaptation effect) [$F_{(1,14)} = 13.44$, $p < .01$, $\eta_p^2 = 0.49$]. On the other hand, for impossible objects, no differences were observed between repeated and alternating trials [$F_{(1,14)} < 1$, $\eta_p^2 = 0.01$] (Fig. 3B). These findings further point to dissociation between these two object categories which in turn, supports the perceptual expectations account. In particular, LOC generates perceptual expectations that are based on the assumption that the probe stimuli would always be possible regardless of the prime identity.

Additionally, we also compared the activation profile of possible and impossible objects in the repeated trials. In accordance with the perceptual expectations account, stronger activation was found for repeated trials of impossible compared to possible objects [$F_{(1,14)} = 4.47$, $p = .05$, $\eta_p^2 = 0.24$].

Finally, our initial procedure for ROI definition yielded considerably large ROIs. To exclude a potential confound of this particular ROI definition, we redefined the LOC but now restricted the size of the ROI to a maximum of 50 functional voxels, which exhibited the strongest object-selective response in the localizer scans ($p < .0006$, uncorrected). This analysis replicated the results reported above, with an interaction between object type and trial type [$F_{(1,14)} = 22.87$, $p < .01$, $\eta_p^2 = 0.62$], that was mediated by a significant adaptation effect for possible objects [$F_{(1,14)} = 20.89$, $p < .01$, $\eta_p^2 = 0.59$] while no such effect was observed for impossible objects [$F_{(1,14)} < 1$, $\eta_p^2 = 0.008$]. Additionally, the comparison of the repeated trials showed greater activation for impossible objects compared to possible ones [$F_{(1,14)} = 8.61$, $p < .05$, $\eta_p^2 = 0.38$], while the comparison between the alternated trials validated the ordering effect reported above with stronger activation in the trials primed by a possible object [$F_{(1,14)} = 7.32$, $p < .05$, $\eta_p^2 = 0.34$].

Behavioral results

The behavioral data of the same/different classification task was analyzed using RT and accuracy as the dependent variables, while prime type (possible/impossible) and pair type (repeated/alternated) served as within subject independent variables.

Accuracy was generally high (mean 88%, SD 8%). Greater accuracy was found for possible objects (89.4%) compared to impossible objects (86.8%) (Fig. 3C). Since there was no effect for pair type (repeated/alternated) [$F_{(1,14)} = 1.9$, $p > .15$, $\eta_p^2 = 0.06$], we calculated sensitivity (d') score that takes into account response bias, separately for possible and impossible objects. This analysis revealed greater sensitivity for trials that were primed by possible objects compared to trials that were primed by impossible objects [$t_{(14)} = 2.11$, $p = .05$, Cohen's $d = 0.56$].

RT results are presented in Fig. 3D. A repeated measures analysis of variance (ANOVA) revealed that repeated presentation did not elicit a behavioral facilitation effect [$F_{(1,14)} < 1$]. This absence of repetition effect could be related to the large physical similarity between the stimuli in the alternating trials (Xu et al., 2007). Similarly to accuracy results, a marginal effect for faster RTs was observed for possible objects compared to impossible ones [$F_{(1,14)} = 3.54$, $p = .08$, $\eta_p^2 = 0.2$].

Taken together, the behavioral results indicate that perceptually, trials in which impossible objects served as primes were harder compared to trials in which the possible object served as a prime, thus providing additional behavioral support for the perceptual expectations account.

Discussion

In the current study we showed that fMRIa for novel objects in the LOC is modulated by long-term perceptual expectations based on the 3D statistical regularities inherent to real-world objects. Unlike possible (and spatially expected) objects, which elicited an adaptation effect, no such effect was found for impossible (spatially unexpected) objects. The differences in the fMRIa levels between the two object categories stemmed from the activation profile in the repeated and alternated trials. Specifically, as predicted by the perceptual expectations account, in the repeated trials, stronger activation was observed for impossible objects compared to possible objects. Yet, this difference might also be accounted for by the incoherency of the 3D information embedded in impossible objects (Freud et al., 2015c) or by differential eye-movement patterns (Shuwairi et al., 2007). Therefore, a more direct support for the perceptual expectations account came from the effect of the stimulus presentation order on LOC activity for the alternating trials. Specifically, greater activation was found for trials in which the possible version preceded the impossible version compared to the reverse order. Such modulation suggests that the visual system is biased to generate a prediction of a possible object, and when an impossible object is presented as the second object within a trial it is perceived as a surprising or an unexpected event (Meyer and Olson, 2011).

Importantly, since the visual information in the alternated trials is completely identical, such a pattern of activation could not be easily accounted for by bottom-up models, attentional factors or potential differential eye-movements patterns specifically. If attentional factors (e.g., impossible objects are more interesting) or eye-movement pattern (e.g., participants make more fixations on impossible objects) modulated the fMRI response, no differences should have been obtained between these two types of alternating trials, since they contain similar levels of “impossible information”. On the other hand, the perceptual expectations account nicely fits to this pattern of results because it directly predicts that the order of presentation would modulate the fMRI response. Moreover, according to the attentional factors/eye-movement pattern accounts, the greatest activation is predicted for trials that were composed of two impossible objects, since they convey more “impossible information” relatively to the alternating trials. However, when comparing the repeated impossible objects to the alternating trials no differences were observed.

The utilization of stimulus order as a tool for examining long-term perceptual expectations is an unstudied property of the fMRIa design. This examination relies on the rationale that the visual system generates a representation based on the prime object and this representation is then compared to the probe object (for a similar logic from a different domain, see Mauro and Kubovy, 1992). Hence, any differences between the alternating trials point to dissociable representations of the prime objects. The results revealed such dissociation between possible and impossible objects, and therefore imply that the order of stimulus presentation could be used in future fMRIa studies in order to elaborate our understanding of different characteristics of visual representations.

Finally, the imaging results were also supported by the behavioral data obtained during scanning. Particularly, better performance was found for trials in which possible objects served as the prime object suggesting that better predictions were generated for spatially valid objects. Taken together the current study provides novel evidence that object representation in the LOC relies on perceptual expectations which are based on long-term statistical regularities.

Previous studies induced perceptual expectations by utilizing specific experimental settings and within-experiment statistical regularities. For example, Summerfield et al. (2008) induced perceptual expectations by increasing the likelihood of repeated trials compared to alternated trials. A different approach, that yielded results along similar lines, was used by Meyer and Olson (2011) who trained monkeys on pairs of images presented in a fixed sequence, such that the first image in a pair became a predictor of the second object. Importantly,

in the current investigation the perceptual expectations could not be formed based on the specific experimental setting since objects were novel, and identical probability of presentation was used for the different conditions. Note, that it is plausible that long-term perceptual expectations may be mediated by different cognitive and neural mechanisms than those employed for perceptual expectations which are formed based on specific, short-term, conditions. Such differences were not in the focus of the current study, however, future studies should further investigate this issue.

The results of the present study could also be accounted for by the coarse-to-fine theoretical framework (Hochstein and Ahissar, 2002) that argues that stimulus processing is mediated by an initial coarse representation of the stimulus and only later in time a fine-grained representation is available. In the context of previous behavioral studies we have argued that while the visual system can overcome object impossibility and generate a coarse description of this object category based on available shape attributes, it cannot support the creation of fine-grained representations of impossible objects (Freud et al., 2015a,b). Accordingly, we found similar levels of fMRIa and similar behavioral performance for possible and impossible objects, while differences between object categories were revealed only in the correlation pattern between the behavioral and fMRIa (Freud et al., 2013), a phenomenon which was associated with late perceptual processes (Sayres and Grill-Spector, 2006). Importantly, in that study, unlike the current one, objects within trials were always from the same category (i.e. possible or impossible) and the alternating trials were composed of completely different objects. Hence, this task could be performed while relying on a coarse description of the objects (Freud et al., 2015a,c; Hochstein and Ahissar, 2002). On the other hand, in the current study, objects were always physically very similar, therefore a fine-detailed perceptual representation was required in order to perform this task.

Yet, the differences between the present study and our previous one (Freud et al., 2013) could also be accounted for by the perceptual expectations account. In particular, the reliance on perceptual expectations is suggested to be more pronounced when the differences between the stimuli are small (i.e., low signal-to-noise ratio) compared to situations in which the differences between objects are large (i.e., high signal-to-noise ratio) (Bogacz et al., 2006; Summerfield and de Lange, 2014). Hence, in the context of the current study, the minimal physical differences between stimuli within the alternating trials (i.e., low signal-to-noise ratio) might have emphasized the reliance of the signal in LOC on perceptual expectations. On the other hand, our previous results (Freud et al., 2013) could be accounted for by the high signal-to-noise ratio available due to the experimental design which minimized the need to rely on perceptual expectations. This interpretation is also in-line with studies suggesting that fMRIa reflects a combined effect of both perceptual expectations and a more automatic neural adaptation (Larsson and Smith, 2012; Grotheer and Kovács, 2014a). In particular, since perceptual expectations were less dominant in Freud et al. (2013), the adaptation effect for impossible objects in this study might have reflected a more automatic effect of neural adaptation.

The role of familiarity in perceptual expectations

The role of perceptual expectations within the framework of fMRIa was initially investigated using faces as the experimental stimuli of choice (e.g., Summerfield et al., 2008; Larsson and Smith, 2012; Kovács et al., 2013; Grotheer et al., 2014). Yet, a macaque electrophysiology study, as well as a recent fMRIa human study, found no evidence for the modulation of the neural response by the repetition probability for non-face objects (Kaliukhovich and Vogels, 2011; Kovács et al., 2013; But see Meyer and Olson, 2011; Mayrhauser et al., 2014).

The differential effects of perceptual expectations found for faces and objects in previous studies were recently attributed to the relatively extensive experience that humans have with faces. This explanation was supported by a study in which repetition probability modulated

fMRIa for Roman alphabet but not for an unfamiliar false font (Grotheer and Kovács, 2014b). This model, taking familiarity into account in relation to fMRIa, is also of relevance to the observed dissociation between possible and impossible objects in the current study. In particular, both possible and impossible objects were novel. Nevertheless, the visual system rarely encounters impossible objects while the identification of novel (but possible) objects is regularly performed. Thus, in that context, impossible objects are not only unexpected but also unfamiliar compared to possible objects.

The role of LOC in depth perception

The present investigation also sheds light on the role of the LOC in depth perception. A growing body of literature suggests that LOC is sensitive not only to the perceived shape (Malach et al., 1995; Kourtzi and Kanwisher, 2001) but also to object 3D structure. Moore and Engel (2001) found that, a mere perceived experience of 3D structure elicited greater fMRI activation in this region compared to the response to the same stimulus when it was perceived as a 2D object. Similarly to the current study, Moore and Engel (2001) used 3D objects that were defined by monocular depth cues. Moreover a similar pattern of relationship between LOC activation and depth perception was also found when binocular depth cues were provided (Chandrasekaran et al., 2007). Accordingly, Welchman et al. (2005) demonstrated that LOC plays an important role, not only in the perception of a particular depth cue, but also in the combination of monocular and binocular depth cues that establish a more coherent perception of 3D structure.

The current study confirms and extends these previous findings. Particularly, the significant role of LOC in representing 3D structure was demonstrated by its susceptibility to even minor changes in object 3D structure, as evident by the adaptation effect obtained for possible objects. Moreover, the absence of adaptation effects for impossible objects in this experiment further demonstrates the importance of coherent spatial information for forming a successful object representation in LOC.

Conclusions

The current study shows for the first time that long-term perceptual expectations affect fMRIa in the LOC. These results strongly suggest that perceptual expectations play an important role in the representation of unfamiliar objects and that perceptual expectations rely not only on specific experimental settings but also on real-world statistical regularities of object 3D structure.

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