NEUROPSYCHOLOGIA

Neuropsychologia 45 (2007) 2191–2200

www.elsevier.com/locate/neuropsychologia

Visual elements of subjective preference modulate amygdala activation

Moshe Bar *, Maital Neta

Martinos Center at MGH, Harvard Medical School, 149 Thirteenth St., Charlestown, MA 02129, United States

Received 28 August 2006; received in revised form 16 February 2007; accepted 1 March 2007
Available online 12 March 2007

Abstract

What are the basic visual cues that determine our preference towards mundane everyday objects? We previously showed that a highly potent cue is the nature of the object's contour: people generally like objects with a curved contour compared with objects that have pointed features and a sharp-angled contour. This bias is hypothesized here to stem from an implicit perception of potential threat conveyed by sharp elements. Using human neuroimaging to test this hypothesis, we report that the amygdala, a brain structure that is involved in fear processing and has been shown to exhibit activation level that is proportional to arousal in general, is significantly more active for everyday sharp objects (e.g., a sofa with sharp corners) compared with their curved contour counterparts. Therefore, our results indicate that a preference bias towards a visual object can be induced by low-level perceptual properties, independent of semantic meaning, via visual elements that on some level could be associated with threat. We further present behavioral results that provide initial support for the link between the sharpness of the contour and threat perception. Our brains might be organized to extract these basic contour elements rapidly for deriving an early warning signal in the presence of potential danger.

Keywords: Arousal; Contour; fMRI; Form; Shape; Threat

We determine our preference towards people and objects in the environment frequently and rapidly (Ambady, Bernieri, & Richeson, 2000; Bar, Neta, & Linz, 2006; Willis & Todorov, 2006). These first-impression preferences must rely on perceptual features in the image, especially when they are derived quickly. What are these features? In addressing this question, we discovered that the nature of an object's contour provides a potent source of influence on preferences (Bar & Neta, 2006). Specifically, emotionally neutral objects comprised of primarily pointed features and sharp angles were liked significantly less than when the same objects were comprised of curved features (e.g., a watch with a sharp-angled contour compared with a watch with a curved contour).

What is the origin of this bias for preferring objects with curved visual elements significantly more than objects with sharp-angled elements? We hypothesize that this preference bias is the result of an elevated level of arousal in the presence of sharp-angled features; an elevated arousal that stems from an implicit association of these sharp features with threat and danger. To test this hypothesis, we compared amygdala response between conditions when participants viewed sharp-angled and curved objects. Specifically, we collected pairs of objects where each pair consisted of one member whose contour is primarily comprised of sharp angles, and a counterpart whose corresponding features are curved. The object pairs could either depict real everyday objects (e.g., a sharp-angled candle and a curved candle) or novel patterns that we created (Fig. 1). We ensured that the semantic meaning of the objects was emotionally neutral (i.e., we refrained from using images of objects such as knives or puppies). Each participant was exposed to only one member of each pair. In a third condition, we used objects with mixed sharp and curved features as a control baseline (see Section 1). Given that the amygdala in particular has been implicated in processing information related to fear and arousal (Adolphs et al., 1999; Whalen, 1998), we concentrated on the difference in functional magnetic resonance imaging (fMRI) activity elicited in the amygdala by these three conditions. If the reduced liking for sharp-angled objects stems from an elevated perception of threat, one would expect increased amygdala activation for this condition compared with both the curved and the baseline conditions.

* Corresponding author. Tel.: +1 617 726 7467; fax: +1 617 726 0504.
E-mail address: bar@nmr.mgh.harvard.edu (M. Bar).

0028-3932/$ – see front matter © 2007 Elsevier Ltd. All rights reserved.
doi:10.1016/j.neuropsychologia.2007.03.008

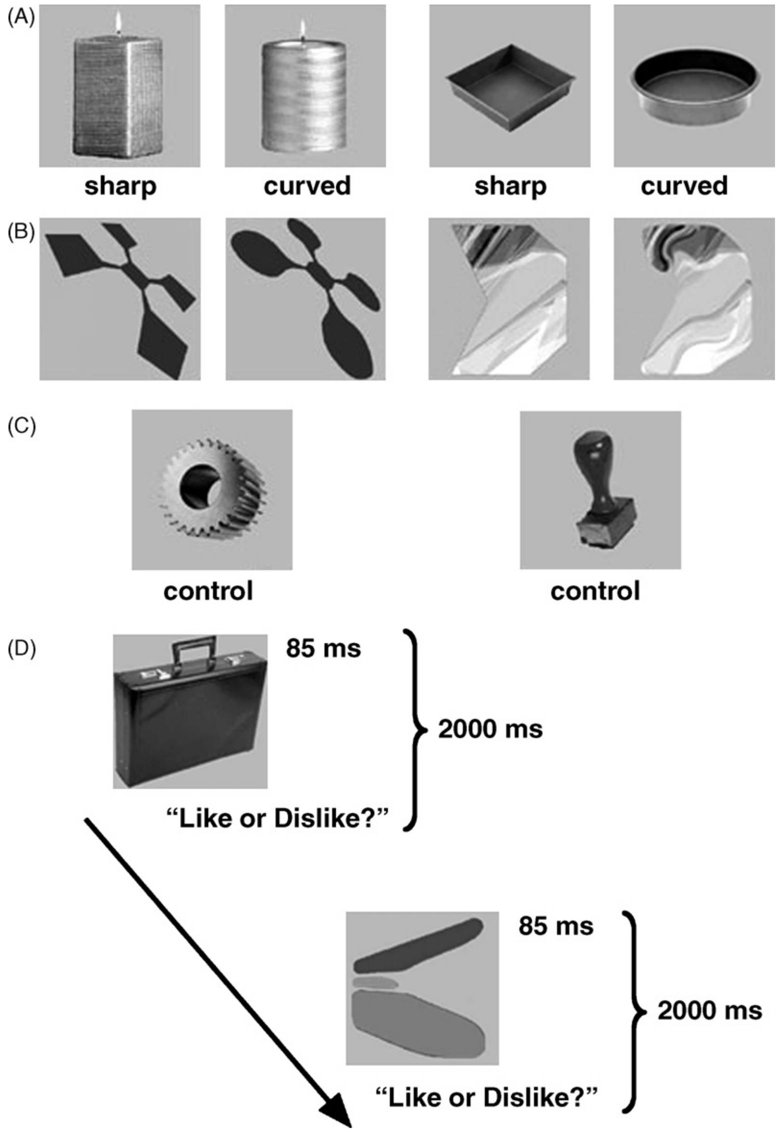

Fig. 1. Examples of the stimuli used in the experiment. (A) Pairs of real objects; (B) pairs of novel patterns; (C) control baseline objects, comprised of a mixture of curved and sharp angles. Pairs of objects and patterns were matched in appearance and in semantic meaning so that the contour was the critical difference between them. (D) A depiction of two trials in the experimental sequence.

We additionally hypothesized that the contour-based preference formation is mediated by the low spatial frequencies (LSFs) of the image, rather than the high spatial frequencies (HSFs). Such LSFs have been shown to be extracted rapidly (Bar, 2003; Bar, Neta, & Linz, 2006; Bullier, 2001) and, critically, have been shown to modulate amygdala response in fear-related situations (Vuilleumier, 2005; Vuilleumier, Armony, Driver, & Dolan, 2003). The prediction that stems from this hypothesis is that the reduced liking of sharp-angled objects relative to curved objects would be significantly stronger when viewing the LSF version of the images than when viewing the HSFs, and we test this prediction directly in Experiment 2. Finally, in Experiment 3, we provide initial evidence linking sharp-angled contour and threat perception. The combination of the results of these three experiments supports our hypothesis that the relative reduced liking of objects with a sharp contour stems from a perception of potential threat conveyed by sharp elements.

1. Experiment 1: Subjective preference and amygdala activation

1.1. Methods

1.1.1. Participants and design

We collected 140 pairs of real objects and 140 pairs of novel meaningless patterns for which the critical difference between the items in each pair was the curvature of their contour, keeping their semantic meaning and general appearance equated (Fig. 1). These were everyday objects whose semantic meaning had no inherent positive or negative valence (e.g., a plant or a chair). The novel patterns provided a further measure for the possible role of semantic meaning, familiarity and associations in preference formation. We also included a control condition of 80 real objects consisting of a roughly equal mixture of curved and sharp-angled features to determine a baseline preference. In sum, we had 140 items in the sharp-angled real object condition, 140 items in the Curved real object condition, 80 items in the control real object condition, 140 items in the sharp-angled novel pattern condition, and 140 items in the curved novel pattern condition.

The real object images were grayscale photographs of everyday objects, such as tools, furniture, clothes, and plants. The novel pattern images were grayscale patterns that we created using Adobe Photoshop 7.0. One picture at a time was presented at the center of the computer screen (visual angle 7°), on a gray background, for 85 ms. Sixteen healthy volunteers (8 female) participated. Each had 60 practice trials consisting of all conditions of real objects, novel patterns, and fixations (prior to image acquisition) with images that were not presented again in the experimental trials. After the practice, each participant then viewed one member from each pair (either the sharp-angled or the curved; counterbalanced across participants), and all the control objects, and made a like/dislike forced-choice decision about each picture based on their immediate "gut" reaction. Participants were given 1915 ms to decide whether they "liked" or "disliked" each object or novel pattern (i.e., "Do you get a good (like) or bad (dislike) feeling from this image?"), and they could make this response at any point during this time (Fig. 1D). For each condition, percent "like" responses was calculated as the proportion of the "like" responses out of the total number of responses. All participants had normal or corrected-to-normal vision, no psychoactive medication, and no significant neurological or psychiatric history. None were aware of the purpose of the experiment, and they were all recruited from the greater Harvard and Massachusetts General Hospital community, and paid for their participation. Informed written consent was obtained from each participant before the session, and all procedures were approved by Massachusetts General Hospital Human Studies Protocol number 2001P-001754.

1.1.2. fMRI data acquisition

Stimuli were back-projected using a Notevision6 LCD projector onto a translucent screen that participants viewed through a mirror mounted on the head coil. A custom-designed magnet-compatible panel of four keys (two of which were used for this experiment) was used for participants' responses. The image presentation and response collection were controlled by a Macintosh G4 running Matlab experimental software at a display resolution of 1024 × 768 pixels and a refresh rate of 75 Hz. The presentation order of trials for the event-related design was randomized across the three categories of stimuli. This was accomplished using the optseq program within the FreeSurfer Functional Analysis Stream (FS-FAST) software tools (http://surfer.nmr.mgh.harvard.edu/optseq); a program that optimizes the presentation sequence of experimental and fixation trials for event-related designs to maximize the efficiency and accuracy of the estimation of the hemodynamic response for each stimulus presentation (Burock, Buckner, Woldorff, Rosen, & Dale, 1998; Dale, Greve, & Burock, 1999). The final sequence presentation order provided by optseq was divided into five sections of 140 consecutive trials, each lasting 2 s, for use in each of the functional runs. Structural images were acquired in a 3T Siemens Allegra system using a series of high-resolution 3-D T1-weighted images, and functional images were then collected using a $T2^*$-weighted gradient echo-planar imaging sequence (TR = 2.00 s, TE = 25 ms, flip angle = 90°, field of view = 256, slice thickness = 3 mm + 1 mm skip, 33 interleaved slices oriented along the AC-PC line).

1.1.3. fMRI statistical analysis

Functional data were analyzed using the FS-FAST analysis tools (see elaborated description of methods in Bar & Aminoff, 2003; Bar et al., 2001). Data from individual fMRI runs were first corrected for motion using the AFNI package (Cox, 1996) and spatially smoothed with a Gaussian full-width, half-maximum (FWHM) filter of 5 mm. The intensities for all runs were then normalized to correct for signal intensity changes and temporal drift, with global rescaling for each run to a mean intensity of 1000. Signal intensity for each condition was then computed, excluding trials with extreme response times (RTs), and averaged across runs. To obtain whole brain group activation maps in the event-related priming task, a Finite Impulse Response (FIR) model was used in which signal intensity was averaged across 2–8 s from trial onset. Motion parameters derived from realignment correction were also entered to the model as covariates. The data were then tested for statistical significance and activation maps were constructed for specific contrasts of interest, namely sharp-angled versus Curved stimuli conditions, as well as individually for the real objects and novel patterns (*t*-test with a minimal threshold set at $p < .001$, uncorrected for multiple comparisons) for each fMRI design.

1.1.4. Cortical surface-based analysis

Once the data from all trials were averaged, the mean and variance volumes were resampled onto the cortical surface for each participant. Each hemisphere was then morphed into a sphere in the following manner: first, each cortical hemisphere was morphed into a metrically optimal spherical surface. The pattern of cortical folds was then represented as a function on a unit sphere. Next, each individual participant's spherical representation was aligned with an averaged folding pattern constructed from a larger number of individuals aligned previously. This alignment was accomplished by maximizing the correlation between the individual and the group, while prohibiting changes in the surface topology and simultaneously penalizing excessive metric distortion (Fischl, Sereno, Tootell, & Dale, 1999).

1.1.5. Region of Interest (ROI) analysis

Our ROIs were limited to the subcortical regions that were hypothesized a priori to show significant activation for sharp over curved objects, namely the bilateral amygdala, using structural and functional constraints of labeling. The structural constraint was based first on labeling the brain structures for each participant. This labeling was accomplished by using the FS-FAST automatic segmentation tools, which uses information about image intensities, global position within the brain, position relative to neighboring brain structures, and anatomical landmarks to determine classification of brain regions. These tools have been optimized with regards to accuracy and test–retest reliability (Fischl et al., 2004). Subsequently, based on this segmentation, the ROI labels were hand drawn on individual participant brains on the areas designated as the right and left amygdala.

The functional constraint of the ROIs was based on a mask selecting only the subset of voxels within each anatomical label that were differentially activated by any component of the task, as revealed by the main effect (i.e., the contrast of all conditions versus baseline), with a threshold of $p < .01$. The activation in the voxels that met these constraints was then averaged for the amygdala in each hemisphere, allowing the contrasts of interest to be computed across the time course. The mean percentage of signal change was then calculated for each condition for the TRs showing peak signal change (time points 2–6 s). One participant was excluded from this analysis for the right hemisphere, and one participant was excluded for the left hemisphere analysis because there were less than 10 voxels activated in the specified region of the amygdala. For the analysis of gender, we averaged the data across hemispheres because the activation was similar in both (see Section 1.2.2).

1.2. Results

1.2.1. Behavioral results

Participants liked the curved objects significantly more than the control objects ($t(15) = 2.20$, $p < .05$), and liked the sharp-angled objects significantly less than the control objects ($t(15) = -3.56$, $p < .005$; mean ± standard error: sharp = 47.2% ± 3.5, curved = 62.9% ± 2.6, control = 57.4 ± 2.7; Fig. 2A and Table 1). Thus, sharp-angled objects were liked significantly less than their curved counterparts ($t(15) = -4.82$, $p < .0005$). A similar outcome was obtained with preference for the novel patterns ($t(15) = -3.28$, $p < .005$; sharp = 24.3% ± 4.8, curved = 34.7% ± 5.6). Note that the cutoff between like and dislike is the percentage of liking responses to the control objects, instead of simply taking the less specific 50% liking as cutoff. In other words, the sharp objects were liked significantly less than the control objects, and the curved objects were liked significantly more than the control objects. Thus, we state that the sharp real objects were disliked relative to baseline and the curved objects were liked relative to baseline.

Overall preference for real objects was significantly higher than for novel patterns, regardless of contour type. A contour (curved, sharp) × stimulus type (real objects, patterns)

Table 1
Summary of percent liking data for Experiment 1

Contour	Mean (%)	Standard error	Significance
Real objects			
Sharp	47.2	3.5	Curved > sharp**
Control	57.4	2.7	Sharp < control**
Curved	62.9	2.6	Curved > control*
Novel patterns			
Sharp	24.3	4.8	Curved > sharp**
Curved	34.7	5.6	
ANOVA: contour (C) × stimulus type (ST)			Main effect: C**, main effect: ST**
Item analysis: real objects			
Sharp	50.5	1.8	Curved > sharp**
Curved	58.0	1.7	
Item analysis: novel patterns			
Sharp	25.4	1.5	Curved > sharp**
Curved	37.0	1.6	

ANOVA revealed a significant main effect for both contour [$F(1,15) = 19.6$, $p < .0005$], and stimulus type [$F(1,15) = 19.4$, $p < .005$] (see Bar and Neta (2006) for a possible account). There was no significant difference in average RT between the sharp and curved items ($t(15) = 1.36$, $p > .1$; $RT_{sharp} = 680\ ms \pm 26$, $RT_{curved} = 687\ ms \pm 28$). No effect of gender was found.

An item analysis also indicated a significant difference between the sharp and curved counterparts of each real object pair ($t(139) = -3.38$, $p < .001$; mean ± standard error: sharp = 50.5% ± 1.8, curved = 58.0% ± 1.7), and of each novel pattern pair ($t(139) = -5.69$, $p < .0001$; sharp = 25.4% ± 1.5, curved = 37.0% ± 1.6), such that the sharp-angled were liked significantly less than the curved stimuli. Therefore, this general pattern of preference judgments was consistent across participants and across items, and provides a replication of our previous findings with a different group of participants. Taken together, contour type has a robust influence on liking preferences.

1.2.2. fMRI results

To test our hypothesis that the origin of this preference bias might stem from processes in the amygdala that are possibly related to the detection of threat-related cues, we conducted a Region of Interest analysis on the amygdala. In the right amygdala, we found significantly greater activation for objects with sharp contours than for objects with curved contours, for both real objects ($t(14) = 2.19$, $p < .03$) and novel patterns ($t(14) = 2.09$, $p < .03$) (Fig. 2B and C, Table 2). We used one-tailed t-tests here because our a priori hypothesis predicted that sharp-angled objects would elicit greater amygdala activation than would objects with curved contours. A contour × stimulus type ANOVA revealed a significant main effect of contour [$F(1,14) = 6.55$, $p < .05$], but no significant main effect of stimulus type [$F(1,14) = .67$, $p > .1$], and no significant interaction of contour × stimulus type [$F(1,14) = .09$, $p > .5$]. The results in the left hemisphere were similar: there was significantly greater amygdala activation for objects with sharp contours than for objects with curved contours, for both real objects ($t(14) = 2.21$, $p < .03$) and novel patterns ($t(14) = 1.87$, $p < .05$). A contour (curved, sharp) × stimulus type (real objects, patterns) ANOVA revealed a significant main effect of contour [$F(1,14) = 7.17$, $p < .02$], but no significant main effect of stimulus type [$F(1,14) = .032$, $p > .8$], and no significant interaction of contour × stimulus type [$F(1,14) = .11$, $p > .7$]. A contour (curved, sharp) × stimulus type (real objects, patterns) × Hemisphere (left, right) ANOVA demonstrated that there was no significant main effect of Hemisphere [$F(1,14) = .46$, $p > .5$] and no significant interactions between contour and Hemisphere [$F(1,14) = .06$, $p > .8$], stimulus type and Hemisphere [$F(1,14) = .78$, $p > .3$] or for the overall interaction of contour, stimulus type and hemisphere [$F(1,14) = .01$, $p > .9$] (Table 2). Overall, these results provide strong support for the proposal that sharp-angled objects are liked less because of an increased perception of threat that they convey, consciously or not, even for visual stimuli whose semantic meaning is emotionally neutral.

The increased bilateral amygdala activation for sharp-angled objects was consistent regardless of participants' sex. For this analysis, we averaged the results of the left and right hemispheres because the activation was shown to be similar in each. A contour (curved, sharp) × stimulus type (real objects, patterns) × gender (male, female) ANOVA revealed no significant main effect of gender [$F(1,14) = 3.22$, $p > .09$], no significant interaction between gender and contour [$F(1,14) = 2.97$, $p > .1$], but a significant gender × stimulus type interaction [$F(1,14) = 8.89$, $p < .02$] on percent signal change in the amygdala. The gender × contour × stimulus type interaction was not significant [$F(1,14) = .41$, $p > .5$] (Table 2).

Contour type was correlated with percent "like" responses such that the majority of objects with sharp contours were disliked relative to baseline, and the majority of objects with curved contours were liked relative to baseline [Point Biserial correlation coefficient: $r(279) = .32$, $p < .0001$. For this correlation, we have compared two variables: contour (sharp, curved) and Percent liking (an average of the like/dislike scores across all participants for each individual item), collapsed across stimulus type. Because one of these variables is discrete (contour)

Table 2
Summary of amygdala ROI data for Experiment 1

ANOVA	Effect	Significance
Contour effect (RH)	Real objects: sharp > curved	*
	Novel patterns: sharp > curved	*
Contour effect (LH)	Real objects: sharp > curved	*
	Novel patterns: sharp > curved	*
Contour (C) × stimulus type (ST) RH	Main effect: C	*
	Main effect: ST	n.s.
	Interaction: C × ST	n.s.
Contour (C) × stimulus type (ST) LH	Main effect: C	*
	Main effect: ST	n.s.
	Interaction: C × ST	n.s.
Contour (C) × stimulus type (ST) × hemisphere (H)	Main effect: H	n.s.
	Interaction: H × C	n.s.
	Interaction: H × ST	n.s.
	Interaction: H × C × ST	n.s.
Contour (C) × stimulus type (ST) × gender (G)	Main effect: G	n.s.
	Interaction: G × C	n.s.
	Interaction: G × ST	*
	Interaction: G × C × ST	n.s.

t-Tests	Conditions	Significance
Collapse across C, ST, H	Like vs. dislike	n.s.
Collapse across liking, ST, H	Sharp > curved	**

and one is continuous (percent liking), the correlation is a Point Biserial. There were a total of 140 sharp items and 140 curved items (hence df = 279)]. We wanted to explore further which of the two factors directly influences amygdala activation: mere liking or contour type. In other words, is amygdala activation stronger for sharp-angled objects because they are liked less, or because of the sharp elements in the image? Here we could not perform an item analysis on the ROI data, and therefore conducted an analysis across participants. When comparing like with dislike responses for each participant, collapsed across contour, stimulus type, and hemisphere, we found no significant difference in amygdala percent signal change ($t(15) = .19$, $p > .4$). However, when comparing sharp contour and curved contour for each participant, collapsed across percent liking, stimulus type, and hemisphere, we found a significant difference in amygdala percent signal change ($t(15) = 3.21$, $p < .003$) (Table 2). These further analyses demonstrate that the amygdala response increased for sharp-angled stimuli because of the presence of the sharp features per se, and not because of a difference in liking. Taken together, contour type is the dimension that drove the difference in amygdala activation, and not the liking response. It is possible that while the perception of threat in these everyday objects and novel patterns is implicit, it has affected, somewhat indirectly, the explicit judgment of liking. In other words, we might not perceive the mundane objects in our everyday environment explicitly as threatening when their contour is composed of sharp elements, but this implicit perception of threat is translated into an explicit preference bias.

Beyond the amygdala, there was significant differential activation for sharp-angled and curved contour items in several other regions on the cortical surface of the brain. These include, in the left hemisphere, the superior temporal gyrus (Talairach peak x, y, z coordinates; −57, −22, −7), anterior cingulate cortex (ACC; −3, +25, +21), and early visual areas including the lingual gyrus (−9, −61, +3). In addition, there was differential activity in the parahippocampal cortex (PHC; −24, −33, −11) and retrosplenial complex (RSC; −7, −58, +27), particularly in the precuneus region. In the right hemisphere, the PHC (+27, −36, −12) and RSC (+9, −50, +22) were again differentially activated, as well as early visual areas, particularly in the calcarine sulcus (+5, −83, +4). In all of these cases, the activity was stronger for the sharp-angled objects than for their curved contour counterparts. While the activation in these cortical regions may be relevant to understanding the broad implications of the effects of these visual qualities (i.e., the sharp angles and curvature in contour) and of liking, the specific interpretations of these data are beyond our present scope of studying the relation between contour type, liking judgments and amygdala activation. Future studies and additional hypotheses would be required to address these additional foci directly.

In the following experiment we tested our second hypothesis: that the bias in preference towards curved objects is mediated by the LSFs in the image. The rationale for this hypothesis was that if the reduced preference for sharp-angled objects relative to curved objects is related to the detection of a potential threat, humans would benefit from extracting the relevant information rapidly. Given that LSFs are known to be extracted faster than HSFs (Bar, 2003; Bullier, 2001; Merigan & Maunsell, 1993; Shapley, 1990), we hypothesized that such contour-based preference formation will rely more on the LSFs than on the HSFs. The specific prediction that stems from this hypothesis is that a preference bias for curved over sharp-angled objects would

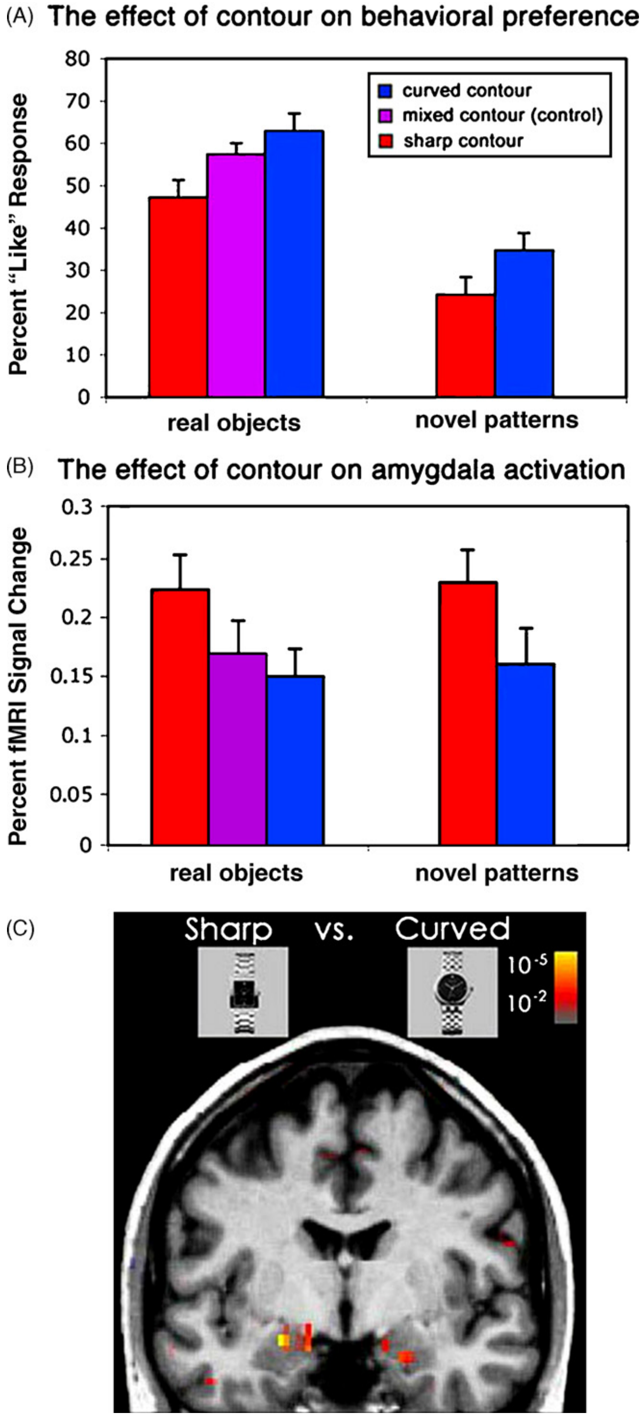

Fig. 2. Decreased preference and increased amygdala activation for items with sharp angles. (A) Percent "like" responses as a function of contour type; (B) percent fMRI signal change in the amygdala, averaged across the left and right hemispheres of fifteen participants during the peak activation time interval (2–6 s). All error bars represent 95% confidence intervals; they reflect standard errors across participants. (C) Statistical map showing a significant differential activation in the amygdala when comparing the activity elicited by sharp-angled objects with their curved counterparts.

be significantly stronger when viewing the LSF version of the images than when viewing the corresponding HSF version.

2. Experiment 2: Low spatial frequencies mediate contour-driven preferences

In this experiment, we tested directly our hypothesis that the aspects of the contour that are critical for this type of preference formation are conveyed primarily by the LSFs in the image. We preceded this experiment with a pilot study, where we wanted to verify that the amount of low and high spatial filtering we employed would create sets of LSF and HSF images that are equally recognizable. By using an equated set of images, we ensure that the differences we might observe are not attributable to differences in performance but to differences in spatial frequency content. In this pilot study the task of the participants was to recognize and name aloud each object. Subsequently, a different group of participants rated preferences for this set of equated LSF and HSF images, using the same task as in Experiment 1 with intact images.

2.1. Methods

The methods for the filtering pilot study were the same as for Experiment 1, except that participants were asked to name each presented object, and a microphone recorded both responses and RTs. Further, because the task is to recognize each object, and the novel patterns are not namable objects that can be identified, they were omitted from this pilot, and from the experiment, as their recognition could not be easily equated. All stimuli were filtered to include either the LSFs (spatial frequencies of lower than: 6, 8, or 10 cycles per image; cpi) or the HSFs (frequencies higher than 24 cpi). The participants consisted of a new group of 26 individuals (4 viewed the LSFs at 6 cpi, 6 viewed the LSFs at 8 cpi, 8 viewed the LSFs at 10 cpi, and 8 viewed the HSFs at 24 cpi). The spatial filtering was applied by using an in-house filtering program written in Matlab. The images were filtered in the frequency domain, employing Gaussian low-pass and high-pass filters implemented using techniques described in Gonzalez, Woods, & Eddins (2004). We modified the filtering level of the LSFs until we found a recognition rate and RT that was equivalent to this of the participants that viewed the HSFs. Based on the data from these participants, we found that the level of LSF filtering that best matches performance with our 24 cpi HSF filtering is 10 cpi. With this filtering cut-off, average recognition difficulty of the items in each condition was equivalent in terms of accuracy and average RTs (LSF at 10 cpi and HSF at 24 cpi; $t(14) = .80$, $p > .2$; mean ± standard error: $RT_{LSF} = 976$ ms ± 51, $RT_{HSF} = 930$ ms ± 26).

Once we have derived sets of LSF and HSF images that were equated in performance, we proceeded to the actual experiment. Methods were the same as for Experiment 1, except as follows: (i) because this experiment had to be piloted without the novel patterns, they were also omitted from the experiment, (ii) all stimuli were filtered to include either the LSFs or the HSFs (as described above) to the degree to which the pilot determined (Fig. 3), and (iii) a new set of 32 participants were recruited (16 viewed the LSFs at 10 cpi and 16 viewed the HSFs at 24 cpi), and made the same like/dislike forced-choice decision about each picture as in Experiment 1, based on their immediate "gut" reaction. All participants had normal or corrected-to-normal vision, no psychoactive medication, and no significant neurological or psychiatric history. None were aware of the purpose of the experiment, and they were all recruited from the greater Harvard and Massachusetts General Hospital community, and paid for their participation. Informed written consent was obtained from each participant before the session, and all procedures were approved by Massachusetts General Hospital Human Studies Protocol number 2001P-001754, and by the Committee on the Use of Human Subjects in Research, Harvard University, FWA #00004837.

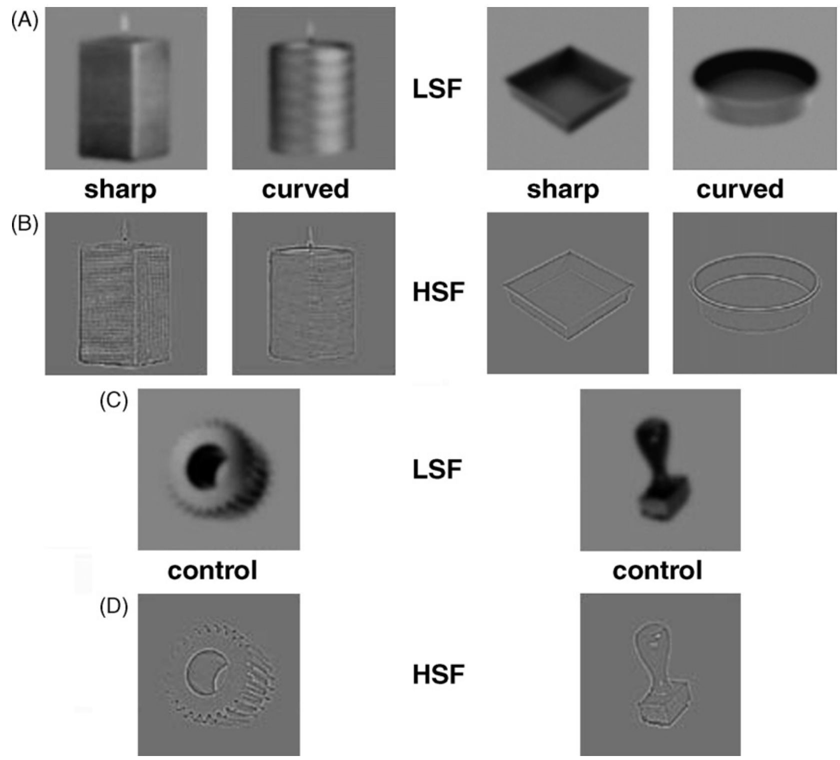

Fig. 3. Examples of the filtered stimuli used in Experiment 2. (A) Pairs of real objects filtered to include the low spatial frequencies (LSFs; up to ten cycles per image); (B) pairs of real objects filtered to include the high spatial frequencies (HSFs; higher than 24 cycles per image); (C) control baseline objects filtered to include the same LSFs; (D) control baseline objects filtered to include the same HSFs. The contrast of the images has been modified slightly from the experimental version to optimize visibility in the figure. Recognition was equated between the two conditions in a pilot experiment.

2.2. Results

When viewing the LSFs of an object, participants liked the curved objects significantly more than the control (i.e. mixed contour) objects, $t(15) = 3.66$, $p < .005$, and liked the sharp-angled objects significantly less than the control objects, $t(15) = -2.75$, $p < .01$; mean ± standard error: sharp = 41.9% ± 3.1, curved = 58.1% ± 3.1, control = 49.2% ± 3.8. Thus, sharp-angled LSF objects were liked significantly less than the curved objects, $t(15) = -5.84$, $p < .0001$. Conversely, when viewing the HSFs of an object, there was no significant difference between preference for the curved objects and the control objects, $t(15) = .30$, $p > .7$, although the sharp-angled objects were liked significantly less than the control objects, $t(15) = -2.74$, $p < .01$; sharp = 53.9% ± 5.5, curved = 60.8% ± 4.8, control = 60.0% ± 4.5; summary in Table 3. The bias in preference for curved objects over sharp objects was significantly greater for the LSF version of the objects than for the HSF version, $t(15) = 3.23$, $p < .005$ (Fig. 4). In other words, when participants viewed the LSFs, they liked the sharp significantly less than the curved, and this difference was much greater than the difference exhibited by participants who viewed the HSFs. Indeed, there was a contour (curved, sharp) × Spatial Frequency (low, high) interaction such that the preference bias for curved objects over sharp-angled objects was greater when viewing the LSFs than when viewing the HSFs [$F(1,30) = 7.09$, $p < .02$]. This specific result demonstrates that the bias in preference against the sharp-angled objects is more readily influenced by the information conveyed by the LSFs of an image. Furthermore, the sharp versus curved bias in preference in the LSF condition in this experiment (16.2%) was almost identical to the corresponding difference when the object images were intact in Experiment 1 (15.7%). Therefore, the rapidly extracted LSFs of an image seem to play a dominant role in shaping our contour-based visual preferences.

Table 3
Summary of percent liking data for Experiment 2

Contour	Mean (%)	Standard Error	Significance
LSFs (8 cpi)			
Sharp	41.9	3.1	Curved > sharp**
Control	49.2	3.8	Sharp < control*
Curved	58.1	3.1	Curved > control**
HSFs (24 cpi)			
Sharp	53.9	5.5	Curved > sharp**
Control	60.0	4.5	Sharp < control*
Curved	60.8	4.8	Curved vs. control n.s.

ANOVA: contour (C) × spatial frequency (SF); interaction: C × SF**.

3. Experiment 3: Subjective ratings of threat for sharp and curve contours

Experiments 1 and 2, while providing critical support for our hypotheses, do not provide a direct link between contour type and an actual perception of threat; so far we primarily inferred

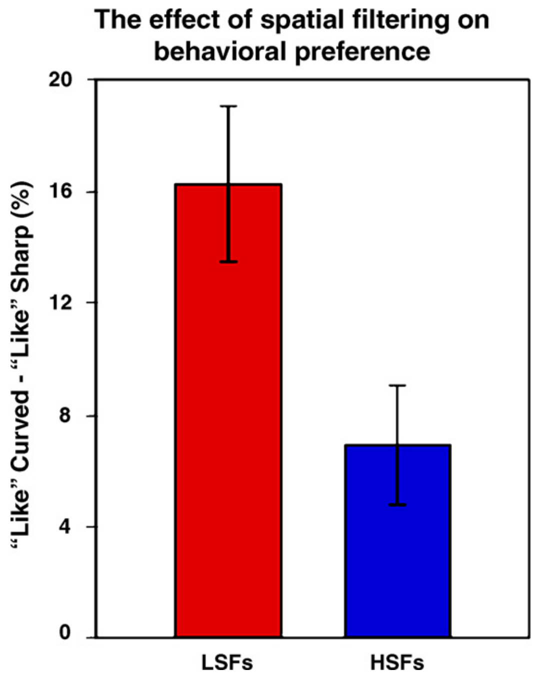

Fig. 4. Low spatial frequencies drive the preference for curved objects. The difference in percent "like" responses between curved and sharp contour objects (i.e., curved-sharp) for low spatial frequencies (LSFs) and for high spatial frequencies (HSFs). The difference for LSFs is significantly greater than the difference for HSFs.

it from the combined decrease in preference and increase in amygdala activation. But amygdala activation could be observed for emotions other than fear, and we decided to test the direct link in a separate behavioral experiment.

3.1. Methods

In this additional experiment, two different groups of eleven participants each saw the same images used in Experiment 1 and, instead of liking, they were required to respond "threatening" or "non-threatening" for each item. One group saw these images exactly under identical conditions as the participants in Experiment 1 (presented for 85 ms), and the second group saw these pictures for 150 ms. The 150 ms version was conducted in parallel in case that the original 85 ms version was too brief for the possible perception of threat to translate into an explicit threat response.

3.2. Results

Critically, in both the 85 and 150 ms groups, we observed a significant difference between the perceived threat for the sharp compared with the curved objects. In the 85 ms group, sharp-angled objects were rated as significantly more threatening than curved objects, $t(10) = 3.71$, $p < .003$; mean ± standard error: sharp = 42.5% ± 5.4, curved = 28.0% ± 5.5 (Table 4). The same was found for the novel patterns, $t(10) = 2.58$, $p < .02$; sharp = 56.8% ± 8.9, curved = 39.8% ± 7.4. This effect was also significant in the 150 ms group, for the real objects $t(10) = 3.01$, $p < .007$; sharp = 38.0% ± 4.2, curved = 29.7% ± 5.3, and for the novel patterns, $t(10) = 3.46$, $p < .003$; sharp = 60.8% ± 7.2, curved = 41.9% ± 8.5. These findings provide essential support for our proposal that the amygdala activation and subsequent effect on liking is a result of threat conveyed by contour elements.

Table 4
Summary of threat data for Experiment 3

Contour/stimulus type	Mean threat (%)	Standard error	Significance
85 ms			
Sharp/real object	42.5	5.4	Curved < sharp**
Curved/real object	28.0	5.5	Curved < control**
Control/real object	48.8	4.3	Sharp < control*
Sharp/novel pattern	56.8	8.9	Curved < sharp*
Curved/novel pattern	39.8	7.4	
150 ms			
Sharp/real object	38.0	4.2	Curved < sharp**
Curved/real object	29.7	5.3	Curved < control*
Control/real object	39.7	2.8	Sharp vs. control n.s.
Sharp/novel pattern	60.8	7.2	Curved < sharp**
Curved/novel pattern	41.9	8.5	
Average			
Sharp/real object	40.2	2.3	Pattern > object**
Sharp/novel pattern	58.8	5.9	

The control (i.e., mixed contour) objects in the 85 ms group were rated as more threatening than the curved objects $t(10) = 5.59$, $p < .0002$, and the sharp-angled objects, $t(10) = 2.91$, $p < .02$; control = 48.8% ± 4.3. However, in the 150 ms group, the control objects were still rated as more threatening than the curved objects $t(10) = 2.22$, $p < .03$, but they were not significantly more threatening that the sharp-angled objects, $t(10) = .54$, $p > .6$; mean control = 39.7% ± 2.8. That the sharp-angled objects were not rated as more threatening than the control objects is somewhat puzzling, and will require further experiments to be fully explained. Independently, for our present purposes, the critical comparison is whether objects with a sharp-angled contour are perceived as relatively more threatening than objects with a curved contour, and these findings indicate unequivocally that they are.

A contour (curved, sharp) × stimulus type (real objects, patterns) ANOVA for the 85 ms group revealed a significant main effect of contour [$F(1,10) = 9.38$, $p < .02$], and a significant main effect of stimulus type [$F(1,10) = 7.88$, $p < .02$], with no significant contour × stimulus type interaction [$F(1,10) = .52$, $p > .4$] (Table 5). This main effect of stimulus type seems to stem from

Table 5
Summary of ANOVAs for Experiment 3

ANOVA	Effect	Significance
Contour (C) × stimulus type (ST) 85 ms	Main effect: C	*
	Main effect: ST	*
	Interaction: C × ST	n.s.
Contour (C) × stimulus type (ST) 150 ms	Main effect: C	**
	Main effect: ST	n.s.
	Interaction: C × ST	n.s.
Contour (C) × stimulus type (ST) × presentation time (PT)	Main effect: PT	n.s.
	Interaction: PT × C	n.s.
	Interaction: PT × ST	n.s.
	Interaction: PT × C × ST	n.s.

the difference in semantic value and subjective associations of the real objects, which were lacking in the novel, meaningless patterns. This is not based on any inherent valence; these items are all devoid of any positive or negative valence. Support for this account can be found in Experiments 1 and 2, where novel patterns were significantly more disliked than real objects, and, in Experiment 3, where the sharp novel patterns were significantly more threatening compared with the sharp real objects when averaging across Presentation Time (85 ms, 150 ms) ($t(10) = 3.58$, $p < .005$; mean ± standard error: sharp real objects = 40.2 ± 2.3, sharp novel patterns = 58.8 ± 5.9). The difference in meaning and subjective associations also seems the best explanation for why some sharp real objects were rated as non-threatening despite their contour. Interestingly, the preference for the novel meaningless patterns is more critically modulated by the effect of contour, because participants had no subjective experience with them. In that sense, the increased threat and disliking that was observed for the novel, compared with real objects, might provide a more realistic estimate of the effect of contour on preference formation.

In the 150 ms group, there was still a significant main effect of contour [$F(1,10) = 14.8$, $p < .003$], but no significant main effect of stimulus type [$F(1,10) = 3.25$, $p > .1$], and a trend for a significant contour × stimulus type interaction [$F(1,10) = 4.57$, $p < .06$].

Finally, an overall contour × stimulus type × presentation Time (85 ms, 150 ms) ANOVA revealed no main effect of Presentation Time [$F(1,10) = .015$, $p > .9$], no significant interactions between presentation time and contour [$F(1,10) = .092$, $p > .7$], or stimulus type [$F(1,10) = 1.64$, $p > .6$], and no overall interaction between presentation time, contour, and stimulus type [$F(1,10) = 1.87$, $p > .2$].

4. Discussion

A critical influence on our preference for objects in the environment is exerted by basic visual elements - whether the contour is curved or sharp (Bar & Neta, 2006). We hypothesized that the bias towards liking sharp-angled objects significantly less than curved objects stems from an elevated perception of threat conveyed by sharp object features, either implicitly or explicitly. To test this hypothesis, we used objects whose semantic meaning is emotionally neutral, and compared amygdala response to these objects when they appear with different types of contour. Our findings indicate that, in agreement with this hypothesis, the amygdala shows significantly more activation for the sharp-angled objects compared with their curved counterparts. This amygdala response is a function of contour type, rather than dependent on liking response, and furthermore seems to be driven significantly more by LSF rather than HSF features in the image.

We concentrate here on the threat-related aspects of amygdala function. Nevertheless, it is important to emphasize that the amygdala has also been implicated in response to positive valence (Gottfried, O'Doherty, & Dolan, 2003; Paton, Belova, Morrison, & Salzman, 2006), vigilance (Whalen, 1998), and a general sensitivity to stimulus' relevance (Vuilleumier, 2005; Zald, 2003). Because the stimuli we have used here were mundane, neutral (and, in the case of the patterns, meaningless) objects, however, they were not likely to elicit a significant level of amygdala activation related to any of these interpretations (e.g., positive affect, relevance and vigilance).

While these findings provide necessary evidence for our proposal that the relatively reduced preference for sharp-angled objects was a result of detecting visual cues that might imply the presence of threat, they are not sufficient on their own; participants' response in the first two experiments was to rate subjective liking, whereas the potential perception of threat conveyed by the sharp-angled contour is presumably implicit in nature and thus cannot be inferred from these responses. Nevertheless, that such elevated amygdala activation was evident for objects that were generally less liked might be safely interpreted as associated with a negative impression, which is what would be expected of stimuli that contain features that signal the presence of potential danger. To study directly our proposed link, therefore we ran an additional behavioral experiment, which indeed showed that when asked explicitly to respond whether each of these stimuli was perceived as threatening or non-threatening, participants tended to find the objects with the sharp elements significantly more threatening than their curved counterparts. This provides an important support for the proposed link between contour type and perception of threat.

The sharp-angled stimuli also elicited a stronger activation in the parahippocampal cortex, the retrosplenial complex and a site within the medial prefrontal cortex. This network has previously been implicated in the analysis of contextual associations (Bar & Aminoff, 2003). Given our proposal that the sharp-angled stimuli convey potential danger, and the idea that dangerous and arousing stimuli are more likely to elicit associative processing than emotionally neutral objects (Medford et al., 2005), it is reassuring that these objects activated the contextual association network to a larger extent than the curved objects.

Research on subjective preference has implicated several brain regions as involved in liking per se, namely the orbitofrontal cortex (Gottfried, Deichmann, Winston, & Dolan, 2002; Ishai, 2007; Kringelbach, O'Doherty, Rolls, & Andrews, 2003; Lewis, Critchley, Rotshtein, & Dolan, in press; O'Doherty et al., 2003; Rolls et al., 2003). As we have shown in the analysis of Experiment 1, amygdala activity was correlated with contour type and not with liking response. Liking itself might have modulated activity in the orbitofrontal cortex also in the present study, and that we did not observe such orbitofrontal liking-based modulation might be a result of the notorious susceptibility artifacts in this region, which typically necessitate an imaging protocol specifically designed to cope with the attenuated signal.

Finally, when decomposing object images to LSFs and HSFs, the consistent preference difference between sharp-angled objects and curved objects was significantly more apparent with the LSF images. This lends support to our proposal that if the reduced liking for the sharp-angled stimuli is a result of potential threat, the extraction of LSF information would critically influence contour-based preference formation. This conclusion fits what is known about the relative faster perception of LSFs (Bar, 2003; Bar, Kassam, et al., 2006; Bullier, 2001; Merigan & Maunsell, 1993; Shapley, 1990), as well as the sensitivity of the amygdala to LSFs (Vuilleumier, 2005; Vuilleumier et al., 2003). If the shape of the contour, even in neutral images, is used to detect potential threat, humans will benefit from extracting the relevant features quickly. That they would rely on the rapidly extracted LSFs, therefore, makes sense in this context.

In conclusion, our findings indicate that humans like sharp-angled objects significantly less than they like objects with a curved contour, and that this bias can stem from an increased sense of threat and danger conveyed by these sharp visual elements. We used objects whose semantic meaning was emotionally neutral, rather than semantically negatively valenced objects (e.g., a knife or a gun), and we know that people do not typically feel explicitly threatened by neutral everyday objects (e.g., a watch or a sofa). Therefore, we propose that the danger conveyed by the sharp-angled stimuli was relatively implicit. Indeed, the amygdala has been shown to respond to implicit, non-conscious cues of threat (Whalen et al., 1998). It is possible that our brains have evolved to detect sharp features rapidly, perhaps using low-level features such as spatial frequencies (Bar & Neta, 2006; Vuilleumier et al., 2003), which can help signal a potential danger. These findings are consistent with our proposal that objects may be perceived as threatening based on the nature of their contour.

Acknowledgements

We thank K. Kveraga for programming tools used for filtering stimuli, as well as those used for both the recording and collection of voice responses to the filtered images used in the pilot for Experiment 3. We also thank E. Aminoff, M. Fenske, N. Gronau, M. Vangel, P. Whalen, and G. Wolford for helpful comments on the manuscript. This work was supported by the James S. McDonnell Foundation #21002039, NINDS R01 NS044319 and NS050615, the MIND Institute, and resource support by #5P41RR014075.

References

Adolphs, R., Tranel, D., Hamann, S., Young, A. W., Calder, A. J., Phelps, E. A., et al. (1999). Recognition of facial emotion in nine individuals with bilateral amygdala damage. *Neuropsychologia*, *37*, 1111–1117.

Ambady, N., Bernieri, F. J., & Richeson, J. A. (2000). Toward a histology of social behavior: Judgmental accuracy from thin slices of the behavioral stream. *Advances in Experimental Social Psychology*, *32*, 201–271.

Bar, M. (2003). A cortical mechanism for triggering top-down facilitation in visual object recognition. *Journal of Cognitive Neuroscience*, *15*, 600–609.

Bar, M., & Aminoff, E. (2003). Cortical analysis of visual context. *Neuron*, *38*, 347–358.

Bar, M., Kassam, K. S., Ghuman, A. S., Boshyan, J., Schmidt, A. M., Dale, A. M., et al. (2006). Top-down facilitation of visual recognition. *Proceedings of the National Academy of Science*, *103*, 449–454.

Bar, M., & Neta, M. (2006). Humans prefer curved visual objects. *Psychological Science*, *17*, 645–648.

Bar, M., Neta, M., & Linz, H. (2006). Very first impressions. *Emotion*, *6*, 269–278.

Bar, M., Tootell, R., Schacter, D. L., Greve, D. N., Fischl, B., Mendola, J., et al. (2001). Cortical mechanisms of explicit visual object recognition. *Neuron*, *29*, 529–535.

Bullier, J. (2001). Integrated model of visual processing. *Brain Research Reviews*, *36*, 96–107.

Burock, M. A., Buckner, R. L., Woldorff, M. G., Rosen, B. R., & Dale, A. M. (1998). Randomized event-related experimental designs allow for extremely rapid presentation rates using functional MRI. *Neuroreport*, *9*, 3735–3739.

Cox, R. W. (1996). AFNI: software for analysis and visualization of functional magnetic resonance neuroimages. *Computers and Biomedical Research*, *29*, 162–173.

Dale, A. M., Greve, D. N., & Burock, M. A. (1999). Optimal stimulus sequences for event-related fMRI. *Human Brain Mapping*, *8*, 109–114.

Fischl, B., Salat, D. H., van der Kouwe, A. J. W., Makris, N., Ségonne, F., & Dale, A. M. (2004). Sequence-independent segmentation of magnetic resonance images. *NeuroImage*, *23*(Suppl. 1), S69–S84.

Fischl, B., Sereno, M. I., Tootell, R. B., & Dale, A. M. (1999). High-resolution intersubject averaging and a coordinate system for the cortical surface. *Human Brain Mapping*, *8*, 272–284.

Gonzalez, R. C., Woods, R. E., & Eddins, S. L. (2004). *Digital image processing using MATLAB*. Prentice Hall.

Gottfried, J. A., Deichmann, R., Winston, J. S., & Dolan, R. J. (2002). Functional heterogeneity in human olfactory cortex: an event-related functional magnetic resonance imaging study. *Journal of Neuroscience*, *22*, 10819–10828.

Gottfried, J. A., O'Doherty, J., & Dolan, R. J. (2003). Encoding predictive reward value in human amygdala and orbitofrontal cortex. *Science*, *301*, 1104–1107.

Ishai, A. (2007). Sex, beauty and the orbitofrontal cortex. *International Journal of Psychophysiology*, *63*(2), 181–185.

Kringelbach, M. L., O'Doherty, J., Rolls, E. T., & Andrews, C. (2003). Activation of the human orbitofrontal cortex to a liquid food stimulus is correlated with its subjective pleasantness. *Cerebral Cortex*, *13*, 1064–1071.

Lewis, P. A., Critchley, H. D., Rotshtein, P., & Dolan, R. J. (in press). Neural correlates of processing valence and arousal in affective words. *Cerebral Cortex*.

Medford, N., Phillips, M. L., Brierley, B., Brammer, M., Bullmore, E. T., & David, A. S. (2005). Emotional memory: Separating content and context. *Psychiatry Research*, *138*, 247–258.

Merigan, W. H., & Maunsell, J. H. (1993). How parallel are the primate visual pathways? *Annual Review of Neuroscience*, *16*, 369–402.

O'Doherty, J., Winston, J., Critchley, H. D., Perrett, D., Burt, D. M., & Dolan, R. J. (2003). Beauty in a smile: The role of medial orbitofrontal cortex in facial attractiveness. *Neuropsychologia*, *41*, 147–155.

Paton, J. J., Belova, M. A., Morrison, S. E., & Salzman, C. D. (2006). The primate amygdala represents the positive and negative value of visual stimuli during learning. *Nature*, *439*, 865–870.

Rolls, E. T., O'Doherty, J., Kringelbach, M. L., Francis, S., Bowtell, R., & McGlone, F. (2003). Representations of pleasant and painful touch in the human orbitofrontal and cingulate cortices. *Cerebral Cortex*, *13*, 308–317.

Shapley, R. (1990). Visual sensitivity and parallel retinocortical channels. *Annual Review of Psychology*, *41*, 635–658.

Vuilleumier, P. (2005). How brains beware: Neural mechanisms of emotional attention. *Trends in Cognitive Sciences*, *9*, 585–594.

Vuilleumier, P., Armony, J. L., Driver, J., & Dolan, R. J. (2003). Distinct spatial frequency sensitivities for processing faces and emotional expressions. *Nature Neuroscience*, *6*, 624–631.

Whalen, P. J. (1998). Fear, vigilance, and ambiguity: initial neuroimaging studies of the human amygdala. *Current Directions in Psychological Science*, *7*, 177–188.

Whalen, P. J., Rauch, S. L., Etcoff, N. L., McInerney, S. C., Lee, M., & Jenike, M. A. (1998). Masked presentations of emotional facial expressions modulate amygdala activity without explicit knowledge. *Journal of Neuroscience*, *18*, 411–418.

Willis, J., & Todorov, A. (2006). First impressions: Making up your mind after a 100-ms exposure to a face. *Psychological Science*, *17*, 592–598.

Zald, D. H. (2003). The human amygdala and the emotional evaluation of sensory stimuli. *Brain Research Reviews*, *41*, 88–123.