There is substantial evidence that object representations in adults are dynamically adapted by learning. Here we show that these effects are induced by active processing of objects in a particular task context, and not merely by visual exposure to objects during training. We derived behavioural sensitivity and neural selectivity for shape differences in a psychophysical and an event-related fMRI-adaptation study, respectively. We had two training conditions: “categorised objects” were categorised at a subordinate level based on fine shape differences, while “control objects” were seen equally often in a task context requiring no subordinate categorisation. After training, categorised objects were more easily discriminable than control objects and object-selective cortex was more selective for differences among categorised than control objects. These results indicate that the task context modulates the extent to which shape similarity is altered as a result of training, both at the behavioural and at the neural level.

Introduction

Human perceivers can categorise an infinite number of perceptual objects into a limited number of categories at various levels of abstraction. By default, we tend to quickly categorise objects at a basic level (e.g., bird), but we are also able to classify objects at a higher level of abstraction (superordinate level, e.g., animal) or to include more details in our categorisation (subordinate level, e.g., canary). This cognitive ability, which is crucial for sur-
vival, requires a specific interaction between the way objects are perceived by our senses and the way we think about the perceived objects. Recently, there has been more attention for the way visual perception is influenced by our knowledge and experiences. In this study, we examined the influence of one particular experience with visual objects, perceptual categorisation at a subordinate level of abstraction.

Traditional approaches made a distinction between processes that are more associated with ‘visual perception’, how objects are represented by high-level properties in order to be recognised, and processes that are more associated with ‘visual cognition’, how objects are identified, categorised and remembered (Palmeri & Gauthier, 2004).

Object recognition is a decision whether a specific object has been seen before. Recognition involves generalisation across size, location, viewpoint and illumination. The main controversy in the literature on object recognition concerns the question whether object representations are viewpoint-independent (e.g., Biederman, 1987) or viewpoint-dependent (e.g., Tarr, 1999), although more recent studies have taken intermediate positions (e.g., Demeyer, Zaenen, & Wagemans, 2007; Vanrie, Beatse, Wagemans, Sunaert, & Van Hecke, 2002; Vanrie & Wagemans, 2001; Vanrie, Willems, & Wagemans, 2001; Willems & Wagemans, 2001). DiCarlo and Cox (2007) propose that objects are represented in a high-dimensional space, and that recognition occurs after untangling the object’s manifold. In humans as well as in monkeys, the occipitotemporal cortex plays a central role in visual object recognition (Grill-Spector, 2003). Several studies have emphasised the role of the lateral occipital complex (LOC), located on the lateral bank of the fusiform gyrus and extending ventrally and dorsally. This area is strongly activated when people view pictures of objects compared to noise or scrambled objects, and shows perceptual constancy under many circumstances. Moreover, the activity in LOC is correlated with successful object identification, hence this area seems to reflect the perceived object rather than the physical stimulus (see Grill-Spector, Kourtzi, & Kanwisher, 2001). Identification is a decision about an object’s unique identity, categorisation about an object’s kind. Identification requires the discrimination between physically similar objects, categorisation the generalisation across physically similar objects. Many studies in the literature on object identification/categorisation suggest that objects can be represented in a multi-dimensional shape space (Edelman, 1998; Op de Beeck, Wagemans, & Vogels, 2001), in which the similarity between objects is inversely related to the distance in space. Category learning can then be conceived as learning the category prototype (‘prototype models’), all exemplars belonging to a particular category (‘exemplar models’) or the association between particular regions in the shape space and particular categories using a decision rule (‘decision
bound’) (Ashby & Maddox, 2005; Sigala, Gabbiani, & Logothetis, 2002). Object-selective areas, like LOC, as well as higher cortical and subcortical areas, like the prefrontal cortex and the basal ganglia, are important for learning new perceptual categories (Freedman, Riesenhuber, Poggio, & Miller, 2003).

As outlined above, visual perception was traditionally thought to generate an object representation, which was subsequently used to identify or categorise the object in a linear fashion. Recently, there has been increasing evidence for an interaction between visual perception and conceptual knowledge. For example, *categorical perception* refers to the observation that human perceivers exaggerate differences among items that fall into different categories relative to physically equivalent differences among items that fall into the same category (Newell & Bülthoff, 2002). *Categorisation uncertainty* refers to the observation that the ease with which an item is categorised, depends on the perceived similarity of that item to items of that and other categories (e.g., Grinband, Hirsch, & Ferrera, 2006). The aim of the current study was to investigate whether categorisation training can modulate the perceived shape similarity of everyday objects.

Previous psychophysical studies showed that categorisation can change the perceptual representations of abstract stimuli (Goldstone, 1994; Op de Beeck, Wagemans, & Vogels, 2003). Categorisation of a shape space can result in an expansion of relevant shape differences (between-category differences or differences on the relevant dimension) (Goldstone & Steyvers, 2001), but also in a compression of irrelevant differences (within-category differences or differences on the irrelevant dimension) (Livingston, Andrews, & Harnad, 1998). Most of these studies used artificially constructed stimuli (Op de Beeck et al., 2003) or faces (Goldstone, Lippa, & Shiffrin, 2001). The first aim of our study was to investigate whether these results can be replicated using everyday objects and ecologically valid shape spaces.

Human functional Magnetic Resonance Imaging (fMRI) studies have suggested several neural correlates of these behavioural changes in object-selective cortex: increased activation (Gauthier, Tarr, Anderson, Skudlarski, & Gore, 1999), altered spatial distribution of activation (Op de Beeck, Baker, DiCarlo, & Kanwisher, 2006), and increased neural selectivity as derived from the release of adaptation (Jiang, Bradley, Rini, Zeffiro, vanMeter, & Riesenhuber, 2007). In addition, behavioural and neural effects of training have also been observed in nonhuman primates (Baker, Behrmann, & Olson, 2002; Op de Beeck, Wagemans, & Vogels, 2007; Sigala & Logothetis, 2002). However, most of these studies compared trained objects with objects that were never seen during training. As a consequence, any difference between these conditions might be caused by the categorisation training as much as by mere exposure to the objects presented during the training. The second aim of
our study was to investigate the effect of categorisation on object representations in LOC, while controlling the amount of exposure across conditions.

The research question of the current study, the influence of categorisation on the perceived shape similarity of everyday object, is two-folded. First, one can ask questions about the effect of the relevance of the dimension during a perceptual categorisation task: Does categorisation result in a higher perceptual sensitivity for differences among objects on the relevant dimension (i.e., expansion) and/or a reduced sensitivity for differences among objects on the irrelevant dimension (i.e., compression)? Are these effects reflected in the Blood-Oxygenation Level-Dependent (BOLD-) signal in LOC? Second, one can investigate whether categorisation training induces categorical perception. Does categorisation training result in a higher perceptual sensitivity for differences among objects that belonged to different categories during training compared to objects that belonged to the same category during training? Is this effect reflected in the BOLD-signal in the LOC? These questions were investigated with a psychophysical and an event-related fMRI study in healthy volunteers. The fMRI study has been reported more fully elsewhere (Gillebert, Op de Beeck, Panis, & Wagemans, 2009).

Stimulus construction

We created four two-dimensional shape spaces (fishes, birds, cars, vases), consisting of 20 exemplars each (see Figure 1).

Each shape space was created by morphing between four stimuli, selected from a larger database (Op de Beeck & Wagemans, 2001), that were rated by subjects as being relatively different in shape compared to other objects from the same basic-level category (Panis, Vangeneugden, & Wagemans, 2008b). The images were generated using a commercially available morphing algorithm, Magic Morph® (http://www.effectmatrix.com/morphing/index.htm). This algorithm generates a continuous set of stimuli by weighing corresponding reference points on a source and a target stimulus. The stimuli were black contour lines (300 × 225 pixels, approximately 9° visual angle) presented on a white background. They were briefly masked by squares (380 × 280 pixels) containing noise. Stimulus presentation and response registration was controlled by a Pentium IV PC running E-Prime software (http://www.pstnet.com/products/e-prime/). Stimuli were shown on a 19 inch CRT monitor (resolution 1024 x 768 pixels, refresh rate 75 Hz) during the psychophysical sessions, and projected on a mirror in front of the head during the fMRI session by means of a liquid crystal display projector (1280 × 1024 pixels; Barco 6300; Barco, Kortrijk, Belgium). Head movements were minimised using a chin rest during the psychophysical sessions and using lateral head pillows during the fMRI session.
Psychophysical study

Subjects

Sixteen neurologically normal subjects participated in this study. Subjects were 4 male and 12 female, with a mean age of 20 years (range 18-22). They were paid € 16 for participation and gave written informed consent in accordance with the Declaration of Helsinki.

Method

Training phase: perceptual categorisation task and odd man out task

Subjects were trained on a perceptual categorisation task (PCT) during three sessions on consecutive days. Each subject learned to categorise two of the four shape spaces (‘categorised’) according to a vertical or horizontal
CATEGORISATION MODULATES SHAPE SIMILARITY

category boundary. In order to control for the effect of perceptual experience unrelated to the categorisation training, shapes of a third shape space (‘control’) were viewed with the same frequency in an odd-man out task (OMOT). Subjects were asked to detect an oddball (a shape randomly chosen from the fourth shape space) within a sequence of shapes selected from the third shape space. Hence, subjects had the same amount of perceptual experience with shapes of three shape spaces, but within-category shape differences were only relevant for two of them. The assignment of shape spaces and category boundaries to conditions was counterbalanced across subjects.

Each trial of the PCT consisted of a shape (200 ms), a brief mask (50 ms) and a response window (1500 ms) during which subjects had to decide whether the shape belonged to category A (left key press) or to category B (right key press) (Figure 2A). Feedback about the correctness of the answer was given by an auditory tone. The same trial sequence was used for the OMOT. In contrast to the PCT, subjects did not have to categorise the shapes at a subordinate level. Instead, they were asked to press a button whenever they noticed the oddball.

Each training session consisted of eight PCT blocks (four blocks for each shape space to be categorised) and four OMOT blocks. The order of the blocks was randomized before each session. One PCT block consisted of 100 trials. Each of the 20 shapes within the shape space to be categorised was presented five times in each block, and 20 times in each session. Subjects received feedback regarding their overall percentage correct at the end of each block. An OMOT block consisted of 110 trials. Each shape from the third shape space was presented five times within each block, and 20 times in each session, in addition to 10 oddballs from the fourth shape space per block. Hence, shapes of three shape spaces were seen equally often during the training, but only some of them were categorised at the subordinate level.

Test phase: same – different task

The training phase was followed by a test phase, in which subjects performed a same-different task (SDT) on shapes selected from the three trained shape spaces. Trials of each shape space were presented in three different blocks. The order of the blocks was randomized for each subject. Each block contained 168 trials: 84 ‘same’ and 84 ‘different’ trials. Shapes of the fourth shape space were not seen during this session. Only the 16 morph stimuli were used during scanning, and not the original four shapes (the ‘corner stimuli’ in Figure 1).

Each trial in this session could be classified according to the training task (PCT, OMOT). Trials of the ‘categorised’ shape spaces could be classified according the dimension from which the shapes in those trials were sampled (relevant, irrelevant), and according to the position of those shapes
on that dimension (central, lateral). Central trials on the relevant dimension contained shapes belonging to different categories during the training (‘between’), lateral trials contained shapes belonging to the same category (‘within’) (see Figure 2B).

Each trial contained a fixation cross (500 ms), an auditory get-ready cue (50 ms), the first stimulus (150 ms), a mask (50 ms), an interstimulus interval (1000 ms), the second stimulus (150 ms), a mask (50 ms), and a response window (1500 ms). Subjects were asked to decide whether two stimuli within a trial were identical or differed with one step in the morphing space.

The proportions of correct responses on ‘same’ and ‘different’ trials were converted to $d'$, a bias-independent measure of perceptual sensitivity for shape differences. $D'$ was normalised to be the same ($d' = 1$) for each object category (birds, cars, fishes, vases) across all subjects.

Results

Training phase: PCT and OMOT

Subjects performed at ceiling in the OMOT. The proportion of correct responses in the PCT increased during the training phase, reaching an average percentage of 91.6% at the end of the last training session (SEM = .003).
We conducted a repeated-measures ANOVA on the proportion of correct responses, with stimulus set (cars/fishes, vases/birds) as a between-subject variable and session (one, two, three) as a within-subject variable. The main effect of session indicated a significantly higher accuracy with increasing training ($F(2, 28) = 99.57, p < .0001$). Performance increased with 13.90% (95% confidence interval (CI) from 13.85 to 13.95%) from session one to session two ($F(1, 28) = 111.2, p < .0001$, planned contrast) and with 3.77% (95% CI from 3.73 to 3.83%) from session two to session three ($F(1, 28) = 8.79, p = .008$, planned contrast). The main effect of stimulus set nor the interaction between stimulus set and session reached significance ($p > .05$).

There was no evidence for a change in mean reaction time (RT) over the course of the training ($F(2, 28) = 1.17, p = .3$ with G-G correction), although we noticed a non-significant decrease in RT from session one ($M = 537$ ms, $SD = 125$) to session two ($M = 518$ ms, $SD = 122$) and session three ($M = 500$ ms, $SD = 126$), ruling out a speed-accuracy trade-off.

Performance was influenced by the distance of the shape to the category boundary, as it was worse for shapes near compared to shapes further away from the category boundary. A repeated measures ANOVA confirmed that accuracy rates ($F(3, 45) = 91.24, p < .0001$ with G-G correction) and RTs ($F(3, 45) = 28.08, p < .0001$ with G-G correction) were influenced by the distance of the shape to the category boundary (see also Figure 2B). Post-hoc Scheffé contrasts suggested that the accuracy rate was lower for stimuli located immediately adjacent to the category boundary (distance 1) compared to stimuli situated further away from the category boundary ($F(1, 15) = 173.39, p < .0001$, tested with a contrast-specific error term and a critical F-value of 43.91). The difference in accuracy rate was estimated to be 19.05% (with a 95% CI from 14.50 to 23.59%), the difference in RT 69 ms (with a 95% CI from 31 to 107 ms, $F(1, 15) = 31.92, p < .001$, post-hoc Scheffé contrast tested with a contrast-specific error term and a critical F-value of 28.01).

Test phase: SDT

Accuracy rates on ‘same’ and ‘different’ trials were converted to $d'$, a bias-independent measure of perceptual sensitivity for shape differences.

Without normalisation, there was a significant difference between shape spaces, ($F(3, 44) = 4.15, p = .01$), with higher discriminability of vases ($M = 1.39$) than of birds ($M = .95$), cars ($M = .87$), and fishes ($M = 1.14$).

First, we investigated whether categorisation training resulted in a differential perceptual sensitivity for differences among objects on the relevant, irrelevant and control dimension. Using a repeated measures ANOVA on normalised $d'$, we found that training altered the perceptual discriminability of shapes depending on the nature of the training task ($F(2, 30) = 3.94, p =$
.039 with G-G correction). We found that categorisation training improved the perceptual discrimination among ‘categorised’ (M = 1.06) compared to ‘control’ shapes (M = .87) (F(1, 15) = 7.48, p = .015, planned contrast, Figure 3A). Post-hoc pairwise comparisons (Tukey HSD) showed that categorisation training improved the discriminability of shapes on the relevant dimension (‘expansion’ of the relevant compared to the control dimension: p = .03), but did not modulate the sensitivity for shape differences on the irrelevant dimension (no ‘compression’ of the irrelevant compared to the control dimension, p > .05; no significant difference between the relevant and the irrelevant dimension, p > .05).

Next, we investigated whether categorisation training induced categorical perception. We ran a repeated-measures ANOVA with relevance (relevant/irrelevant) and position (central/lateral) as within-subjects variables. We observed a trend for an interaction between relevance and position (F(1, 15) = 3.55, p = .079). The perceptual sensitivity for differences among objects belonging to different categories was higher than that among objects belonging to the same category during the PCT (F(1, 15) = 12.77, p = .003). Post-hoc pairwise comparisons (Tukey HSD) suggested a significant difference between central and lateral trials on the relevant dimension (p = .01), but not on the irrelevant dimension (p > .05). This is illustrated in Figure 3B.

![Figure 3](image)

**Figure 3**

*Behavioural sensitivity after training*

Average sensitivity for shape differences, as measures in a same-different task. Error bars indicate the standard error of the mean. A. Normalised d’ in function of the training task. For the categorised shape spaces, we made a distinction between the dimension that was relevant and the dimension that was irrelevant for the PCT. B. Normalised d’ in function of the position of the shape pair within a categorised shape space (see also, Figure 2B). ‘Central’ trials on the relevant dimension contained two shapes belonging to different subordinate categories during training, the other trials consisted of two shapes belonging to the same category.
In summary, performance during the training phase followed a typical learning curve (Ashby & Maddox, 2005). We observed that the distance of the shape to the category boundary modulated the difficulty of the categorisation task, a phenomenon that has been referred to as ‘categorisation uncertainty’ (Grinband et al., 2006). In the test phase, we found that training improved the perceptual discrimination among ‘categorised’ compared to ‘control’ shapes, but no evidence was found for a higher sensitivity for differences on the ‘relevant’ compared to the ‘irrelevant’ dimension, nor for a reduced sensitivity for differences on the ‘irrelevant’ compared to the ‘control’ dimension. Hence, categorising objects at a subordinate level increased their discriminability compared to merely being exposed to objects, independent of the relevance of the object differences for the categorisation task. We observed a trend towards a higher sensitivity for differences among shapes that crossed the category boundary compared to shapes that belonged to the same category during training, hence the occurrence of categorical perception.

Event-related fMRI adaptation study

The same research questions were investigated using an event-related fMRI adaptation paradigm. fMRI adaptation refers to the phenomenon that the BOLD-signal of higher order cortical areas is reduced when the same stimulus is repeatedly presented. In fMRI adaptation, responses are compared between a condition with an exact stimulus repetition (‘same’ trials), and a condition with a sequential presentation of two stimuli that differ on one particular dimension (‘different’ trials). Higher responses in ‘different’ trials compared to ‘same’ trials suggest a release of adaptation during the ‘different’ trials. This release of adaptation is interpreted as selectivity of the BOLD-response for the dimension that is manipulated in the ‘different’ trials (Grill-Spector & Malach, 2001; Krekelberg, Boynton, & van Wezel, 2006). Hence, adaptation can be used to investigate neural selectivity for shape differences. More adaptation means less selectivity, less adaptation (more ‘release from adaptation’) more selectivity. Several studies have used this paradigm to investigate the functional properties of face-selective (e.g., Gilaie-Dotan & Malach, 2007; Leopold, O’Toole, Vetter, & Blanz, 2001) and object-selective cortex (e.g., Kourtzi, Erb, Grodd, & Bülthoff, 2003; Kourtzi & Kanwisher, 2001; Panis, Vangeneugden, Op de Beeck, & Wagemans, 2008a). In a previous fMRI adaptation study, we have already shown that LOC is sensitive to within-category shape similarity (Panis et al., 2008a), but now we use fMRI adaptation to investigate the influence of categorisation on the neural selectivity of LOC (see also Gillebert et al., 2009).
Methods

Subjects

Nineteen neurologically normal subjects (15 females, aged 20-26) participated in this study. None of them had participated in the psychophysical study. They were paid € 50 for participation and gave written informed consent in accordance with the Declaration of Helsinki. The data of one subject were removed due to excessive head motion. Informed consent was obtained from all subjects prior to the experiment. All procedures were approved by the ethical committee of the Faculty of Psychology and Educational Sciences (K.U.Leuven) and the committee for medical ethics of the University Hospital.

Training phase: PCT and OMOT

The training phase was similar to that of the psychophysical study. Because the SDT in the psychophysical study showed that the vases were more discriminable than other shapes, this shape space was not used as a ‘categorised’ or ‘control’ shape space in the fMRI study. Instead, shapes of this shape space functioned as ‘oddball’ in the OMOT for all subjects.

Each subject learned to categorise two out of the three shape spaces (PCT) and saw the shapes of the third shape space in a control task (OMOT).

Test phase: event-related fMRI adaptation study

All subjects were scanned post-training at the Department of Radiology of the K.U.Leuven. The functional runs consisted of nine experimental runs and two localiser runs. Localiser runs were acquired after the experimental runs and followed by the acquisition of a T1-weighted anatomical scan (9.6 ms repetition time (TR), 4.6 ms echo time (TE), 256 x 256 acquisition matrix, 1 x 1 mm in-plane resolution, 1.2 mm slice thickness, 182 coronal slices). Functional images were acquired with an echo-planar imaging (EPI)-sequence (30 ms TE, 90° flip angle, 80 x 80 acquisition matrix, 2.75 x 2.75 mm in-plane resolution, 3 mm slice thickness, no interslice gap, 36 axial slices including most of the cortex except the most superior parts of frontal and parietal cortex).

The EPI images from the two localiser runs were used to define the object-selective LOC (164 time points per time series; 3000 ms TR). Localiser runs consisted of blocks of fixation spot, intact familiar, intact new, scrambled familiar and scrambled new objects (Kourtzi & Kanwischer, 2000). Each block lasted 30 s and was repeated three times within each localiser run. This sequence was followed by an 18 s fixation period. The sequence of the blocks was randomized prior to the experiment and was different for both runs. Subjects performed a colour-change detection task. They were asked to
press a button each time the fixation cross changed in colour. This occurred approximately every 3 seconds.

The EPI images from the experimental runs were acquired with an event-related adaptation design (152 time points per time series; 2000 ms TR). Each trial in the experimental runs lasted 2000 ms. The first image was presented for 350 ms, followed by a mask of 150 ms, the second shape (150 ms) and a second mask (1050 ms). The mask was included in the first few subjects scanned, but we decided to include the presence of a mask as an extra between-subject variable because most fMRI adaptation studies in the literature do not use a mask between first and second stimulus. Furthermore, to our knowledge no study has been published with information about whether such a mask has any effect on the degree of adaptation. No effect was seen in our study: we analysed the fMRI data with “mask presence” as a between-subject variable, and this variable did not interact with the degree of adaptation or any other variable. So we did not include this variable in the analyses reported in the Results section.

In each block, we presented 144 trials, preceded by 4 and followed by 4 fixation trials. One block contained 10 ‘catch trials’, 14 fixation trials and 120 event trials. The catch trials consisted of a bird, car or fish, followed by a vase. The event trials consisted of two birds, two cars, or two fishes. Both shapes within each event trial were selected from the same shape space and were either the same or different. In different trials, we used the smallest difference on the morphing line. The conditions were randomized a priori using a genetic algorithm (Wager & Nichols, 2003).

Shapes within a trial were ‘categorised’ during the training (PCT) or were seen equally often in a ‘control’ task (OMOT). Subjects performed a vase detection task. They were asked to press one button whenever they saw two birds, two fishes, two cars, and another button whenever they saw a vase. Hence, any effects of categorisation could not be attributed to a task confound during the scanning.

Analysis of imaging data

Data were analysed using the Statistical Parametric Map software package (SPM5, Wellcome Department of Cognitive Neurology, London), as well as custom Matlab code. Preprocessing included time slicing, realignment, co-registration, segmentation, normalisation and smoothing.

The BOLD-signal during the localiser runs was modelled using a boxcar response model smoothed with a hemodynamic response function (Friston, 2003). The general linear model contained four independent conditions (intact familiar, scrambled familiar, intact new, scrambled new) and six regressors (motion parameters needed for the realignment). LOC was defined as those voxels in the lateral occipital and ventral occipitotemporal
cortex with a larger BOLD-activity while subjects viewed intact versus scrambled objects (uncorrected $p$-value of .0001). Figure 4 illustrates the distribution of LOC among the subjects.

For the experimental runs, the time course of the BOLD-signal intensity was extracted by averaging the data from all the voxels within the independently defined LOC. We averaged the signal intensity across the trials in each condition from 0 to 10 s post trial onset (6 time points). These event-related time courses of BOLD-signal intensity were then converted to percent signal change (PSC) by subtracting the corresponding value for the fixation condition and dividing by that value. We then computed the peak for the time courses across conditions for each subject (occurring 4 or 6 s after trial onset). The percent signal change at the peak served as the measured response for each condition and was used in a repeated-measures ANOVA.

**Results**

**Training phase: PCT and OMOT**

Participants were trained to categorise two out of the three shape spaces according to a vertical or a horizontal category boundary. Accuracy and RT data were submitted to a repeated-measure ANOVA with two factors (session, distance). Accuracy increased from session one to session two ($F(1, 17) = 72.03, p < .0001$) and was modulated by the distance of the stimulus to the category boundary ($F(3, 15) = 94.16, p < .0001$). RTs decreased from session...
one to session two \( (F(1, 17) = 27.14, \ p = .0001) \), and participants tended to be slower for stimuli near the category boundary \( (F(3, 15) = 16.46, \ p = .0001) \). Participants saw shapes of the third shape space in an OMOT. In this task, they could detect 99% of the oddballs \( (SEM = .003) \).

Test phase: behavioural data

Analyses on the behavioural data were performed using the data of 16 subjects, as responses were not properly encoded due to technical problems for the remaining two subjects. Responses were coded as correct or incorrect and RTs were registered after the offset of the second stimulus. Subject detected 88% of the vases \( (SEM = .02) \) and made a false alarm in 12% of the trials in which two birds, two fishes or two cars were presented \( (SEM = .04) \). They responded significantly slower on catch trials \( (M = 396 \text{ ms}, \ SD = 20) \) than on the other trials \( (M = 296 \text{ ms post stimulus offset}, \ SD = 15), t(15) = 7.63, \ p < .0001 \). There was no significant difference between the other conditions in the proportion of hits \( (t(15) = 1.12, \ p = .28) \), false alarms \( (t(15) = .43, \ p = .67) \) or in the RTs \( (t(15) = .70, \ p = .49) \).

Test phase: imaging data

For statistical analyses, we defined the timing of the peak of the response per subject (occurring 4 or 6 s after trial onset). Using these peak responses as dependent variable, we performed a repeated-measures ANOVA with one between-subject factor (mask vs. no mask) and two within-subject factors (same vs. different and categorised vs. control). The main effect of mask was not significant, nor did it interact with any other variable \( (p > .05) \). We observed a significant difference between same and different trials \( (same < different: F(1, 16) = 15.32, \ p = .001) \), an effect that is traditionally interpreted as reflecting a release of adaptation related to the neural selectivity of the underlying neuronal population (Grill-Spector & Malach, 2001). There was no significant difference between categorised and control objects, with a small trend towards a greater signal for categorised objects than for control objects \( (categorised > control: F(1, 16) = 3.69, \ p = .07) \). However, using paired t-test, we found an effect of categorisation for different trials \( (t(17) = 2.57, \ p = .02) \), but not for same trials \( (t(17) = .79, \ p = .44) \) (see Figure 5).

Most importantly, we found a significant interaction between the adaptation effect and the effect of categorisation \( (F(1, 16) = 7.29, \ p = .016) \). As can be seen in Figure 5, the adaptation effect was larger for categorised objects than for objects that were seen equally often in a control task.

The PSC for ‘different’ trials on the relevant, irrelevant and control dimensions were analysed in a separate ANOVA. The main effect of dimension was significant \( (F(2, 32) = 5.19, \ p = .01) \). As shown above, we found evidence for an expansion of the relevant and irrelevant dimension compared
to the control dimension \( F(2, 32) = 5.98, p = .026 \), but no significant difference between the relevant and the irrelevant dimension \( p > .05 \).

Second, we checked whether the training induced any effect of the position of the categorised shapes in each shape space relative to the learned category boundary. As illustrated in Figure 2B, shapes could be at a different side of this boundary (cross-category), or at the same side of the boundary (within-category). We observed no significant differences in release of adaptation between these conditions \( t(17) = 1.03, p = .32 \), suggesting that the enhanced neural selectivity for objects that crossed the category boundary transferred to objects that belonged to the same subordinate category during training.

In summary, we found a higher release from adaptation within LOC when pairs of ‘categorised’ shapes were presented, compared to pairs of ‘control’ shapes. Among the trained objects, there was no difference in selectivity depending on whether the shape differences were relevant or irrelevant for the learned category rule, or whether two shapes crossed the category boundary or not. These results indicate that subordinate categorisation per se, independent from visual exposure, results in a higher selectivity for shape differences in the LOC.

**Figure 5**

*Neural selectivity after training*

The average percent signal change in LOC from a fixation baseline, in function of the task during training. Higher responses in ‘different’ trials compared to ‘same’ trials suggest a release of adaptation, and this release of adaptation is used as an index for neural selectivity. Error bars indicate standard errors of the mean across subjects.
Discussion

The aim of the current study was to examine the influence of categorisation training on the perceived shape similarity of everyday objects. We described a psychophysical and an event-related fMRI experiment in which we derived behavioural sensitivity and neural selectivity from respectively the proportion of hits and false alarms and the release of adaptation in trials with two different stimuli compared to trials with twice the same stimulus. We compared these measures for objects that were categorised at a subordinate level during a training phase with control objects that were seen equally often, but without subordinate categorisation. We found a higher behavioural sensitivity and a higher neural selectivity for the categorised objects compared to the control objects. These results confirm earlier findings (Goldstone, 1994) and indicate that subordinate categorisation per se, independent from visual exposure, results in a higher selectivity for shape differences in the LOC.

First, we investigated the effect of the relevance of the dimension during a perceptual categorisation task. In the psychophysical study, we found evidence for an expansion of the relevant compared to the control dimension, but not compared to the irrelevant dimension. Hence, expansion effects (Goldstone & Steyvers, 2001; Levin & Beale, 2000) can be replicated using psychophysically determined shape spaces containing everyday objects. We did not find evidence for compression effect of the irrelevant dimension compared to the control dimension. Similarly, in the fMRI adaptation study, the release of adaptation was higher for the relevant and irrelevant dimension compared to the control dimension, without significant differences between the relevant and the irrelevant dimension.

Next, we examined whether subordinate categorisation could induce the occurrence of categorical perception (Newell & Bulthoff, 2002). In the psychophysical data, we observed a trend towards a higher sensitivity for ‘between-category’ compared to ‘within-category’ differences. Our event-related fMRI study did not provide evidence for a higher neural selectivity for ‘between-category’ compared to ‘within-category’ differences. These data are in line with other human fMRI (Jiang et al., 2007) and single cell recordings (Op de Beeck et al., 2001) studies showing no task-independent category effects after a training of categorisation. On the contrary, Sigala and Logothetis (2002) did report higher selectivity for diagnostic over non-diagnostics features (but see Baker et al., 2002; Tanaka, 2004). Debaene, Ons, Wagemans, and Vogels (2008), who counterbalanced the relevant categorisation dimension across animals, only obtained minor category related effects on the shape tuning of IT neurons, after controlling for the pre-training selectivity. It must be noticed in this context that we did not ask
our subjects to categorise objects during the test phase. Thus, it might still be possible to observe category-selective responses in the object-selective and frontal cortex when making explicit judgments at a subordinate level (Jiang et al., 2007). In this context, we emphasise that one should be careful in directly comparing adaptation of the BOLD-response with adaptation at the level of single cells. There is still some debate about whether the same underlying mechanisms are responsible for adaptation measured by single-cell recordings as compared to fMRI, and about the relationship between adaptation and neural selectivity (Grill-Spector, Henson, & Martin, 2006; Sawamura, Orban, & Vogels, 2006).

It is important to stress that the observed effects cannot be attributed to the effects of perceptual experience with the categorised shapes. Studies of object learning typically do not control for this. A few studies have used an internal control by designing the training task so that some object features are irrelevant and some are relevant for the task, and relevance is counterbalanced across subjects. If a difference is seen in performance or selectivity between the irrelevant and the relevant features, then these effects indicate that the task matters. However, while this procedure is possible for a task like categorisation, it is not straightforward to apply it on a task like discrimination where all objects need to be discriminated. Furthermore, mixed results were obtained when applying this procedure in studies of category learning. At a behavioural level, strong effects of feature relevance are only found for very distinct features (e.g., size and colour, see Goldstone, 1994), relatively simple shape properties (e.g., aspect ratio and curvature, see Op de Beeck et al., 2003), and features that are located in different parts of the objects (e.g., Sigala & Logothetis, 2002). In other cases, including everyday objects with a complex shape, category learning seems to induce no difference in sensitivity for relevant and irrelevant dimensions (Jiang et al., 2007; Op de Beeck et al., 2001; Op de Beeck et al., 2003). As a result, even these studies with this theoretically ideal control did not tell us whether it is the active training task that matters, or just the mere exposure to the objects. Within the literature on perceptual expertise, some behavioural between-subjects studies showed that the level of categorisation during training profoundly influenced the discriminability of novel exemplars or novel categories (Tanaka, Curran, & Sheinberg, 2005).

So, what is the crucial difference between the PCT and the OMOT? The most obvious difference between the PCT and the OMOT is the level of categorisation. During the PCT, shapes had to be categorised at a subordinate level. During the OMOT, shapes had to be categorised at a basic level. However, the level of categorisation will inevitably influence many cognitive processes. For example, attentional processes might be more recruited for subordinate categorisation than for categorisation at a higher level of abstrac-
tion. Murray and Wojciulik (2004) showed that attention not only increases the BOLD-response in LOC, it also increases the neural selectivity of this region, as measured by the release of adaptation. Could it be that subjects paid more attention during the fMRI task to objects that were previously categorised at a finer level of discrimination? Several aspects of our data suggest that this explanation cannot fully account for our results. First, while we observed a difference in task performance during training, no differences in performance between categorised and control objects were present during the fMRI session. Second, when asked to explicitly pay attention to the difference between two subsequently presented shapes, subjects showed a higher d’ (bias-independent measure of perceptual performance) for shapes that were previously categorised compared to shapes that were seen equally often in a control task. Third, while the data of Murray and Wojciulik (2004) showed a main effect of attention, even in their ‘same’ condition, we failed to find evidence for an effect of categorisation in the ‘same’ condition. We observed a trend towards a main effect of training task when including all trials, but subsequent paired t-tests showed that this effect could be accounted for by the effect on ‘different’ trials. Hence, we propose that attention might explain part of the effect in our study, as well as in previous studies that investigated the neural mechanisms of object learning, but that this argument cannot fully explain our results.

Furthermore, previous behavioural studies suggest that human perceivers use different object features when judging an object, depending on the nature of the categorisation task (e.g., Schyns, Bonnar, & Gosselin, 2002; Schyns, Goldstone, & Thibaut, 1998; Tanaka et al., 2005; Van der Linden, Murre, Van Elswijk, & Van Turennout, 2005). These studies add evidence to the hypothesis that the crucial difference might be the level of detail – or depth of processing – with which the stimuli had to be processed during the training phase (see also Op de Beeck, Beatse, Wagemans, Sunaert, & Van Hecke, 2000). Thus, our results suggest that the effect of categorisation training on the perceptual sensitivity and on the neural selectivity depends on the level of categorisation and the differences in cognitive processing associated with it.

Conclusion

In sum, our study provides evidence that the level of categorisation required during category learning influences the behavioural sensitivity and the neural selectivity in object-selective cortex for fine shape differences between the categorised objects afterwards. This study is the first study to investigate the effect of category training on top of the effect of perceptual
experience with the categorised objects. Our design allowed us to investigate whether the categorisation training matters, or whether perceptual experience with the trained objects is sufficient to elicit the effects. Moreover, we used everyday objects with a higher ecological validity than the stimuli in other studies. We conclude that perceptual categorisation and object representations are not independent, as categorisation can influence the perceived similarity between the categorised objects. Further studies are needed to examine the processes underlying these effects.

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Received November 15, 2008
Revision received May 1, 2009
Accepted May 5, 2009