



## Representation of possible and impossible objects in the human visual cortex: Evidence from fMRI adaptation

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### ABSTRACT

Impossible objects are defined as 2D drawings that represent objects that could not exist in real 3D space. Previous studies have proposed that such objects are represented differently in long-term memory due to their invalid spatial structure. Nevertheless, it is not clear whether these discrepancies reflect early perceptual processes or late, post-recognition, processes. Here, we address this issue by using fMRI adaptation. Interestingly, equivalent adaptation levels were obtained for repeated compared to non-repeated possible and impossible objects in object selective regions within the human high-level visual cortex. Yet, a significant correlation between fMRI adaptation and behavioral facilitation was found for possible but not for impossible objects, thus exhibiting some dissociation in the representation of the two object categories. Overall, our findings suggest that the initial perception of possible and impossible objects is mediated by shared neural mechanisms whereas the observed differences between the two types of objects may reflect higher post-recognition processes.

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### Introduction

Impossible objects are defined as 2D drawings that represent 3D objects that could not exist in real 3D space (Penrose and Penrose, 1958; Schacter et al., 1990). Due to their unusual structure, impossible objects were often used in the literature as a tool for investigating the representation of structural, spatial information using various behavioral (e.g. Schacter et al., 1990; Soldan et al., 2009; Williams and Tarr, 1997) and imaging experiments (e.g. Schacter et al., 1995; Habeck et al., 2006). Despite some discrepancies across studies, it has mostly been argued that different cognitive processes mediate long-term representations of possible compared to impossible objects (e.g. Schacter et al., 1990, 1995). Yet, it is still not clear whether such differences between these two object categories could be attributed to early perceptual mechanisms (Soldan et al., 2006) or to higher cognitive functions (see Friedman and Cycowicz, 2006), and whether such differences suggested for long-term memory, are also applicable to immediate perception of objects.

In an early PET study, Schacter et al. (1995) were the first to examine the neural representation of impossible objects. They showed that when subjects performed a possible/impossible classification task, different activation patterns were observed for the two object categories. These imaging findings were consistent with earlier behavioral findings by the same group (Schacter et al., 1990) and were

interpreted as evidence for the existence of a perceptual mechanism termed SDS (structural description system) that creates a 3D representation for possible objects having a coherent 3D structure. According to their account, due to the spatial ambiguity inherent to impossible objects, no such representation can be created for this class of objects.

More recently, Soldan et al. (2006) found that repeated presentations of objects elicited repetition enhancements at early posterior ERP component (N1, N2) but only for possible objects. Hence, these authors suggested that in line with the SDS theory, the visual perceptual system differentially encodes globally coherent (possible) and incoherent (impossible) 3D objects. On the other hand, Friedman and Cycowicz (2006) used ERP and found late repetition enhancement effect (> 500 ms) only for possible objects and argued that the differences between the two object types rely on late conceptual and semantic, rather than early perceptual processes.

Additionally, using fMRI, Habeck et al. (2006) showed that the fMRI BOLD response for repeated possible and impossible objects was accompanied by a decrease in activation in several high-level visual areas as well as the frontal cortex; however, similar to Soldan et al.'s (2006) results, the decrease in activation was correlated with RT facilitation in the object decision task for possible but not for impossible objects, suggesting that their processing could be mediated by a different cognitive mechanism (Habeck et al., 2006). Note, that in this study, participants performed an object decision task in which they were asked to classify each stimulus as possible or impossible. Such classification, however, is problematic because subjects' decisions are always confounded by the object category. Therefore, the

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true nature of the representations mediating the perception of possible and impossible objects might be obscured when using the object decision task.

To summarize, the ambiguous nature of impossible objects leads to some differences in their neural representation compared to possible objects, yet, the origin of these differences remains elusive. In particular, it is not clear whether such differences stem from early perceptual processes, such as figure-ground separation, which are crucial for successful object recognition, or from higher perceptual processes that occur after the initial recognition and could be subjected to top-down modulations.

Careful examination of the fundamental features of impossible objects could provide predictions about the processes that mediate their early representation. In particular, despite the fact that impossible objects have an atypical shape, this object category still has valid shape attributes such as object closure, distinguishable surfaces and volume properties (see Fig. 1). These properties are known to critically affect perceptual organization and to support holistic encoding of the visual environment in line with the Gestalt principles (e.g. Geisler et al., 2001; Koffka, 1935; Kovacs and Julesz, 1993; Wertheimer, 1923). Thus, the visual system may overcome the ambiguity inherent to impossible objects and successfully represent them similarly to possible objects, while the perceived impression of impossibility could rely on higher cognitive functions.

In the current study, we hypothesized that the perception of possible and impossible objects relies, at least partially, on shared neural representation in the human high-level visual cortex. To test this proposal we used fMRI adaptation which utilizes the change in the fMRI BOLD signal of a particular brain region following repeated presentation of images to 'tag' the underlying response properties of neurons within that area. In particular, in the high level visual cortex, a repeated presentation of a stimulus usually leads to reduced fMRI activation compared to the signal obtained when two different stimuli are presented consecutively (Grill-Spector et al., 1999) and the level of signal attenuation is taken as evidence for the representation of the repeated stimulus in regions showing the adaptation effect. If the structure of impossible objects can be effectively represented in the visual cortex, we expect to find similar adaptation effects for possible and impossible objects in object-selective regions (e.g. LOC; Malach et al., 1995).

Importantly, we do not argue that impossible and possible objects are processed similarly throughout the entire identification process.

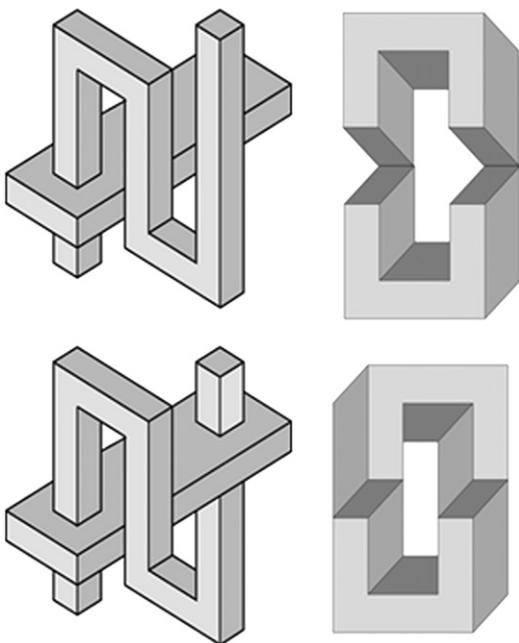


Fig. 1. Possible (upper row) and impossible objects (bottom row) from two matched sets.

After all, perceivers can effectively distinguish between the two types of objects. However, and in line with Friedman and Cycowicz's (2006) proposal, we argue that the differences between object types could emerge after the initial recognition process.

The correlation between behavioral performance and the level of fMRI adaptation could be used to confirm this assumption. In an attempt to explore whether adaptation effects in the high-level visual cortex reflect processes occurring concurrently with initial recognition or following it, Sayres and Grill-Spector (2006) conducted two studies where stimulus exposure duration was manipulated. In their first experiment, exposure duration was relatively long (2 s), whereas in the second, exposure duration was very short and was in the range of the minimum time required for recognition (85–101 ms). fMRI adaptation and RT facilitation were found for both long and short durations. However, a significant correlation between RT facilitation and the adaptation effect was only found when the images were presented for the longer duration. The authors argued that the differences between the experiments could be related to post-recognition processes, which are not required for simple classification and could be elicited for fine discriminations during long stimulus presentation durations.

Following Sayres and Grill-Spector's (2006) ideas, we propose that if the correlation between adaptation effects and behavioral performance (following long exposures) would be observed only for possible objects, it could be argued, in agreement with Friedman and Cycowicz's (2006) assumption, that the differences in the representation of possible and impossible objects reflect post-recognition processes rather than early perceptual processes.

## Methods

### Participants

Twenty two healthy, right handed participants with normal or corrected to normal vision provided informed consent to participate in the experiment. Three participants were excluded from the study: two were excluded due to artifacts in the BOLD signal and one participant was excluded since we were not able to localize his object selective regions. The experiment was approved by the Helsinki committee of the Soroka Medical Center, Beer Sheva, Israel.

### Stimuli

Stimuli were grayscale line-drawing of possible and matched impossible objects adopted with permission from two sources (a. Soldan, et al., 2009, b. Impossible world website <http://impossible.info/english/index.html>). Matched objects are identical objects, except for one or a few features that change the object's global 3D structure from possible to impossible or vice versa. Shading and grayscale colors were added to the original set that was adopted from Soldan and her colleagues. The stimuli adopted from the "Impossible world website" contain only impossible objects; therefore, a matching set of possible objects was created for these stimuli by using Photoshop CS (Fig. 1). For each participant, only one version of the stimuli was used in the experiment (balanced across subjects) to avoid cross categorical priming effect (Williams and Tarr, 1997) and each stimulus was used twice during the experimental session.

### Procedure

#### MRI setup

Data was collected on a 1.5 Tesla Philips Intera scanner equipped with a standard head coil located at the Soroka Medical Center, Beer Sheva, Israel. fMRI BOLD contrast was acquired using gradient-echo echo-planar imaging sequence. Specific scanning parameters were as follows: whole brain coverage 20 slices, transverse orientation, 5 mm thickness, no gap, TR = 2000 ms, TE = 40 ms, flip angle = 90°, FOV =

240 × 240 mm<sup>2</sup>, and matrix size 128 × 128. High-resolution anatomical volumes were acquired with a T1-weighted three-dimensional (3D) pulse sequence (1 × 1 × 1 mm<sup>3</sup>) to permit coregistration of functional data.

#### Visual stimulation

Visual stimuli were projected to a screen mounted on the head coil above the participants' eyes and generated using the E-prime IFIS software (Psychology Software Tools, Inc., Pittsburgh, PA, USA). Prior to the scan, participants completed a short training session to familiarize them with the experimental tasks.

#### Localizer scan

Participants were presented with a standard blocked-design localizer experiment that allows defining object selective regions. Stimuli were presented in 10 s blocks composed of 9 images of either faces, houses, daily objects, novel objects or scrambled objects. Participants performed a one-back task to maintain their attention throughout the experiment and there was one image repetition per block.

#### Possible/impossible scans

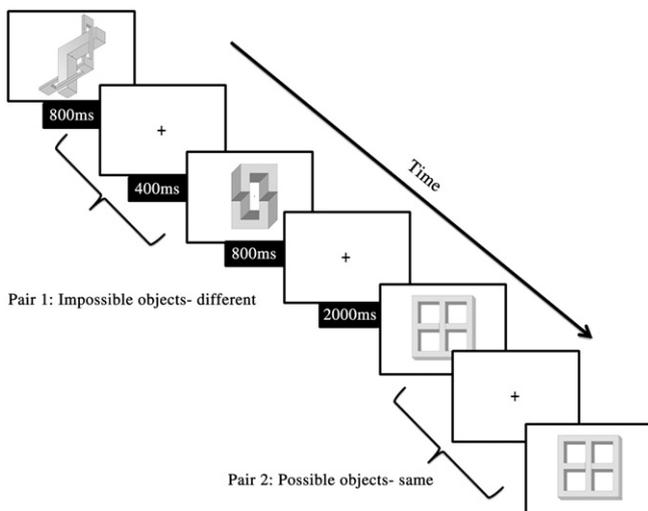
Participants completed two fast event-related runs in which 72 pairs of possible and 72 pairs of impossible objects were presented and were asked to make speeded same/different judgments for the first and second object presented for each stimulus pair. Half of the pairs (36) were of the same object and half were of different objects. Experimental trials were 4 s long. Each stimulus was presented for 800 ms, the inter stimulus interval was 400 ms and a 2000 ms fixation was presented at the beginning of each trial (Fig. 2).

#### Data analysis

fMRI data was processed using the BrainVoyager QX software (BrainInnovations, Maastricht, Netherlands) and complementary in-house software written in Microsoft Excel (Microsoft Corporation, 2010) and Matlab (The MathWorks, Inc., Natick, MA, USA). Preprocessing included 3D-motion correction and filtering of low frequencies (slow drift) and was followed by concatenation of the two experimental runs for each participant.

#### Rapid event-related experiment

The time-course for each condition was estimated using a deconvolution algorithm implemented in BrainVoyager. This algorithm



**Fig. 2.** Experimental design: during an fMRI scan, subjects performed a same/different classification task in which pairs of possible or impossible objects were shown consecutively, the two images in each pair could be either same or different.

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. Beta weights refer to the scaling of regressors in a GLM, in which the BOLD response is reconstructed.

Adaptation effects were calculated similarly to other studies (e.g. Grill-Spector et al., 1999; Andresen et al., 2009), comparing the mean peak response of the non-repeated trials to the mean peak response of the repeated trials separately for possible and impossible objects. Specifically, adaptation ratio was calculated as follows:

$$\frac{(\text{Beta weights non repeated} - \text{Beta weights repeated})}{(\text{Beta weights non repeated} + \text{Beta weights repeated})},$$

where 0 represents the absence of adaptation and 1 reflects maximal adaptation (Avidan and Behrmann, 2009). For each region, we initially measured the adaptation effect with hemisphere as an independent variable, however, since there were no significant hemisphere effects in any ROI, 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 previous studies (Harel et al., 2010):

$$\frac{((\text{RH beta weight} \times \text{RH ROI size}) + (\text{LH beta weight} \times \text{LH ROI size}))}{(\text{RH ROI size} + \text{LH ROI size})}.$$

Behavioral data (RT and accuracy) that were obtained during the imaging session were also analyzed. Object type (possible/impossible) and pair type (repeated/non-repeated) served as within subject independent variables. Similar to the adaptation ratio, we also calculated a behavioral facilitation ratio:

$$(\text{RT non repeated} - \text{RT repeated}) / (\text{RT non repeated} + \text{RT repeated}),$$

where 0 represents the absence of RT facilitation for repeated items and positive values represent greater facilitation. Due to a ceiling effect we did not calculate the same ratio for accuracy (see the Behavioral results section for details).

#### 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 and averaged across subjects. For each subject, ROIs (LOC, pFUS and mFUS) were defined at a significance level of  $q(\text{FDR}) < 0.05$ . Table 1 includes the mean Talairach coordinates of the selected ROIs, the mean cluster size and the number of participants exhibiting each ROI.

All ROIs were defined by the contrast of novel objects and daily objects compared to scrambled objects (Malach et al., 1995). The lateral occipital complex (LOC) was defined as the region which is located on the lateral occipital cortex posterior and adjacent to MT and also extended ventrally (Vinberg and Grill-Spector, 2008). Additional object selective regions were defined as ROIs along the fusiform gyrus and termed pFUS and mFUS. Previous studies have showed that these regions are involved in object perception (Grill-Spector, 2003; Grill-Spector and Malach, 2004; Malach et al., 1995), and perception of 3D properties of objects based on binocular (Chandrasekaran et al., 2007; Gilaie-Dotan et al., 2002) and monocular cues (Georgieva et al., 2008; Moore and Engel, 2001; Welchman et al., 2005).

The maps shown in Fig. 3 were generated by contrasting objects and drawings conditions vs. the scrambled objects condition and the data are projected on group-averaged folded meshes. These meshes were created separately for each hemisphere, using a cortex-based alignment algorithm implemented in the BrainVoyager QX software. Next, each subject's individual mesh time course was incorporated into a group general linear model, which allows for the creation of functional activation maps in cortically-aligned space.

**Table 1**  
Talairach coordinates.<sup>a</sup>

	Hemisphere	n	X	Y	Z	Cluster size (voxels)
LOC	R	18	41 ± 5	-75 ± 6	-6 ± 4	1321 ± 1258
	L	18	-47 ± 5	-75 ± 4	-8 ± 5	1389 ± 1111
pFUS	R	10	37 ± 7	-55 ± 5	-17 ± 4	318 ± 237
	L	6	-34 ± 5	-56 ± 6	-17 ± 2	310 ± 276
mFUS	R	8	28 ± 4	-44 ± 4	-15 ± 3	354 ± 287
	L	9	-31 ± 3	-46 ± 6	-18 ± 5	220 ± 237

<sup>a</sup> Average Talairach coordinates of ROIs. Note that the LOC was localized bilaterally for 17 participants and unilaterally for 2 participants. mFUS was localized bilaterally for 5 participants and unilaterally for 7 participants. pFUS was localized bilaterally for 5 participants and unilaterally for 6 participants.

## Results

### fMRI adaptation for possible and impossible objects

Subjects viewed pairs of possible and impossible objects and performed same/different judgments (Fig. 2 and see the Procedure section). We examined whether possible and impossible objects elicited equivalent or differential fMRI adaptation effects in the predefined object selective ROIs in the visual cortex and correlated the adaptation effect with behavioral facilitation.

### Behavioral results

The behavioral data from this experiment was analyzed using RT and accuracy as dependent variables and object type (possible/impossible) and pair type (repeated/non-repeated) as within subject independent variables. Data from two subjects were excluded from this analysis because their behavioral data was corrupted due to a technical failure. Participants (N=17) were very accurate (>95%) and there were no significant differences in response times [ $F_{(1,16)} < 1$ , ns] or accuracy [ $F_{(1,16)} = 1.14$ ,  $p > 0.25$ ] between possible and impossible objects. However, as presented in Fig. 4a, there was a main effect for pair type, with repeated items classified faster compared to non-repeated items [ $F_{(1,16)} = 28.4$ ,  $p < 0.0001$ ,  $\eta_p^2 = 0.64$ ]. The interaction between pair type and object type was not significant [ $F_{(1,16)} < 1$ ]. The similarity of the behavioral performance across object categories serves as some evidence

that similar representations underlie the initial perception of possible and impossible objects.

### Adaptation effects

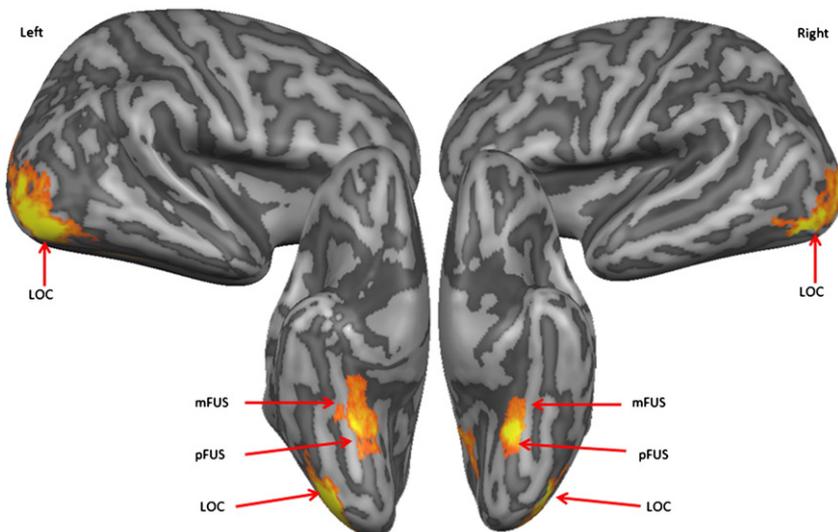
Adaptation effects were tested separately within each of the object selective ROIs and then averaged across the two hemispheres (see the Data analysis section for details).

In LOC (N=19), a repeated measures ANOVA with object type (possible/impossible) and pair type (repeated/non-repeated) as within-subject factors revealed a significant adaptation effect [ $F_{(1,18)} = 19.2$ ,  $p < 0.001$ ,  $\eta_p^2 = 0.51$ ], with no interaction between object type and adaptation effect [ $F_{(1,18)} < 1$ ]. Planned comparisons revealed significant adaptation effects for possible objects [ $F_{(1,18)} = 5.16$ ,  $p < 0.05$ ] and impossible objects [ $F_{(1,18)} = 17.25$ ,  $p < 0.001$ ] (Fig. 4b). A similar pattern was observed in the pFUS (N=11) which also exhibited a main effect of adaptation [ $F_{(1,10)} = 7.21$ ,  $p < 0.05$ ,  $\eta_p^2 = 0.41$ ], again with no interaction with object type [ $F_{(1,10)} < 1$ ]. Planned comparisons revealed that the adaptation effects were significant for both possible [ $F_{(1,10)} = 3.54$ ,  $p < 0.05$ , one tail] and impossible objects [ $F_{(1,10)} = 6.48$ ,  $p < 0.05$ ] (Fig. 4c). Finally, adaptation effect was also evident in the mFUS [ $F_{(1,11)} = 6.26$ ,  $p < 0.05$ ,  $\eta_p^2 = 0.36$ ], again with no interaction with object type [ $F_{(1,11)} < 1$ ]. Planned comparisons showed that despite a clear trend, the adaptation effect was not significant for possible objects [ $F_{(1,11)} = 2.31$ ,  $p = 0.15$ ] in this region. For impossible objects however, a significant adaptation was observed [ $F_{(1,11)} = 7.1$ ,  $p < 0.05$ ] (Fig. 4d). These findings reinforce the notion that similar representation processes mediate the perception of possible and impossible objects across high-level object selective regions.

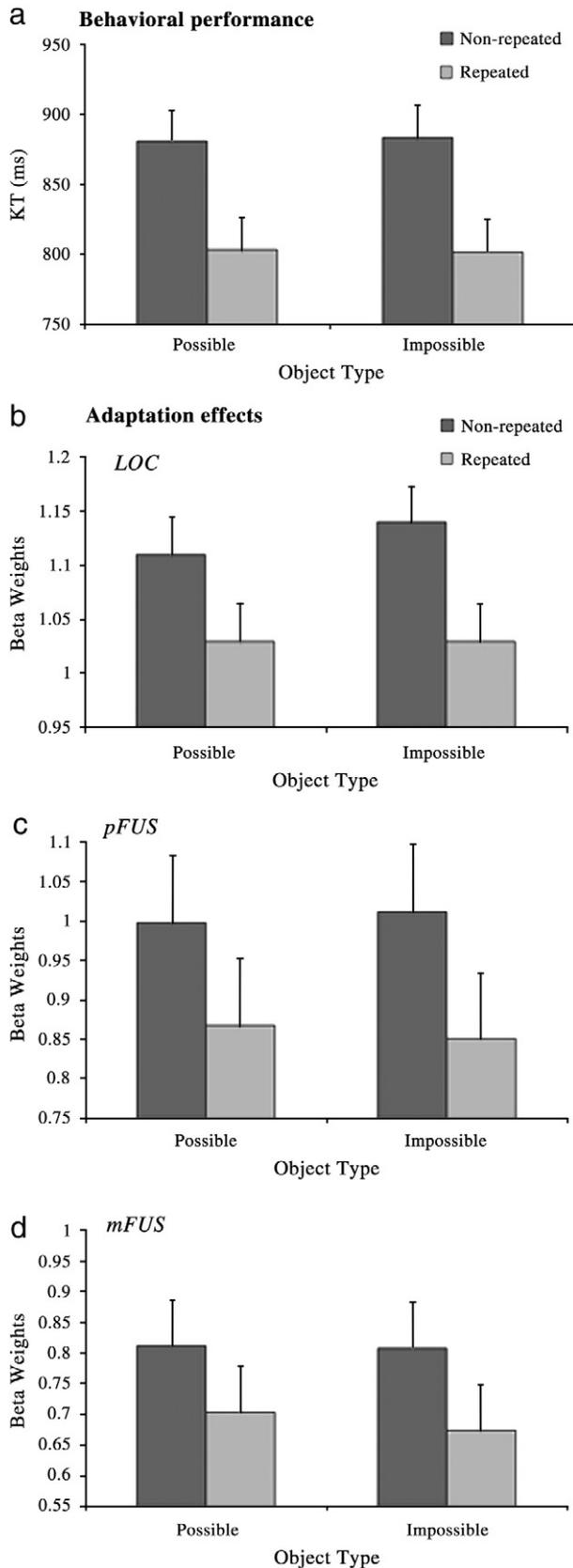
### The relationship between adaptation effect and behavioral facilitation

We calculated Pearson correlations between the behavioral facilitation ratio and the adaptation ratio in each of the predefined ROIs in order to evaluate the correlation between fMR-adaptation and RT facilitation (see the Data analysis section).

Interestingly, this analysis revealed a clear dissociation between possible and impossible objects. In particular, for possible objects, a significant correlation between adaptation ratio and facilitation ratio was found in LOC [ $R^2 = 0.54$ ,  $p < 0.001$ ], while no such correlation was found for impossible objects [ $R^2 = 0.001$ ,  $p > 0.8$ ] (Figs. 5a and



**Fig. 3.** Activation maps of object selective regions. The activation maps of the three object selective ROIs (LOC, pFUS, mFUS) are overlaid on a group-averaged folded cortical mesh and are presented in a lateral view and in a ventral view. The maps for the object-selective regions were obtained by the contrast (objects + drawings) > buildings (red to yellow colors). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)



**Fig. 4.** (a) Reaction times in the same/different task that was performed during the scanning. No differences were observed between possible and impossible objects. A facilitation effect was found for repeated pairs compared to non-repeated pairs with no interaction with object type. (b–d) Similar adaptation effects for possible and impossible objects were observed in LOC, pFUS and mFUS. Error bars represent confidence intervals as calculated for repeated measure ANOVA's (Jarmasz and Hollands, 2009).

b). This correlation indicates that the decrease in fMRI BOLD signal for repeated possible objects is accompanied by a comparable decrease in reaction time.

A similar pattern was observed in the pFUS [possible:  $R^2 = 0.3$ ,  $p = 0.12$ ; impossible:  $R^2 = 0.01$ ,  $p > 0.7$ ] and mFUS [possible:  $R^2 = 0.3$ ,  $p = 0.07$ ; impossible:  $R^2 = 0.02$ ,  $p > 0.6$ ]<sup>1</sup> (Figs. 5c–f) such that a correlation between adaptation ratio and facilitation ratio was found only for possible objects.

To examine whether the correlations for possible and impossible objects were statistically different (Nieuwenhuis et al., 2011), we applied an additional analysis in which the difference between two correlation coefficients was computed using the  $r$  to Fisher  $z$  transformation (STATISTICA, data analysis software system, StatSoft, Inc. 2011). This analysis revealed a significant difference between the correlation for possible and impossible objects in the LOC [ $p < 0.05$ ] but not in the mFUS [ $p = 0.24$ ] or pFUS [ $p = 0.21$ ]. These differences across ROIs however, may be attributed to reduced statistical power in mFUS and pFUS due to the fact that fewer subjects exhibited activation in these foci.

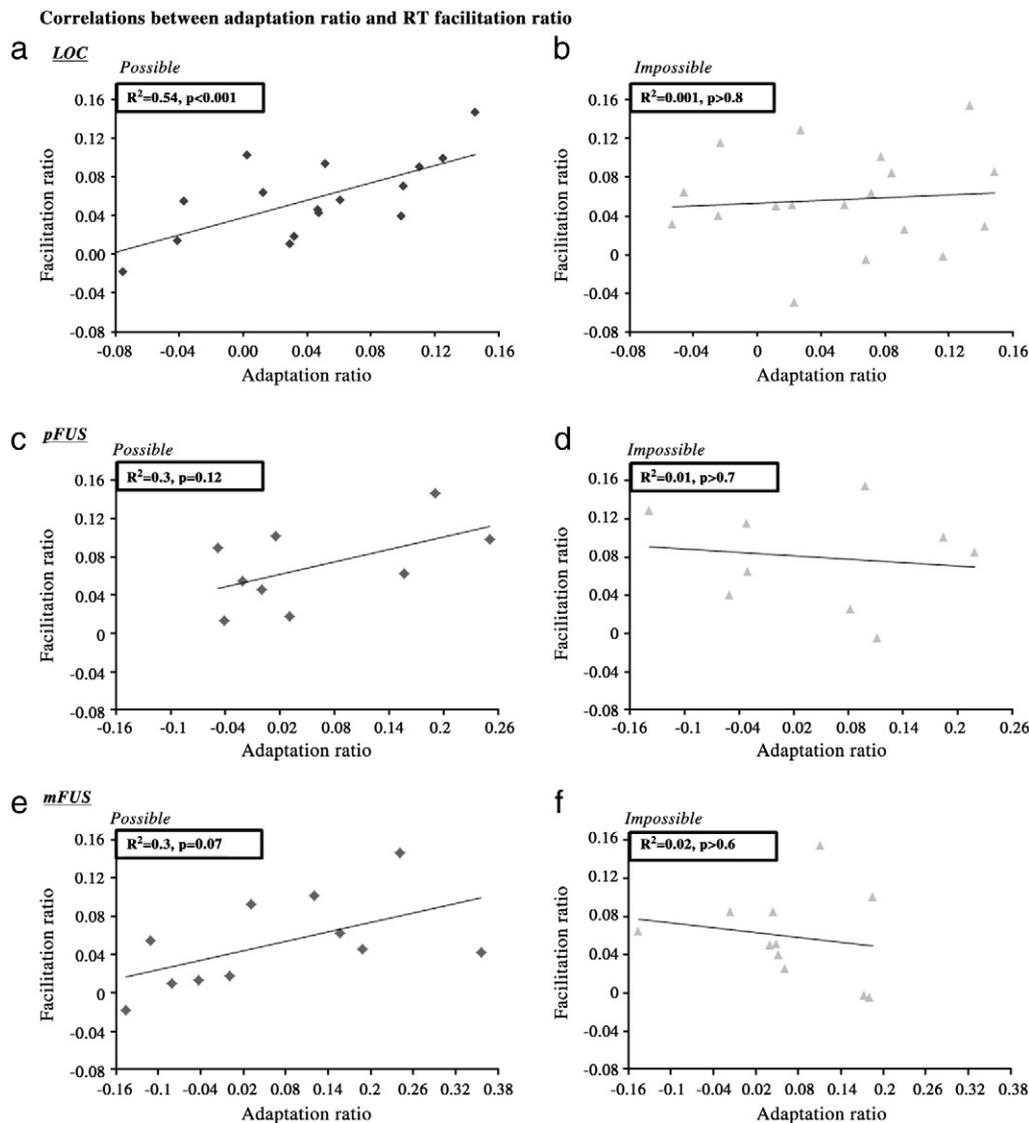
## Discussion

The main objective of the present study was to explore the neural processes mediating the perception of impossible objects. Previous studies used repetition priming to examine the representation of possible and impossible objects in long-term memory. Evidence from behavioral (Schacter et al., 1990; Soldan et al., 2009), neuroimaging (Habeck et al., 2006; Schacter et al., 1995) and electrophysiological studies (Soldan et al., 2006) suggest qualitative differences between the long-term memory representations of these objects. In the current study, we present new evidence suggesting that the initial perception of possible and impossible objects may rely on shared neural mechanisms, and thus the differences between these object types may be attributed to late processing stages, that occur after initial object recognition.

We used the fMRI adaptation paradigm to probe the nature of the representation of possible and impossible objects under a simple perceptual task such that participants' attention was not directed to object possibility. Previous fMRI adaptation studies have used fMRI adaptation to test the invariance of object representation to different visual properties using the following logic; to the extent that no adaptation is found in a given brain region when an object is transformed across a particular visual property (e.g. shape, size, viewpoint, position or illumination), it can be argued that representations in this region are sensitive to this visual property. Conversely, the existence of adaptation effect reflects invariance of the particular neuronal population to the manipulated visual property (e.g. Grill-Spector et al., 1999; Kourtzi et al., 2003; Andresen et al., 2009). This logic has been applied to explore the nature of representation of conventional as well as of atypical stimulus classes. For example, it has been found that unlike upright faces, inverted faces do not elicit adaptation in the FFA. This finding was taken as evidence that the neural population in the FFA could not discriminate between different inverted faces in contrast to upright ones (Brandman and Yovel, 2010; Yovel and Kanwisher, 2005). Accordingly, the existence of adaptation effects for impossible objects could serve as first evidence that these objects could be effectively represented in the visual cortex.

Previous studies found adaptation effects in the LOC for both familiar and unfamiliar objects (Grill-Spector and Malach, 2001; Kourtzi et al., 2003), suggesting that this region is effectively tuned to the object form rather than to its higher semantic properties. In the current study, similar adaptation effects were found for possible and impossible

<sup>1</sup> For both pFUS and mFUS, we excluded one outlier participant (different for each ROI) from this particular analysis. It is important to mention that including these participants in the analysis, did not elicit significant correlation for impossible objects, thus maintaining the main findings reported in this study. Moreover, exclusion of these participants from other analyses did not change the reported results.



**Fig. 5.** (a–d) Correlations between neural adaptation in the LOC, pFUS and mFUS and behavioral facilitation for possible and impossible objects; the adaptation ratio was significantly correlated with the facilitation ratio for possible objects (a, c, e), while no such correlation was found for impossible objects (b, d, f).

objects. Because both object categories possess valid shape attributes such as object closure, distinguishable surfaces and volume properties; the similarity of the adaptation effects for the two object classes indicates that similar representations could mediate their perception.

The adaptation effect was not restricted to the LOC and was also found in two additional object selective regions along the fusiform gyrus (mFUS and pFUS). Previous studies argued that high-order object representation is also mediated by these regions (Grill-Spector, 2003; Grill-Spector and Malach, 2004). Hence, the existence of adaptation effects in pFUS and mFUS further establishes the notion that possible and impossible objects are represented by shared neural mechanisms in the visual cortex. Additional support for our assumptions was provided by the behavioral data obtained during the scanning session. A similar pattern of performance was found in the same/different classification task for possible and impossible objects and object category did not modify reaction time, accuracy or repetition effects. Taken together with the imaging results, our data strongly supports the notion that similar perceptual processes mediate the perception of possible and impossible object.

In contrast to the similarity in the magnitude of fMRI adaptation and behavioral performance obtained for possible and impossible objects, we found differences between the two object categories when

adaptation was correlated with behavioral performance. In particular, a correlation between the adaptation ratio and RT facilitation ratio was observed for possible objects but not for impossible objects in object selective regions. Such findings are in line with ERP findings reported by Soldan et al. (2006) who showed repetition enhancement (increased signal for studied compared to unstudied items) in two early posterior components (N1, N2) for possible objects. The N1 component was correlated with the behavioral priming effect only for possible objects. Along similar lines, Habeck et al. (2006) showed that the fMRI BOLD response for repeated possible objects was correlated with RT facilitation in the object decision task. The current study provides novel evidence for the existence of such dissociation under an immediate perceptual task and even when participants are not explicitly engaged in classifying object possibility.

The relationship between RT facilitation and decreased neural signal is a well-replicated finding and was observed in studies that used both short-lag and long-term adaptation designs. Yet, it was also reported that adaptation effects could be observed in the visual cortex even in the absence of RT facilitation (Xu et al., 2007; and also see Wig et al., 2005). Sayres and Grill-Spector (2006) found that the correlation between adaptation and behavior depends on stimulus exposure duration, particularly, such correlation was found only for long exposure durations.

These authors have therefore concluded that such correlations are mediated by post-recognition cognitive processes.

In the current study, stimuli were presented for 800 ms which is well above the minimum threshold required for successful recognition. The observed correlation between RT facilitation and adaptation ratio for possible objects is therefore not surprising. The lack of adaptation–facilitation correlation for impossible objects suggests that the differences in the representation for possible and impossible objects may emerge from post-recognition processes. This assumption is in line with a previous ERP study that found differences in ERP priming effects between possible and impossible objects, an effect which was observed only 500 ms following stimulus onset (Friedman and Cycowicz, 2006). The exact nature of these processes remains speculative. For example, one option is that the lack of correlation between the adaptation ratio and facilitation ratio for impossible objects reflects top-down processes that modulate the activation in LOC (e.g. Rose et al., 2005; Sigman et al., 2005). Future studies are required in order to address this issue and pinpoint the source of differentiation in the representation of possible and impossible objects.

#### *Behavioral task considerations in imaging studies*

Several different tasks have been used in the literature to investigate the processing of possible and impossible objects. The object decision task was introduced by Schacter et al. (1990) and has been extensively used since (e.g. Habeck et al., 2006; Soldan et al., 2009; Williams and Tarr, 1997). However, the suitability of this task to imaging studies is questionable. In particular, it has been suggested that attention can modulate visual processing and the corresponding neural response (e.g. Reynolds and Chelazzi, 2004). Therefore, the pattern of activation observed during possible/impossible classifications could be modulated by the subjects' decisions rather than to reflect the nature of the representations of the objects in hand. In an attempt to overcome this difficulty, several ERP studies used indirect tasks such as left–right orientation classifications. However, such tasks do not always include an objective measure of classification performance and therefore the correlation between behavioral and neural measures could not be calculated (e.g. Friedman and Cycowicz, 2006).

To address these concerns, we used a simple perceptual task involving only same/different classifications. This task has the advantage of having an objective response criteria and avoids attentional confounds that are part of possible/impossible classification. Additionally, the strong facilitation effect for repeated objects in our study implies that this task is sensitive enough to detect differences between the different experimental conditions. Yet, this task also has potential disadvantages. Particularly, it could be conducted without processing the 3D information, which is part of the illusion of impossibility. Although we could not completely rule out this possibility, there is good evidence to suggest that 3D information is automatically processed even when subjects are asked to ignore this aspect of the stimuli (Atchley and Kramer, 2001; Goldfarb and Tzelgov, 2005). Additionally, previous studies that utilized the object decision task (i.e. possible/impossible classification) have shown that participants are sensitive to object structure even after very rapid presentations (i.e. around 100 ms) (e.g. Schacter et al., 1991; Soldan et al., 2009; Williams and Tarr, 1997). Thus, it seems that exposure times of 800 ms should support full processing of the presented stimuli, including the coherency or incoherency of the 3D structural information.

#### *Implications for object recognition models*

The investigation of the representation of impossible objects could shed light on the cognitive and neural mechanisms that mediate the perception of novel possible objects. In particular, the results of the current experiment suggest that similar mechanisms mediate the perception of the two objects categories. Possible and impossible

objects do share common features, and those features may be crucial for successful object recognition.

Impossible objects possess atypical spatial information; nevertheless, similar to possible objects, these objects still have valid shape attributes which enable the creation of global shape. The importance of such attributes for successful object recognition was demonstrated in behavioral (e.g. Geisler et al., 2001; Koffka, 1935; Kovacs and Julesz, 1993; Wertheimer, 1923) and imaging studies (e.g. Appelbaum et al., 2010; Hasson et al., 2001; Lerner et al., 2002; Moore and Engel, 2001).

Another example demonstrating the importance of global shape for the creation of object representations in the visual cortex was reported by Vinberg and Grill-Spector (2008) who showed that LOC is sensitive to the global shape of objects and not to local disconnected edges or surfaces defined by stereo and motion cues. Additionally, LOC exhibited greater sensitivity to objects compared to holes with the same shape. Overall, these findings were taken as evidence for the central role of LOC in the representation of global shape and border ownership.

Our results are in line with previous findings from behavioral and imaging studies that highlighted the importance of Gestalt principles for the creation of valid object representations in high-level visual regions. Moreover, the current study also extends previous results to suggest that these attributes could be successfully used even for non-ordinary stimuli that contain atypical spatial information.

#### *Conclusions*

We conclude that the initial perception of possible and impossible objects is mediated by shared cognitive and neural mechanisms. High-level regions in the visual cortex seem to overcome the atypical spatial information and to successfully generate a representation for impossible objects. However, our data also provides evidence for differences between possible and impossible objects, with a different pattern of correlations between fMRI adaptation and behavioral performance for impossible and possible objects. We argue that these differences may reflect later cognitive processes that occur following the successful initial recognition of impossible objects.

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