

Cultural objects modulate reward circuitry

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Using event-related fMRI we investigated the rewarding properties of cultural objects (cars) signaling wealth and social dominance. It has been shown recently that reward mechanisms are involved in the regulation of social relations like dominance and social rank. Based on evolutionary considerations we hypothesized that sports cars in contrast to other categories of cars, e.g. limousines and small cars, are strong social reinforcers and would modulate the dopaminergic reward circuitry. Twelve healthy male subjects were studied with fMRI while viewing photographs of different car

classes followed by an attractivity rating. Behaviorally sports cars were rated significantly more attractive than limousines and small cars. Our fMRI results revealed significantly more activation in ventral striatum, orbitofrontal cortex, anterior cingulate and occipital regions for sports cars in contrast to other categories of cars. We could thus demonstrate that artificial cultural objects associated with wealth and social dominance elicit activation in reward-related brain areas. *NeuroReport* 13:2499–2503 © 2002 Lippincott Williams & Wilkins.

Key words: Attractivity; Cars; Emotion; Reward; Ventral striatum

INTRODUCTION

Rewards induce subjective feelings of pleasure and contribute to positive emotions. They can act as positive reinforcers by increasing the frequency and intensity of goal-directed behavior. Objects that signal reward have a positive motivational value and thus can elicit effortful behavioral responses. Neurobiologically, reward is mediated by dopaminergic systems involving the ventral striatum in which the nucleus accumbens is located. Drugs like amphetamine and cocaine can prolong the dopaminergic influence on target neurons such as the nucleus accumbens [1]. The activity of dopaminergic neurons in the nucleus accumbens of the rat has been shown to increase their activity by self-administration of cocaine [2]. In monkeys, dopaminergic neurons show phasic activation after the presentation of liquid and solid rewards and after the presentation of stimuli predicting reward [3,4]. Human neuroimaging studies have demonstrated that the ventral striatum is activated by the presentation of natural rewards such as sexual stimuli [5], food (e.g. chocolate) [6] or mate attributes such as beautiful faces [7]; money is the probably strongest learned reinforcer [8,9].

Recently, it has been shown that these reward mechanisms are also involved in the regulation of social relationships such as dominance and social rank. Macaque monkeys differ in the number and availability of dopamine D₂ receptors after 3 months of social housing in relation to their social rank [10]. In contrast to subordinate monkeys dominant monkeys showed an increase in the number and

availability of D₂ receptors in the ventral striatum and less cocaine self-administration.

Dominance and social rank are mediated by individual attributes signaling wealth and superfluity. A classical example is the peacock's elaborate tail: this has no apparent survival value and might actually hinder survival in making its owner more conspicuous to its predators and too clumsy to escape [11,12]. The tail thus fulfills no meaningful function except to signal that its owner is obviously strong enough to be able to invest energy in such a useless structure. In fact, peacocks who are able to produce the most fancy and ornamental tails are fitter in the darwinian sense; this has been shown in a study reporting that the offspring of those peacocks grew faster and had better survival rates [13]. In human societies the demonstration of wealth and superfluity is also a strong signal of social dominance. This is seen in rural societies such as the indian tribe of the Kwakiutl in British Columbia, where the aim of a feast called Potlatch is to give away or to destroy more goods than other competing chieftains. By this behavior the chieftain demonstrates his power and wealth [14]. Based on these evolutionary considerations, we hypothesized that cultural objects signaling wealth and superfluity will act as strong social reinforcers and will activate the dopaminergic reward circuitry. Examples of such objects are sports cars. These differ from natural reward stimuli like food, sex and faces (mates) and do not have an intrinsic reward value. In contrast, they are neither economically nor ecologically appropriate, certainly not spacious for more than two persons and often dangerous for their owners or drivers.

However, they signal high social rank, social dominance and wealth, and can be regarded as the human equivalent to the peacocks tail.

MATERIALS AND METHODS

Subjects: Twelve male subjects participated in the experiment who were highly interested in cars according to a pre-scan self-rating procedure (with a rating of ≥ 4 on a five-point scale) and had participated at least once in a car purchase. Mean age of the subjects was 31.4 ± 6.9 years, and they had no history of neurological or psychiatric illness and no use of stimulating drugs or medicine. All subjects gave written informed consent. The study was approved by the local ethics committee.

Experimental design: We used different categories of cars, i.e. sports cars, limousines and small cars, to investigate the neural correlates of indirect social reinforcement. Our stimuli consisted of 66 grey-scaled car photographs, 22 of sports cars, 22 limousines and 22 small cars. All photographs were taken from the same perspective and car brand names were eliminated (Fig. 1). We used an event-related fMRI activation paradigm with car pictures presented for 6000 ms each in randomised order, immediately followed by an attractivity rating of the previously shown car indicated by a five-point-scale for 1500 ms in order to induce an evaluation process. Subjects had to rate the attractiveness of the previously seen car by button press. Interstimulus interval was jittered between 0.7 and 2.5 TR. After the fMRI procedure, subjects underwent a post-scan semiquantitative interview, i.e. about their preferences and indifferences concerning cars in general and their individual criteria for the evaluation of a car.

Data acquisition and analysis: fMRI data were acquired on a 1.5T Siemens Magnetom Symphony whole-body MRI system equipped with a head volume coil. T2* weighted functional MR images were obtained using echo-planar imaging in an axial orientation. Image size was 64×64 pixels, with a FOV of 192 mm. One volume covering the whole brain consisted of 22 slices with 3 mm slice thickness. Volumes were obtained every 2.5 s (TE 60 ms).

Data preprocessing and statistical analysis was carried out with SPM 99 (Statistical Parametric Mapping, Wellcome Institute of Cognitive Neurology, London, UK) and MATLAB 6.1 (MathWorks, Natick, Massachusetts, USA). Individual functional images were corrected for motion artifacts by realignment to the first volume of each session. All images were spatially normalized ($3 \times 3 \times 3$ mm) to an echo-planar image in MNI space. Volumes were resliced by sinc interpolation. Images were spatially smoothed with an 8 mm full width at half maximum (FWHM) isotropic Gaussian kernel. For each trial the variance of every voxel was estimated according to the general linear model. Images were globally scaled, high frequency noise was removed using a low pass filter (Gaussian kernel with 4.0 s FWHM) and low frequency drifts were removed via a high pass filter.

The evoked hemodynamic response for the different pictures were modeled in a single subject analysis for the different car classes as canonical hemodynamic response

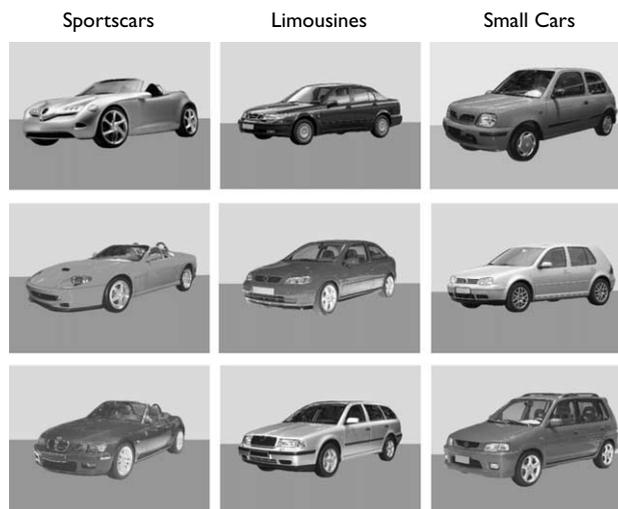


Fig. 1. Picture stimuli. Example of photographs of sports cars, limousines and small cars as used in the experiment.

function. Picture stimuli were modeled as box-car responses convolved with the hemodynamic response function. To account for interindividual variance a random effect group analysis (second level analysis) was performed using the appropriate individual statistical contrast images from single subject analyses. Individual regionally specific effects of conditions for each subject were compared using linear contrasts, resulting in a *t*-statistic for every voxel. *t*-statistics for each voxel were thresholded at $p < 0.001$ uncorrected for multiple comparisons. Results were extent threshold corrected resulting in $p < 0.05$ at the cluster level. All areas were identified using the atlases of Talairach and Tournoux [15] and Duvernoy [16].

RESULTS

Behavioral results: As expected, behavioral results showed that sports cars were rated significantly more attractive than limousines and small cars. Mean attractivity rating for sports cars was 3.79 ± 0.14 , limousines 2.46 ± 0.09 , and small cars 2.03 ± 0.08 ($F(2,33) = 68.299$, $p < 0.0001$; Fig. 2). There was no effect of car category on reaction times for attractivity rating. Mean reaction time for sports cars was 629.5 ± 30.27 ms, limousines 602.5 ± 27.9 ms and small cars 582 ± 27.7 ms ($F(2,33) = 0.69$, $p = 0.508$). Although a trend to shorter reaction times between sports cars and small cars can be seen, this difference was not significant.

fMRI results: fMRI data were analyzed for the three different categories of cars. To account for interindividual variance we performed a group analysis on a second level using a random effects model. Compared to small cars, sports cars elicited activation in right ventral striatum, left orbitofrontal gyrus, left anterior cingulate, bilateral dorsolateral prefrontal gyrus, right fusiform gyrus and left occipital cortex. Compared to limousines, sports cars elicit more activation in left occipital cortex and right anterior

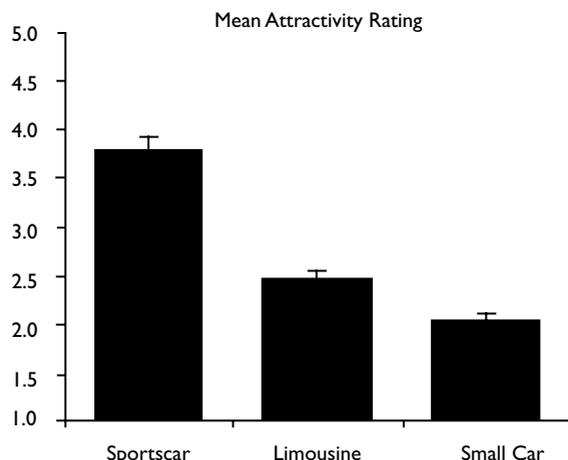


Fig. 2. Mean attractivity rating. Mean rating scores of sports cars, limousines and small cars as rated by the subjects during the fMRI experiment. Sports cars were rated significantly more attractive than limousines and small cars ($F(2,33) = 68.299, p < 0.0001$). Mean attractivity rating for sports cars 3.79 ± 0.14 , limousines 2.46 ± 0.09 , and small cars 2.03 ± 0.08 .

cingulate (Table 1). For limousines *vs* small cars we found significantly more activation in left lingual gyrus and right dorsolateral prefrontal cortex, whereas limousines elicit more activation in right insula and left lingual gyrus compared with sports cars. No significant activation at our chosen level of significance was seen for small cars compared to limousines or sports cars.

DISCUSSION

In our study we wanted to test whether sports cars, which as explained above signal higher reward than limousines or small cars, elicit reward-related activations in the hypothesized brain regions. We addressed this by comparing neural responses associated with the presentation of sports cars *vs* the presentation of small cars. This contrast revealed significantly more activation for sports cars in brain regions associated with reward and reinforcement, i.e. right ventral

striatum, left orbitofrontal cortex, left anterior cingulate and bilateral prefrontal cortex. We also observed significant activation in right fusiform gyrus and left lateral occipital complex (Fig. 3).

Thus, our hypothesis of an activation of the reward circuitry by attractive sports cars was confirmed. The ventral striatum as well as the orbitofrontal cortex were activated more by sports cars than by small cars. The mean signal difference in ventral striatum for activation elicited by limousines was lower than for sports cars but higher than for small cars. This confirms that the degree of attractiveness activates the above-mentioned structures, as would be expected from their intermediate attractivity scores. Given these results, the question arises, why the reward circuitry would be activated by the degree of attractiveness. Recently, it has been demonstrated that passive viewing of female attractive faces activates the ventral striatum in heterosexual male subjects [7]. From an evolutionary perspective there may be a good explanation for the activation of the ventral striatum in that attractive female faces can be regarded as a potentially rewarding stimulus, i.e. the initiation of a social interaction. This consideration can be supported by the recent finding that reward anticipation leads to an increase of ventral striatal activation [17]. It is a possibility that our attractive car stimuli function as predictors of potential social reward because the category of the car one owns is a highly reliable predictor for social dominance and high social rank [18].

We further suggest that cars are processed in a similar way to faces. Evidence for this suggestion comes from the fact that nearly all subjects described the headlights of the cars as eye-like with the cars facing the observer. If this is true, one might expect that attractive cars seen from the back or the side would not elicit activation in the ventral striatum. An interesting observation supporting our suggestion is the activation of the fusiform face area [19], especially by attractive cars in our study. It has also been shown recently that car stimuli activate the fusiform face area in car experts [20]. Thus, it remains open whether activation of the fusiform face area is due to the face-like appearance of the cars or expertise in processing [21].

Table 1. Regions activated in the random effects analysis ($p < 0.001$ uncorrected) for the respective contrasts.

Contrast	Region	Talairach coordinates			Z-score
		x	y	z	
Sports cars > small cars	L occipital gyrus	-48	-78	0	4.63
	R fusiform gyrus	30	-54	-15	3.78
	R ventral striatum	9	3	-6	4.30
	L orbitofrontal gyrus	-3	33	-18	3.68
	L anterior cingulate	-3	45	12	3.50
	R dorsolateral prefrontal cortex	45	15	30	4.08
	L dorsolateral prefrontal cortex	-45	3	36	4.27
	L anterior cingulate	-3	54	12	4.94
Sports cars > limousines	L occipital gyrus	-42	-45	-6	3.44
Limousines > sports cars	R insula	33	-18	15	3.84
	L lingual gyrus	-6	-87	-6	3.77
Limousines > small cars	L lingual gyrus	-9	-96	-15	4.86
	R dorsolateral prefrontal cortex	54	15	30	4.04

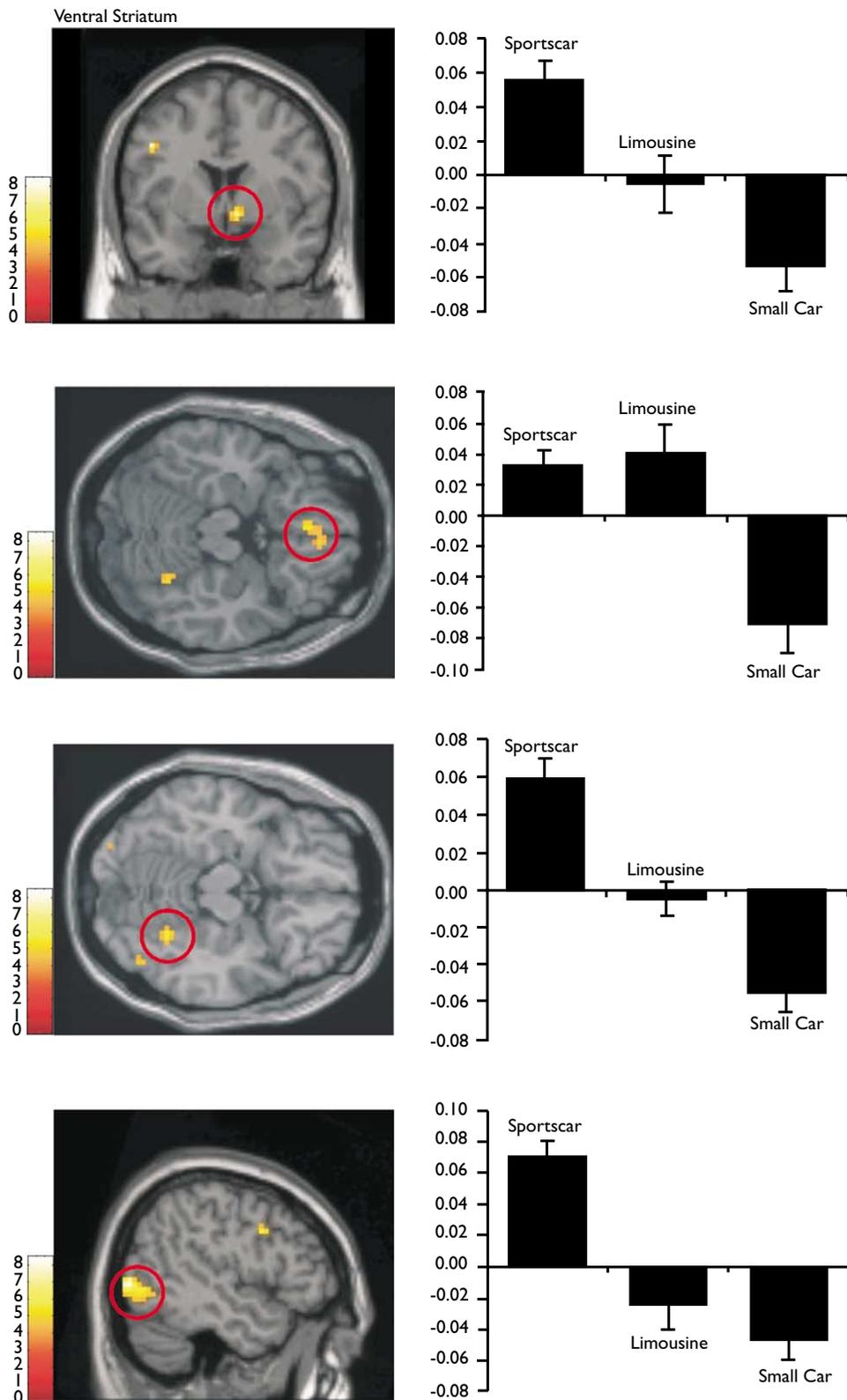


Fig. 3. Images of statistic parametric mapping for the contrast sports car > small car projected onto sections of the standard T1-template of SPM 99 (all images: random effects analysis, $p < 0.001$ uncorrected for multiple comparisons). T-values are color coded, regions are described by their respective x, y, and z-coordinates in the standard T1-template in Table I. Bars on the right show the scaled fMRI signal intensity with s.e. not only for sports cars and small cars but also for limousines. From above (marked in red circle): right ventral striatum, left orbitofrontal cortex, right fusiform gyrus and left lateral occipital complex.

The marked activation in the lateral occipital complex might be due to the fact that the lateral occipital complex is known to process shape information [22] and that all subjects told in the postexperimental debriefing that it was the shape of the car which influenced their judgement mostly. Another possible explanation may be that the incentive value of the objects being processed modulates attention in this area.

Apart from the ventral striatum and the orbital frontal cortex we found several other areas to be activated depending on the attractiveness and category of the car evaluated. The anterior cingulate is part of a network that forms the rostral limbic system, including also the OFC and the ventral striatum, and assesses the motivational content of internal and external stimuli [23]. This explains the activation of the anterior cingulate. In primates reward related activity has been found in neurons of the dorso-lateral prefrontal cortex depending on the expected reward during a delayed response task [24].

In summary, we have shown that artificial stimuli which do not act as natural reinforcers do elicit activation in the ventral striatum and the orbitofrontal cortex in dependence of the degree of attractiveness. These results may be explained by the hypothesis that cars do signal social dominance and rank and are associated with potential reward.

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