

University of Groningen

Aesthetics by numbers

Jacobs, Richard Henrikus Augustinus Hubertus

IMPORTANT NOTE: You are advised to consult the publisher's version (publisher's PDF) if you wish to cite from it. Please check the document version below.

Document Version

Publisher's PDF, also known as Version of record

Publication date:

2011

[Link to publication in University of Groningen/UMCG research database](#)

Citation for published version (APA):

Jacobs, R. H. A. H. (2011). Aesthetics by numbers Groningen: s.n.

Copyright

Other than for strictly personal use, it is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), unless the work is under an open content license (like Creative Commons).

Take-down policy

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

Downloaded from the University of Groningen/UMCG research database (Pure): <http://www.rug.nl/research/portal>. For technical reasons the number of authors shown on this cover page is limited to 10 maximum.

RIJKSUNIVERSITEIT GRONINGEN

Aesthetics by Numbers

Proefschrift

ter verkrijging van het doctoraat in de
Medische Wetenschappen
aan de Rijksuniversiteit Groningen
op gezag van de
Rector Magnificus, dr. E. Sterken,
in het openbaar te verdedigen op
woensdag 7 september 2011
om 11.00 uur

door

Richard Henrikus Augustinus Hubertus Jacobs

geboren op 25 oktober 1972
te Eindhoven

Promotores: Prof. dr. J.M.M. Hooymans
Prof. dr. A. Aleman

Copromotores: Dr. F.W. Cornelissen
Dr. R. Renken

Beoordelingscommissie: Prof. dr. K.R. Gegenfurtner
Prof. dr. H.P.H. Kremer
Prof. dr. N. Petkov

Contents

1. Introduction	1
2. Consistency in beauty ratings to visual textures	6
3. Aesthetics by numbers - deriving perceived texture qualities from computed visual texture properties	12
4. Neural correlates of visual aesthetics - beauty as the coalescence of stimulus and internal state	32
5. Amygdalar guidance of feature-based attention during aesthetic judgments	44
6. Different judgments about visual textures invoke different eye movement patterns	52
7. The amygdala, top-down effects, and selective attention	67
8. Conclusions	84
9. Summary	86
10. Samenvatting (Nederlands)	87
11. Full publications by the author	88
12. Publication status of the chapters	88
13. Acknowledgments	89
14. Epilogue	91
15. References	94

1. Introduction

This thesis is about empirical research into the perception of *beauty*. Beauty is often said to be in the eye of the beholder. This does not mean that empirical investigations of beauty perception are impossible. The aim of this thesis is to get a grip on the mechanisms underlying beauty judgments. I will establish quantitative relationships between texture features and beauty judgments. I will then look at the neural machinery underlying the assessment of beauty. Finally, I will investigate what role attention plays in these processes.

Recently, advances in neuroimaging techniques have enabled the investigation of neural substrates underlying beauty perception. Using these techniques, neural substrates have been identified that respond depending on the perceived beauty level of stimuli (Aharon et al., 2001; Calvo-Merino, Jola, Glaser, & Haggard, 2008; Cela-Conde et al., 2004; A. Chatterjee, A. Thomas, S. E. Smith, & G. K. Aguirre, 2009; Di Dio, Macaluso, & Rizzolatti, 2007; Kawabata & Zeki, 2004; Vartanian & Goel, 2004). Another study has identified regions that appear to be involved in beauty, as opposed to symmetry, judgments (Jacobsen, Schubotz, Hofel, & Cramon, 2006). These studies, together with plans to start a journal of neuroaesthetics (Zeki, personal communication, the term neuroaesthetics was coined by Zeki to refer to this growing field), and a volume written about neuroaesthetics (Zeki, 1999), testify to the increasing interest in the neural foundations of aesthetics.

In this thesis, I will examine beauty judgments to *visual textures*. Textures are patterns. They can consist of objects, but a single object is not a texture. They often are repetitive, and they are typically found on surfaces. A perfectly smooth surface may be said to have no texture, although one could also defend that it contains an extreme texture, namely a perfectly smooth one, for which many features achieve extreme values. Textures can be observed both in the tactile and the visual modality. Color is a feature that is only observable in the visual modality. It definitely is a surface property, but one can dispute whether it should be included as a texture property, or whether it should be seen as separate from it. Visual textures can be defined purely on the basis of color differences, and in particular cases, grey-scaling a colored texture will result in loss of the pattern, i.e., of the texture. So in this thesis, we will assume that color is an integral part of texture.

Visual textures are interesting in themselves, as evidence is accumulating that textures are processed in specialized cortical regions (Beason-Held et al., 1998; J.S. Cant, Arnott, & Goodale, 2009; J. S. Cant & Goodale, 2007; Cavina-Pratesi, Kentridge, Heywood, & Milner, 2010a, 2010b; Peuskens et al., 2004; Puce, Allison, Asgari, Gore, & McCarthy, 1996; Stilla & Sathian, 2007). Hence, visual texture processing may be different from object perception. Also for practical purposes, investigating feelings associated with textures is important, for example to aid in decisions about the coating of the inside of elevators, to induce feelings of comfort, etcetera.

Besides being inherently interesting, the use of visual textures has a number of advantages over other stimuli that are often used to investigate aesthetics (beauty), such as paintings or faces. First of all, many features of textures can be computed, allowing for a quantification of the relationship between stimulus features and beauty ratings. Second, semantic associations can be assumed to be minimal in textures. Hence, the relationship between features and beauty judgments can be studied with little contamination by semantic factors. Nevertheless, some semantic associations remain to be recognizable, familiar textures, such as fur, velvet, stone, wood. Third, the features that are present in textures are typically present all over the stimulus. For example, the spatial frequencies, the colors, and the contrast present in a texture will often be similar all over the texture. This property of textures makes them well suited to investigate *feature-based attention*, a topic that I will focus on in this thesis.

Feature based attention consists of attending to one particular feature, or a group of features, over other features that are present in a stimulus. For example, one can attend to the shape of a bar, or to its orientation, or to its color, or to its width, even though these features can be present at the same location. With the use of visual textures, many features are present all over the stimulus, so that attending to one feature or another should involve feature-based attention with minimal contributions from spatial attention – another form of attention, consisting of attending to different locations. In this thesis, we will argue that judging visual textures for beauty involves attending to other features than judging visual textures for roughness or naturalness.

Overview of the thesis

To get a grip on the processes involved in forming a beauty judgment, we will employ behavioural as well as imaging techniques. At the behavioural level, we will examine relationships between visual texture features and beauty judgments. Neuroimaging will be used to localize brain regions involved in making beauty assessments. As one of these brain regions, the amygdala, appears to play a role in selective attention, we then focus on the role selective attention, and in particular feature based attention, plays in the assessment of beauty.

Before embarking on an examination of beauty in visual textures, it is important to determine whether beauty responses to visual textures are *consistent*, between individuals, and between multiple ratings within one individual. This was our first aim. We examined the consistency of beauty ratings to visual textures, and found consistency to be high, provided that we employ textures that are rated as most and least beautiful to start with. These results are presented in chapter 2. Without consistency in the judgments, the enterprise of examining systematic relationships between texture features and beauty judgments would have been futile. In addition, consistency in the beauty ratings is required to present observers with equal amounts of beautiful, neutral, and ugly stimuli, for example in neuroimaging experiments.

Our second aim was to determine the relationship of beauty judgments to other judgments, such as roughness judgments. In neuroimaging experiments, if you want to examine processes related to beauty judgments, it is necessary to contrast these judgments to other judgments. Some judgments, such as ratings of the elegance of textures, may be more related to beauty judgments than for example roughness judgments. There are numerous judgments one can think of making about visual textures. To make an inventory of these judgments, we asked observers to generate many words describing textures, as is described in the appendix to chapter 3. Next, we made a selection of the most commonly used words, and investigated their interrelationships using factor analysis, in a separate experiment. The results are described in chapter 3. The judgments appear to be captured efficiently by two judgment factors, one capturing the evaluative aspects (beauty, elegance, warmth) and the other capturing more descriptive aspects (roughness, complexity) of the visual textures. Based on these results, we decided to use beauty judgments as representative for the evaluative judgments, and roughness judgments as representative for the descriptive judgments.

Our third aim was to determine the relationships between texture features and beauty and roughness judgments. To this end we computed texture features for the set of textures that were judged for beauty and other aspects. We removed redundancy in the feature space by performing factor analysis, and determined the relationships between the resulting feature factors and average beauty judgments, and between feature factors and average roughness judgments. These results indicate that beauty judgments rely to a large extent on low spatial frequencies, color information, and directionality, while roughness judgments rely to a large extent on low spatial frequencies and image intensity (chapter 3).

Our fourth aim was to investigate the neural basis for the different judgments. Both the effects of beauty level of stimuli and of beauty judgments on neural activation have been investigated before, but the results are puzzling because studies rarely find the same brain regions as being involved in aesthetics. The discrepancies may be explained by the different stimuli that are employed. It is quite conceivable that the brain regions supposedly responding to stimulus beauty are actually responding to features that are predictive of beauty. If the stimulus type and hence the relevant features vary from experiment to experiment, the results are then also likely to vary from one experiment to another. We argue that beauty assessments are reflected in brain regions responding to beauty level during beauty judgments, but not during roughness judgments. We designed an fMRI experiment investigating brain responses to beautiful, neutral, and ugly visual textures while observers judged these for beauty, naturalness, and roughness. The results indicated that the frontomedian cortex and the amygdala respond to beauty level during beauty judgments but not during roughness judgments, so these regions may be making beauty assessments (Chapter 4).

Based on literature pointing to the amygdala as a key node in guiding attention to emotionally relevant information (Adolphs et al., 2005), we predicted that the amygdala should be more active during the emotionally tinged beauty judgments than during the non-emotional naturalness and roughness judgments, in the previous experiment. This prediction was confirmed in our fMRI experiment, mentioned above. As we employed visual textures, in which featural information is omni-present, and where a (spatial) re-allocation of attention does not lead to substantially different information falling on the retina, we believe this constitutes strong evidence for an amygdalar role in feature-based, rather than spatial attention (Chapter 5).

After finding support for an amygdalar role in attention, we became curious whether the differences in attention would be detectable in the observers' eye movements. We designed an experiment in which observers judged visual textures for beauty and for roughness, while their eyes were being tracked (Chapter 6). We found that observers made shorter fixations and covered a larger distance with their eyes, when making beauty judgments. This suggests to us that the extraction of features relevant for roughness judgments takes longer than the extraction of features relevant for beauty judgments. Analysis of the featural information around the fixations showed that observers tend to fixate more on colored information during beauty judgments than during roughness judgments. These findings both point to differences in feature-based attention during the two judgments, although the latter finding suggests that there may still be a spatial component involved.

After finding that the amygdala differentiated between beauty judgments and roughness judgments about visual textures, and finding that also eye movements differ between both judgments, I became curious about further evidence pointing to an amygdalar role in selective, feature-based, attention. The evidence for such a role is reviewed in chapter 7. I present a framework unifying the findings of an amygdalar involvement in top-down attention, spatial attention, feature-based attention, fear conditioning, and responses to facial expressions.

I conclude that beauty and roughness judgments about visual textures are independent, and that these judgments rely mostly on different features. Longer fixations during roughness judgments suggest that the extraction of the features relevant for roughness decisions (uniformity, image intensity) takes longer than extraction of the features relevant for beauty decisions (color features, directionality, and also spatial frequency). The amygdala may mediate these differences between beauty and roughness judgments in feature based attention. Its involvement in spatial attention may only be secondary, as feature-based attention often precedes shifts in spatial attention (Hopf, Boelmans, Schoenfeld, Luck, & Heinze, 2004). Besides the amygdala, the frontomedian cortex appears to be involved in making beauty assessments.

Methods used

Functional magnetic resonance imaging (fMRI)

Magnetic resonance imaging obtains an image of a section of a subject by means of the interaction between the spins of nuclei (usually the hydrogen nuclei, or protons, in water) and an imposed magnetic field. Because the protons possess a small magnetic moment, a steady magnetic field tends to align them in the field direction. By imposing a radio frequency pulse with precisely that frequency that corresponds to the energy difference between alignment parallel to and antiparallel to the steady field, the spins can be flipped into an alignment that is no longer along the field direction. Following the radiofrequency pulse, the energy is reemitted by the nuclear spins, in the form of a radiofrequency magnetic field decaying over some tens of milliseconds as the spin system returns to equilibrium. This field can be detected by a coil.

As neurons do not have internal reserves for glucose and oxygen, more neuronal activity requires more glucose and oxygen to be delivered rapidly through the bloodstream. The delivery of glucose results in a so-called hemodynamic response, which is greater for active than for inactive neurons. Higher Blood Oxygen Level Dependent (BOLD) signal intensities arise from increases in the concentration of oxygenated hemoglobin. The BOLD-response peaks at about 5 seconds after presentation of a stimulus. By asking participants to perform tasks, and/or observe stimuli, differing only in one critical aspect, one can contrast the BOLD-responses associated with each task/stimulus. The resulting activation maps will show brain regions where the activation correlates with the critical aspect that was varied. As these activations are related to the processing taking place in the brain, this method is known as functional magnetic resonance imaging (fMRI).

fMRI is non-invasive, and it usually has a spatial resolution of about 3-4 mm³. In practice, the temporal resolution is usually limited to one full-brain scan every 2 seconds.

Eye tracking

When inspecting our environment, our eyes jump from one fixation spot to the next, resting briefly between jumps. Exceptions to this pattern consist of smooth pursuit movements, for following moving targets, and eye blinks. Thus, eye movements during the observation of stationary pictures can be adequately summarized by the fixation durations and locations, and the saccade durations.

Eye trackers follow the eye movements at a high temporal resolution, in the milliseconds range. Besides keeping track of eye position, they also allow for registering pupil size and eye blinks. All these variables may change according to the questions posed to the observer, or the stimuli presented. Eye movements are a good indicator of where someone is attending, although the relationship is not perfect: It is possible to attend to some spot in your visual field, without focusing on that spot. Pupil size is thought to be an indicator of interest in visual stimuli, and it reflects processing effort.

In my experiments, I used an EyeLink 1000 (SR Research, Canada). It uses infrared light to record images of the eye, in my experiments 500 times per second. The system measures the pupil size and shape and corneal reflections to determine eye position. In my experiments, the observer's head was supported by a standard at the chin and forehead, to minimize head movement.

Factor analysis

Factor analysis attempts to identify underlying variables, or factors, that explain the pattern of correlations within a set of observed variables. It can be used to reduce data to a small number of factors that explain most of the variance in the original variables.

Factor analysis consists of a factor extraction method (such as principal component analysis) plus a rotation of the data. In principal component analysis, the retained dimensions are orthogonal (in contrast to independent component analysis), or perpendicular, to each other. As a consequence, the dimensions are also independent of each other. How many dimensions to retain is a somewhat arbitrary decision. Usually, the variance explained by each component is plotted against the component number, the components being ordered according to the amount of variance in the original data that is explained by each of them. This yields a decreasing curve, called a scree plot. The number of components to retain is sometimes determined by looking for a place in this scree plot where the curve levels off, or has a sharp knick. Another criterion is to retain all components with an eigenvalue greater than 1. Each component has an eigenvalue, and eigenvalues are proportional to the variance explained. Yet another technique is to compare the scree plot for the actual data with the scree plots for random data, e.g. the columns in the original data randomly permuted, such that the relationships between the columns are disturbed, but the distribution of the values per column is retained. Many permutations, typically around 1000, lead to as many scree plots. From these, an average value and standard deviation in explained variance can be computed. As long as the variance explained by the components determined for the actual data remains above the variance explained by the components determined for the permuted data, the components are considered to contribute something non-random, and these should thus be retained. The rotation of the extracted components to the data (or of the data to the components) serves to facilitate interpretation of these components. Varimax rotation rotates the data such that they fall as closely to the extracted dimensions as possible. Many of the data will thus end up with a high score on one of the extracted components, and low scores on the other components. This facilitates interpretation of the extracted components.

Chapter 2.

Consistency in beauty ratings to visual textures

Richard H.A.H. Jacobs^{1,2}

Remco Renken^{1,2}

Frans W. Cornelissen^{1,2}

There are suggestions in the literature that texture affects aesthetics. Interested in texture's effects on beauty judgments, we set out to determine the consistency of these judgments, within and between subjects. We find that consistent beauty ratings can be obtained, even between subjects, provided that textures are chosen that are sufficiently diverse in terms of initial beauty ratings.

Affiliations:

1. Laboratory for Experimental Ophthalmology, School for Behavioral and Cognitive Neurosciences, University Medical Center Groningen, University of Groningen, PO Box 30001, 9700 RB Groningen, the Netherlands

2. BCN NeuroImaging Center, School for Behavioral and Cognitive Neurosciences, University Medical Center Groningen, University of Groningen, PO Box 30001, 9700 RB Groningen, the Netherlands

Introduction

There are sporadic suggestions in the literature that texture information, in particular spatial frequencies or fractal dimension present in stimuli, affects emotional and aesthetic judgments (Aks & Sprott, 1996; Kawamoto & Soen, 1993; Schira, 2003; Soen, Shimada, & Akita, 1987) and brain responses (Delplanque, N'Diaye, Scherer, & Grandjean, 2007; Holmes, Winston, & Eimer, 2005; E. T. Rolls et al., 2003; Vuilleumier, Armony, Driver, & Dolan, 2003). This suggests that people may show systematic preferences for textures, despite their apparent affective neutrality. In the tactile domain, a systematic relationship between smoothness and preference for textures has already been demonstrated (Ekman, Hosman, & Lindstroem, 1965). To investigate further, in the visual domain, we perform two experiments asking for repeated beauty judgments to textures. In the first, we ask people to judge textures twice, after which we select the extreme textures on an individual basis for a third judgment, to see if this selection results in stronger correlations between ratings. Encouraged by these findings, we proceed to a second experiment, in which we select extreme textures in terms of group average beauty ratings. This allows for a correlation between average beauty ratings, over participants, to textures. Participants return to judge these textures twice more, and high correlations are found.

Method

In the first study, six male and eight female colleagues participated. They viewed 305 textures, taken from our database (available on request), one by one on a 30'' Apple Cinema HD Display, and rated them for beauty by moving a slider along a horizontal bar (right side = beautiful), in a self-paced task, under instructions to respond based on their first impression. Textures were presented against a grey background, in which they gradually faded (see figure 2.1). Judgments took place on separate days.

In the second study, a different but overlapping set of 300 textures is drawn from the same large texture database. Twelve male and twelve female participants enrolled in exchange for course credits, and all but seven females returned for a second and third rating, which took place on a later day, and were separated by a number (about 9) of other judgments about the textures. The main difference with study 1 was that this time extreme textures were selected based on group average beauty ratings in the first round. The twenty most and least liked textures were taken, as well as twenty from the middle of the range.

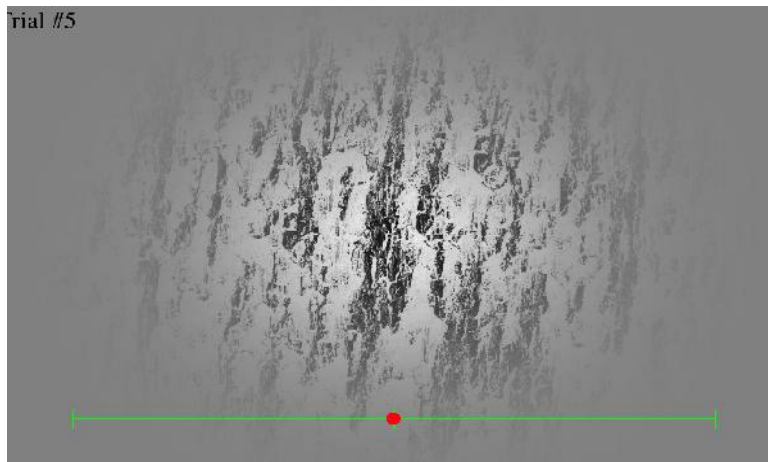


Figure 2.1. Example texture, as shown on screen, with a green slider bar at the bottom.

Results

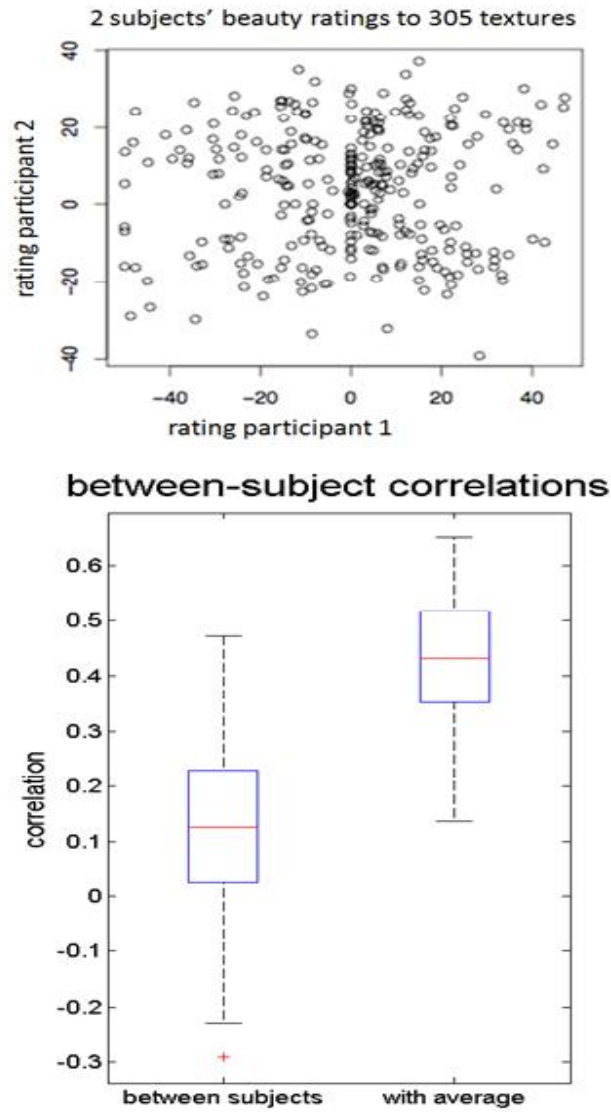


Figure 2.2. Representative example of two subjects' ratings to 305 textures (top panel), showing low correlation. Bottom panel: average between-subjects correlation and spread, and the correlations with the average beauty rating, in the second session, study 1.

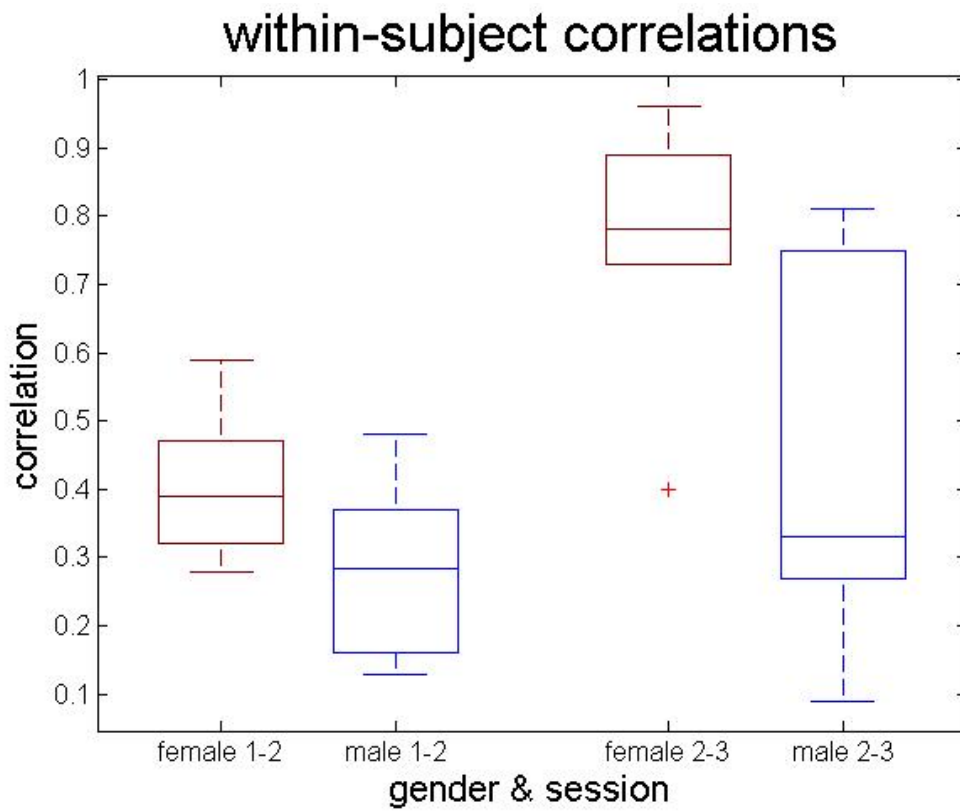


Figure 2.3. Within-subject correlations (r), calculated between the first and the second session (left) and the second and third session (right), for females (red) and males (blue). Within-subject correlations are higher than the between-subject correlations above (figure 2.2, left box). The selection of extremes for the third session appears to further enhance correlations.

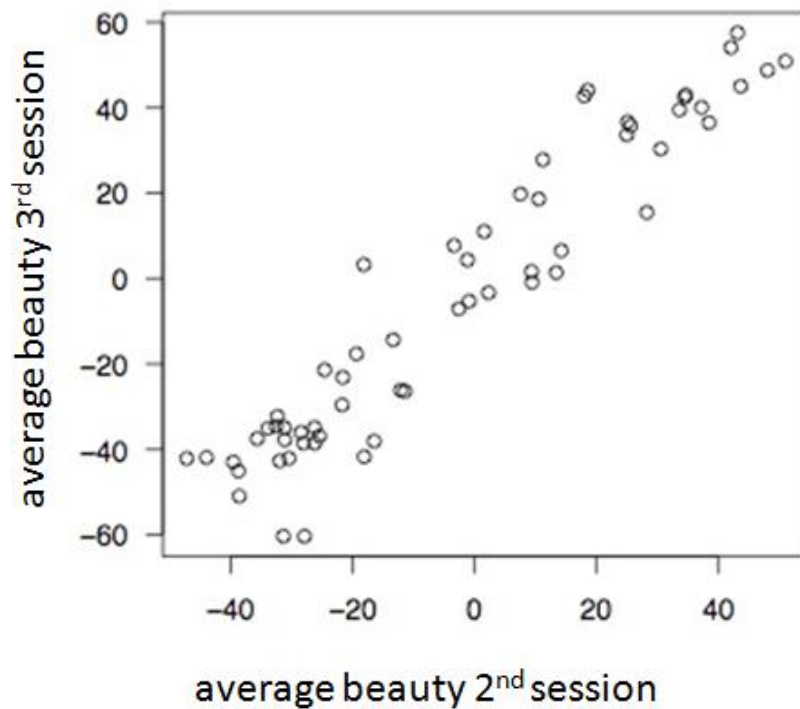


Figure 2.4. Correlation between mean ratings, over subjects, from the second and third session. An r-value of .95 was obtained.

Beauty ratings between different people are close to 0 (figure 2.2). Within subjects, correlations between repeated beauty ratings reach r-values of 0.3 (figure 2.3). After a pre-selection of the individually most and least liked textures, correlations between repeated beauty ratings reach values from 0.3 to 0.8 (figure 2.3). Pre-selecting based on group-averaged ratings results in a high correlation between the means of repeated ratings of textures, over subjects.

Discussion

When taking a random sample of textures, correlations between beauty ratings from different people are quite low (figure 2.2). Within subjects, correlations are better ($r \approx 0.3$; figure 2.3, left part), but we aimed for higher reliability, because we want to obtain reliable beauty judgments in a brain imaging experiment, based on a pre-selection of textures. By selecting the extremes at an individual level, a strong enhancement of within-subject correlations can be obtained (figure 2.3, right panel), showing that there is some consistency in the ratings of the textures, and beauty judgments are not merely a result of random fluctuations in, for example, the state of the viewer. Selecting extremes on beauty can even be done on group-average ratings, resulting in consistent average ratings ($r = .95$; figure 2.4) between sessions, over subjects.

There is a suggestion that females are more consistent in their beauty ratings than males. However, the number of participants (6 males, 8 females) does not allow for any definitive conclusions regarding this matter.

In a similar study (Hofel & Jacobsen, 2003), subjects judged abstract graphic patterns multiple times over several days. Beauty judgments appeared to be quite inconsistent in that study, but consistency improved when judgments to these items were repeated. The authors interpreted this to be a reflection of subjects' desire to maintain consistency, and thus not a genuine aesthetic response. Similar factors may have been at work here. Although mnemonic factors may play a role, we think the consistency in ratings to extremely rated textures is a valuable starting point for further research.

Chapter 3.

Aesthetics by numbers: deriving perceived texture qualities from computed visual texture properties

Richard H.A.H. Jacobs^{1,2}

Koen V. Haak^{1,2}

Stefan Thumfart³

Remco Renken^{1,2}

Brian Henson⁴

Frans W. Cornelissen^{1,2}

Our world is filled with textures. Despite their abundance, there have been few systematic attempts to reveal the relationships between texture features and high-level judgments, even though there are indications that such systematic relationships exist. Exploration of such relationships is desirable, not only from a psychological/neuroscience perspective, but also for applied fields such as design, architecture, and the visual arts. In this study, we explored these relationships for visual textures. In two separate studies, observers judged visual textures for qualities such as beauty, roughness, naturalness, elegance, and complexity. Using factor analysis, we first determined the relationships between these different judgments. We found that 73-76% of the variability in the judgments could be explained by a judgment space with two dimensions, which we called the evaluative and descriptive dimensions. Next, for each of the texture stimuli we derived the values for 188 features. Redundancy in this feature space was removed by performing factor analysis. Of the 20 retained feature factors, 5 were significantly related to the beauty ratings. Higher beauty ratings were associated with lower spatial frequencies and higher intensity variation, saturation, redness, and a diagonal orientation. Feature factors capturing image intensity and uniformity significantly predicted roughness ratings. We found that two dimensions, which are closely associated with beauty and roughness, captured most of the variability in the judgments about textures. Surprisingly, for predicting roughness judgments, uniformity and intensity appeared to be more relevant than some computational features that were explicitly meant to reflect the roughness of texture images. In addition to corroborating the influence of spatial frequency on beauty ratings, we found that element directionality and color also affect these ratings. Thus, beauty is not entirely in the eye of the beholder, and can be accurately predicted from computed features contained in the texture images.

Keywords: Aesthetics, beauty, roughness, features, evaluative, descriptive, semantic differential

Affiliations:

- 1. Laboratory for Experimental Ophthalmology, School for Behavioral and Cognitive Neurosciences, University Medical Center Groningen, University of Groningen, PO Box 30001, 9700 RB Groningen, the Netherlands**
- 2. BCN NeuroImaging Center, School for Behavioral and Cognitive Neurosciences, University Medical Center Groningen, University of Groningen, PO Box 30001, 9700 RB Groningen, the Netherlands**
- 3. Machine Vision Group, Profactor GmbH, Im Stadtgut A2, A-4407, Steyr-Gleink, Austria**
- 4. School of Mechanical Engineering, University of Leeds, LS2 9JT, Leeds, United Kingdom**

Introduction

Working definitions

This paper is about textures and about aesthetics. Aesthetics often refers to beauty and related judgments, such as preferences. In a broader sense, it often refers to other impressions, such as judgments of naturalness. Both interpretations apply to this paper; the focus is on beauty, but we also incorporated other judgments about visual textures.

We found no general consensus on the definition of texture. In our study, we therefore used the following working definition of texture: any pattern in which no single object outline can be discerned. We used 'single' because an outline of one stone would count as an object, but a field of stones would count as a texture. Textures typically contain repetitive information. For the present study, color was defined as an integral part of textures.

Background, general

Visual and tactile textures are widely used in industrial design, art, and architecture to convey information (e.g. about the atmosphere or safety of buildings, or the strength, quality, or intended use of objects) and to influence aesthetic experience. Despite this widespread use, there have been relatively few systematic attempts to reveal the relationships between such perceived aesthetic qualities and their bearing on image textural features.

Using textures to examine aesthetic responses

The study of texture processing is interesting in itself because evidence is accumulating that textures are processed in dedicated visual processing regions, which are located mainly along the medial visual cortex (J. S. Cant & Goodale, 2007; Peuskens et al., 2004a; Puce, et al., 1996). Investigations of texture perception may therefore lead to insights into the functioning of human perception that may not be found when investigating other stimulus types. In addition, texture is an important source of information for assessing material properties. Understanding texture perception will therefore contribute to our understanding of the perception of material properties.

Texture processing is not only inherently interesting. If we improve our understanding of texture processing mechanisms, this may shed a light on the processing of other, more meaningful stimuli that are typically investigated in aesthetics research, such as faces or paintings. Compared to objects, faces or paintings, the use of textures as stimuli has advantages, such as minimizing semantic associations that are hard to control for. Semantic information has been shown to be an important factor for determining preferences (Martindale, Moore, & Borkum, 1990; Vessel & Rubin, 2010). With textures, semantic influences are strongly attenuated, although some textures may still elicit associations through recognition of the material of which it is composed (e.g., stone, wood, silk or fur). If we understood the texture features that influence aesthetic responses, then we could point out systematic relationships between aesthetic appreciation and the textural properties of more complex stimuli, such as photographs or paintings. Moreover, the results could possibly point out confounds in other studies. A second important advantage of using textures over objects is the availability of a large number of computational algorithms to derive image features, allowing the relationship between aesthetic qualities and these features to be quantified. We refer to this process as aesthetics by numbers.

Previous research into texture perception

Research examining texture perception has, in the visual domain, focused primarily on lower-level texture processing, such as texture segmentation and discrimination (Abbey & Eckstein, 2007; Ben-Shahar, 2006; Bergen & Adelson, 1988; Hollingworth & Franconeri, 2009; Julesz, 1981; Knill, Field, & Kersten, 1990; Landy & Bergen, 1991; Merigan, 2000; Sireteanu, Goertz, Bachert, & Wandert, 2005; Victor, Chubb, & Conte, 2005; Victor & Conte, 1996; D. Williams & Julesz, 1992; Yeshurun, Montagna, & Carrasco, 2008). Studies of higher-level processing of visual textures have focused on judgments of appearance and material properties related to glossiness (Motoyoshi, Shin'ya Nishida, & Adelson, 2007; Pont, 2006), illumination (Pont, 2006), metallic appearance (Motoyoshi, Nishizawa, & Uchikawa, 2007), transparency (Fleming & Bühlhoff, 2005; Watanabe & Cavanagh, 1993), estimated weight (Buckingham, Cant, & Goodale, 2009), roughness (Ho, Landy, & Maloney, 2006), and slipperiness (Lesch, Chang, & Chang, 2008).

The number of studies investigating preferences for texture or features that can be regarded as texture features (Aks & Sprott, 1996; Kawamoto & Soen, 1993; Schira, 2003; Soen, et al., 1987) is greatly exceeded by the vast amount of research that has been devoted to understanding the affective responses to objects. Aesthetics research has often focused on stimuli such as paintings or faces, in which featural information is hard to control, and such control is usually not even attempted. Several studies have found relationships between preference and color features (Ball, 1965; Valdez & Mehrabian, 1994). One study has examined the frequency content of paintings, albeit without relating this aspect to actual beauty judgments (D.J. Graham & Redies, 2010; Redies, Hänisch, Blickhan, & Denzler, 2007).

Evidence for a textural influence on preferences

The small number of studies into the relationships between textural image features and beauty ratings is somewhat surprising, given the many indications in the literature that texture may have an impact on preferences. Such indications come from studies investigating the relationship between preference and the fractal dimension (Aks & Sprott, 1996), entropy (Stamps, 2002), spatial frequency content (Kawamoto & Soen, 1993; Schira, 2003; Soen, et al., 1987) or certain colors (Jacobs, Renken, Thumfart, & Cornelissen, 2010; Valdez & Mehrabian, 1994) of stimuli (usually not textures – but such features are present in textures), as well as from work showing that paintings contain certain spatial frequency characteristics (D. J. Graham & Redies; Redies, et al., 2007). Moreover, texture influences facial attractiveness to a large extent (Jones et al., 2004). In line with the reported relationship between spatial frequencies and beauty ratings, the brain responses to affective stimuli – such as expressive faces – depend on the frequency bands present in the stimulus (Alorda, Serrano-Pedraza, Campos-Bueno, Sierra-Vázquez, & Montoya, 2007; Delplanque, et al., 2007; Holmes, et al., 2005; Vuilleumier, et al., 2003). Moreover, brain centers regarded as emotion processors (such as the amygdala) respond to features such as angularity (Bar & Neta, 2007), which are both object and texture features.

To summarize the above, there are indications that texture features influence beauty ratings. These influences have not yet been systematically investigated. To acquire insight into the features that influence beauty and some other high-level judgments, we decided to embark on an exploratory study investigating the relationships between a large set of texture features and two representative judgments – roughness and beauty. We used the following approach.

Approach – step 1: searching for the relevant judgments

Several authors (Jacobsen, et al., 2006; Mandler & Shebo, 1983) have distinguished between evaluative and descriptive judgments. This distinction seems to be based largely on intuition. Semantic differential studies have repeatedly pointed out some orthogonal dimensions in judgment space, where observers have to judge stimuli, indicating redundancy and underlying structure in the many different possible judgments. We therefore selected relevant dimensions and chose judgments that are representative for these dimensions. Compared to examining the presence of relationships for all the judgments separately, this reduced the number of statistical tests (and thus chance findings). We asked participants to judge textures on a number of aspects, in two separate studies. Factor analysis indicated that two judgments dimensions adequately cover most of the variability in the judgments. We chose beauty and roughness judgments as representatives for these judgments based on their high and exclusive loadings on the evaluative factor (beauty) and the descriptive factor (roughness).

Approach – step 2: searching for the relevant features

Texture features other than the ones mentioned (spatial frequency, entropy, fractal dimension) are potentially relevant for affective responses, but so far these have not been systematically investigated. Because it is hard to predict what other features may prove to be relevant for biasing affective responses, we took an exploratory approach by focusing on many features at the same time. We selected a varied set of visual textures, taken from several sources, in such a way that we covered a large range of values for most of the 188 ($n = 188$) computed features (see methods). Factor analysis was used to remove redundancy from this high-dimensional textural feature space.

Approach – step 3: relating features to judgments

Finally, using linear regression, we determined the relationship between the textures loadings on the feature factors and beauty and roughness judgments.

To anticipate our results, we find that textures varying in intensity, with low spatial frequencies, saturated (red) colors, high intensity, and diagonally oriented elements tend to be rated as beautiful. Textures with low intensity and low uniformity tend to be rated as rough.

Materials and Methods

Participants

There were 19 participants (12 male) in the first study. All of them also participated in the texture selection phase (see supplementary materials, Part II). There were 20 participants (ten male) in the second study. All participants were students in higher education, between 18 and 29 years old.

Stimuli

Texture stimuli (see figure 3.1) were taken from a database containing textures originating from various sources. In the first study, these were presented in their original size (height 3.3 to 31.9 degrees, width 5.7 to 37.1 degrees), and in the second study they were all re-sized 24.2 (width) by 20.2 (height) degrees, by cropping larger textures, or by ‘growing’ smaller textures, using a standard algorithm (Efros & Leung, 1999). Stimuli were displayed on a gray background, into which they blended smoothly (see figure 3.1). Viewing distance was about 70-80 cm. Sixty textures were presented in the first study, and 70 in the second.

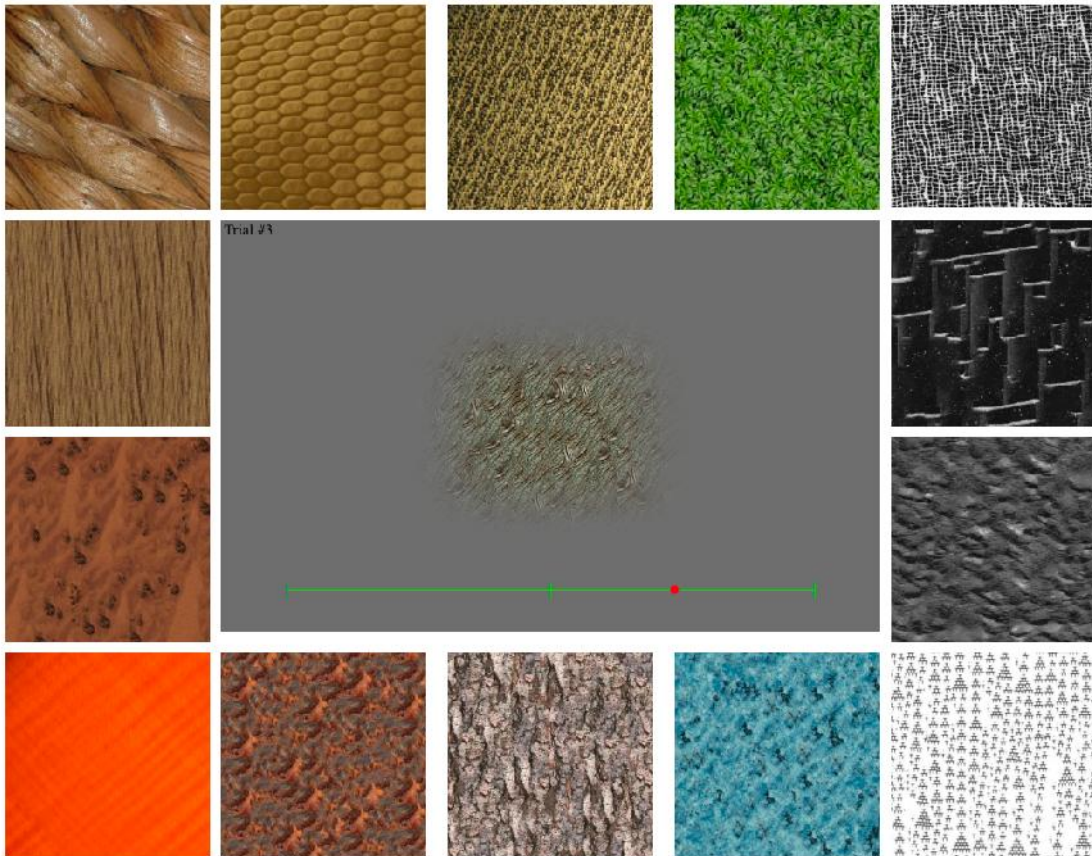


Figure 3.1. Example textures. Thumbnails of textures used in the experiments. The enlargement shows a texture sample, as displayed on screen, with a green slider bar at the bottom.

Feature computation

Computed features are based on Gray-Level Co-occurrence Matrices (Haralick, Shanmugam, & Dinstein, 1973), a set of features related to psychological judgments (Tamura features) (Tamura, Mori, & Yamawaki, 1978), Neighborhood Gray-Tone Difference Matrices (Amadasun & King, 1989), the Fourier spectrum (Laws, 1980; Tuceryan & Jain, 1998), Gabor energy features, and features expressing the presence of colors, brightness, and saturation (Datta, Joshi, Li, & Wang, 2006).

The Tamura features are based on psychological evaluations, and comprise coarseness, contrast, directionality, line-likeness, regularity, and roughness. The Gray Level Co-occurrence Matrices are used to compute statistical properties like entropy, energy, and homogeneity and indicate how often particular gray

levels co-occur at a certain distance. For our purposes, we computed them for distances of 1, 2, 4, and 8 pixels. A Neighborhood Gray Tone Difference Matrix is a vector containing, for each gray level, a sum of the differences in gray tone with all the surrounding pixels, for each pixel with that gray tone. The size of the neighborhood is variable, and we computed matrices for sizes of 3 by 3 and 5 by 5 pixels. Based on these matrices, the features coarseness, contrast, busyness, complexity, and strength were computed.

Fourier features are based on the spatial frequencies in the brightness variations. The extent to which a certain spatial frequency is present is expressed as its energy or power. First, a two-dimensional image is transformed into the frequency domain using the fast Fourier transform, to obtain the Fourier spectrum. Each component of the spectrum is represented by a complex number that describes a frequency in the two-dimensional image by means of amplitude and phase. The component coordinates in the spectrum determine the frequencies wave length and direction. The spatial frequency with highest wavelength (uniform signal, i.e. average brightness) is represented in the centre of the spectrum, while high frequencies can be found on the outside.

The average energy of circular bands around the average brightness was computed for different radii. Also, the energy of wedges with their peak at the average brightness was computed, yielding a measurement of the orientation of the image. In this way, 12 circular energy features and 24 wedge energy features were computed, each reflecting the presence of information at a different spatial frequency (circular rings) and at a different orientation (wedges). In addition, a number of features summarizing their distribution were computed. Similar to Fourier features, Gabor features capture the spatial frequencies in pictures, but they preserve some spatial information. The human visual system is known to contain cells that work as Gabor filters. Gabor 'energy', over the entire texture, was computed for four spatial frequencies, in six orientations. Average saturation and intensity were assessed after converting the image from RGB to HSV color space. The presence of the colors red, green, yellow, cyan, blue, and magenta, was computed by partitioning the hue component of HSV color space into six sectors, and counting the relative frequency of pixels within each sector. The sector frequency was normalized to the average image value and saturation.

We verified that the use of the texture growth algorithm did not affect the feature values by computing the texture features before and after application of the algorithm. The feature values after application of the algorithm were obtained by averaging the feature values over 30 patches of each texture. We determined the percentage of feature values falling outside a range of two standard deviations (the 95% confidence interval) from the original textures, in the distribution of original texture feature values. Across all features and textures, 0.7% of the feature values fell outside this interval, indicating that the feature values were hardly affected by the texture growth algorithm.

Equipment

Stimuli were displayed on a 30'' Apple Cinema HD Display monitor (study 1) or on a 19'' LaCie CRT monitor (study 2).

The programs displaying the textures and recording the responses were programmed in Matlab v7.4 (Mathworks, Natick, Massachusetts), using Psychophysics toolbox (version 3.0.8) extensions (Brainard, 1997). Experiments were run under Mac OS X v. 10.4.10 (Apple, Cupertino, California).

The studies were performed in a room that was completely dark except for the illumination provided by the screen.

Procedure

Two very similar studies were performed, because replications are required for small sample sizes (Guadagnoli & Velicer, 1988). In the first study, textures were selected to maximize differences on our dependent variable, beauty, as explained in the appendix. In the second study, textures were selected to include corners of the feature space. Different textures were used in the two experiments, and a different set of participants judged the textures, but in other respects both studies were similar.

This study conformed to the tenets of the Declaration of Helsinki. The experiments were carried out as part of a psychology bachelor's course. The ethical review board of the Department of Psychology of the University of Groningen approved the study. Participants gave their written informed consent prior to participation. Participating students received course credits.

In a trial, participants were presented with a texture on a computer screen, and were asked to judge it on one of several dimensions. Judgments were made for the following dimensions: beautiful-ugly, smooth-rough, hard-soft, colorfulness, warm-cold, young-old (age), natural-artificial, fuzziness-sharpness, and interestingness-boringness. These dimensions were selected based on results obtained from a pilot study (see supplementary materials). Dimensions were evaluated in separate runs, in random order.

Participants indicated their preference by adjusting the position of a slider at the bottom of the screen (Figure 3.1) by moving a mouse along a bar corresponding to the judged dimension. The poles of the judgments were randomly assigned to either the left or right side of the slider bar. Satisfaction with the judgment was indicated by pressing a mouse button, after which the screen went blank. The next trial started 1000 ms later.

Instructions were given orally, as well as written on the screen, prior to the start of each run. Beauty and naturalness judgments were assessed twice, to assess the consistency of the judgments (see supplementary materials, Part I). All other judgments were assessed once. Presentation order of the textures was random. All textures were presented once in a block.

In the second study, judgments were made for the dimensions beautiful-ugly, smooth-rough, hard-soft, colorfulness, warm-cold, complex-simple, natural-artificial, elegance, and feeling ('How does this texture make you feel?': positive-negative). In this study, we aimed for a larger variation along the feature dimensions in our texture set by selecting textures with extreme values on some features.

Analysis: Pre-processing

The individual judgments, per adjective, were linearly re-scaled to a range between -100 and +100. Next, the average judgments were computed over subjects. For the beauty and naturalness ratings, which were assessed twice per subject in study 1, the two ratings were again averaged.

Analysis: Factor analysis

The resulting scores were subjected to a factor analysis, using Varimax rotation and Kaiser normalization (Kaiser, 1958) in SPSS. The number of factors to be retained was determined by parallel analysis (Hayton, Allen, & Scarpello, 2004; Kaufman & Dunlap, 2000), using 100 permutations of the average judgments about the textures. The eigenvalues exceeding those for the permuted data were taken as indicating factors to be retained.

In both studies, two judgment factors were to be retained, and these were very similar across both studies. We picked beauty and roughness as representative judgments for these two factors, as these judgments loaded strongly and exclusively on one of both factors.

Analysis: Removing redundancy from feature space

To remove redundancy in the textures' feature space, factor analysis was performed on the feature values of the 129 textures used in the experiments. There is no agreed upon method or criterion to decide on the number of factors to retain. We doubled the number of factors indicated by parallel analysis and retained 20 factors.

Analysis: Relationship between features and ratings of beauty and roughness

In order to determine the relationships between features and ratings of beauty and roughness, matrices complementing the feature loadings were computed by multiplying the pseudo-inverse of the rotated feature loadings with the transpose of the feature matrix (the matrix containing the feature values for all used textures), and transposing the outcome. These matrices can be seen as containing the texture loadings, except that these 'loadings' are not constrained to the range of -1 to 1 . We refer to these loadings as texture loadings. Multiple regressions were performed between the beauty and roughness ratings, across both studies, and the texture loadings on the twenty factors.

To determine the relationships between features and ratings of beauty and roughness, we performed regression analyses, once with beauty as the dependent variable and once with roughness. The texture loadings on the feature factors were used as independent variables. This resulted in a regression weight (β), a t -value, and a p -value for each factor on both the beauty and the roughness rating.

Clarification of the factors

The feature factors that are related to beauty or roughness judgments were labeled based on the features loading high on them. To specify the direction of the relationship, which is obscured by rotations occurring in the factor analysis, we took representative features and correlated them directly with the judgments. The signs of these correlation coefficients indicate the direction of the relationships.

Results

Judgments

For the judgments, parallel analysis indicated that two factors should be retained in a factor analysis, both in our first and in our second study. In the first study, the first two factors explained 73% of the variance in the judgments. In the second study, the first two factors explained 76% of the variance in the judgments. The resulting dimensions – and the loadings of the individual judgments on these dimensions (Figure 3.2) – showed that results of both studies were highly similar, despite the involvement of only a limited number of participants, the use of different textures, and the substitution of some judgments by others. In particular, in both studies judgments such as warmth, beauty, and colorfulness loaded strongly on the first factor, while the judgment of roughness loaded strongly on the second factor. Also in both studies, naturalness fell in between, with moderately positive loadings on both factors. Hardness had low loadings on both factors. The other judgments, which were not assessed in both studies, showed that elegance and interestingness had high loadings on the first factor, and that age (young-old) and complexity had high loadings on the second judgment factor.

Factor analysis thus indicated that two judgments dimensions would adequately cover most of the variability in the judgments. We chose beauty and roughness judgments as representatives for these judgments. This choice was based on their high and exclusive loadings on the evaluative factor (beauty) and descriptive factor (roughness).

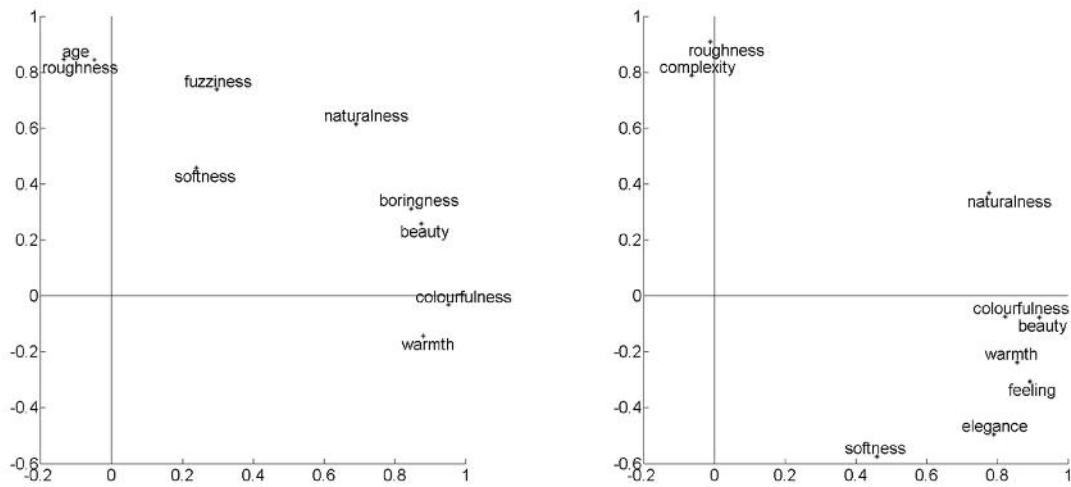


Figure 3.2. Judgments loadings on the varimax rotated factors, for both studies. Two factors were retained. Most judgments load selectively on one of both factors. Results for the first study (left panel) and second study (right panel) are very comparable.

Linear regression between judgments and feature factors

Factor analysis was performed with the 20 feature components explaining most of the variance in the feature values. Subsequently, a linear regression was performed between these twenty feature factors on the one hand, and beauty and roughness judgments on the other, in order to determine which feature factors significantly predicted the beauty and roughness judgments. The 20 factors together explained 63% of the variance in feature values. They explained 59% of the variance in the beauty ratings and 50% of the variance in the roughness ratings. Feature Factors 4, 6, 9, 13, and 17 exerted a significant effect on beauty judgments, and Feature Factors 3 and 9 exerted a significant effect on roughness (Table 3.1).

Correlating judgment	Factor	Features	<i>r</i>	Description
Beauty	4 $r^2 = 0.22$ intensity variation	Mean correlation (d = 8)	0.39	Mean intensity variation of pixel pairs at a distance of 8 pixels Presence of low spatial frequency content in the texture
		C_energy2	0.40	
	6 $r^2 = 0.09$ Gabor frequency	Roughness	0.43	Low spatial frequencies from the Gabor domain, with different orientations
		M_correlation (d = 4)	0.44	
		C_energy3	0.33	
		O2s1	0.11	
O3s1		0.11		
9 $r^2 = 0.04$ intensity	O6s1	0.14	Mean over the average texture intensity; i.e. average texture intensity	
	O5s1	0.15		
	C_energy5	0.03		
	Avg. texture int. (d = 8)	0.18		
	Avg. texture int. (d = 4)	0.18		
13 $r^2 = 0.21$ saturation, intensity	Avg. texture int. (d = 2)	0.19	Range of the weighted sum of the GLCM secondary diagonal entries	
	Avg. texture int. (d = 1)	0.20		
	Average intensity	0.33		
	Average saturation	0.45		
	Degree of redness	0.26		
17 $r^2 = 0.08$ directionality	Regularity	-0.07	Presence of texture elements with orientation 67.5° from vertical Presence of texture elements with orientation 60° from vertical Skewness of the distribution of wedge energy features Presence of texture elements with orientation 52.5° from vertical Presence of texture elements with orientation 70.5° from vertical	
	Average intensity	0.33		
	R_sumVar	-0.39		
	Wedge energy 67.5	0.26		
	Wedge energy 60	0.23		
	Wedge kurtosis	0.00		
Roughness	3 $r^2 = 0.34$ uniformity	Wedge energy 52.5	0.11	Mean over the sum of squared GLCM entries. A measure of uniformity
		Wedge energy 70.5	0.20	
		Mean angular second moment (d = 2)	0.58	
	9 $r^2 = 0.13$ intensity	Mean angular second moment (d = 1)	-0.43	Mean entropy
		Mean angular second moment (d = 4)	-0.45	
		Mean angular second moment (d = 8)	-0.45	
9 $r^2 = 0.13$ intensity	Average intensity	-0.47	Mean over the average texture intensity; i.e. average texture intensity	
	Avg. texture int. (d = 8)	-0.39		
	Avg. texture int. (d = 4)	-0.40		
	Avg. texture int. (d = 2)	-0.40		
	Avg. texture int. (d = 1)	-0.39		

Table 3.1. The feature factors that significantly predicted beauty and roughness ratings. The first column contains the number of the feature factor, and a label attached to these factors, based on the most relevant features. The second column contains the features with the highest absolute loadings on each of the relevant feature factors. The third column gives the correlation coefficients per feature, to confirm the relevance of these features, and to ascertain the directionality of the relationship to the ratings. The fourth column gives a brief description of the features. Factors exerting a significant effect on beauty, at a Bonferroni-corrected two-sided α -threshold of $0.05/20 = 0.0025$ (109 degrees of freedom per test), were Factors 4 ($t = -6.84, p < 0.0001$), 6 ($t = -4.03, p = 0.0001$), 9 ($t = 3.14, p = 0.0022$), 13 ($t = -5.38, p < 0.0001$), and 17 ($t = -3.17, p = 0.0020$). Factors exerting a significant effect on roughness were Factors 3 ($t = -6.90, p < 0.0001$) and 9 ($t = -3.54, p = 0.0006$).

The features loading strongest, whether positively or negatively, on these factors are displayed in Table 3.1. Based on these features, we labeled Feature Factor 4 as a correlation factor, Factor 6 as a low spatial frequency Gabor factor, Factor 9 as an intensity factor, Factor 13 as a saturated redness factor, Factor 17 as a directionality (diagonality) factor, and Factor 3 as a uniformity factor.

The direction of the relationships

To determine the direction of the relationships, and to confirm the findings of our analysis, direct correlations were computed between beauty and the features loading strongly on the feature components that were relevant for beauty. Similarly, correlations were computed between roughness and the features loading strongly on the feature components that were relevant for roughness.

Low spatial frequencies, computed according to Fourier principles (as in Factor 4), were associated with higher beauty ratings. Accordingly, high spatial frequencies computed according to Gabor principles (as in Factor 6) were negatively associated with beauty ratings. Saturation and redness were positively associated with beauty ratings. The presence of diagonal elements in the textures (the wedge energy features in Factor 17) was associated with higher beauty ratings. Uniform textures were rated as smooth or not rough. High average intensity (luminance) led to low roughness ratings.

Discussion

Judgment factors

We found that two judgment factors captured 73% (study 1) and 76% (study 2) of the variance in the judgments. The first factor was associated with the judgments of beauty, elegance, 'feeling', warmth, colorfulness, and interestingness. With the exception of colorfulness, these judgments seem to have an affective or evaluative element in common. The second factor had high and exclusive loadings of roughness, complexity, and age, and seems to be more descriptive in nature. These two factors are orthogonal, so judgments loading exclusively on one component are in general unrelated to the judgments loading exclusively on the other component. The judgments loading high on the same component are highly correlated.

These two judgment factors correspond well to judgment factors obtained in other studies, where different stimuli were employed (Osgood, Suci, & Tannenbaum, 1957; Takahashi, 1995). Such studies typically found an evaluative factor with high loadings of subjective judgments such as beauty, elegance, warmth, and another factor with high loadings of more descriptive judgments such as roughness. These studies labeled these factors as 'evaluative' and 'potency', respectively. We prefer to label the second factor as descriptive rather than potency, a term we borrowed from Jacobsen et al. (Jacobsen & Hofel, 2003).

Relationships between judgments and features

Our main finding is that both beauty and roughness judgments about textures show systematic relationships to visual features present in the textures. Even though individuals differ, there is a common element in beauty judgments across individuals, which can be related to specific features.

As mentioned in the introduction, no systematic investigation of the relationship between texture features and beauty judgments has been performed so far. For this reason, we took an exploratory approach, and used a diverse texture set. We also computed a large set of features to examine their importance for

beauty and roughness judgments. Because so many parameters lead to a loss of degrees of freedom in statistical testing, we reduced feature space to the 20 most important dimensions. Linear regressions showed that these 20 factors explained 59% of the variance in beauty judgments, and 50% of the variance in roughness judgments. We identified five feature factors that significantly predicted beauty judgments: a factor capturing intensity variation, a factor capturing the spatial frequency information, a factor capturing the luminance, a factor capturing the color information (saturation and the degree of redness, mainly), and a factor capturing directionality/diagonality information. We also identified two feature factors that significantly predicted roughness judgments: a luminance factor (the same factor that influenced the beauty judgments) and a uniformity factor.

Previous studies have highlighted relationships between beauty ratings and low spatial frequencies (Kawamoto & Soen, 1993; Schira, 2003; Soen, et al., 1987) or between pleasure and color information (Valdez & Mehrabian, 1994). We have confirmed that these relationships are present, and have extended the findings to patterned stimuli, rather than only completely uniform stimuli. To our knowledge, a relationship between intensity variation and beauty ratings has not previously been reported. The relationships we found between color information and beauty ratings agree with those found by Valdez and Mehrabian in the sense that saturated and intense colors are rated as more beautiful.

Some of the features employed in our study were designed to capture the roughness of textures, as is apparent from their names: roughness and coarseness. Surprisingly, these features appeared to bear little relation to the roughness ratings. Features that emerged with much stronger relationships to the roughness ratings were the uniformity measures, called “angular second moment features” (based on the GLCM). These features should be regarded as reflecting the smoothness-roughness information more effectively than any of the other features that we computed. The other feature factor that emerged was average intensity. A lower average intensity was related to higher roughness ratings. One way to interpret this finding is that weathered, rough surfaces tend to be of low intensity, whereas unscratched, shiny surfaces tend to reflect much light and are rated as smooth.

Limitations of the current study and future directions

We conducted an exploratory study to examine the effects of many features simultaneously. This allowed us to find some features that influence beauty and roughness ratings that have not been reported before. But a limitation of this exploratory approach is that we did not vary certain features systematically, while controlling for the effects of others. Hence, it is possible that the features that grouped together on our feature factors did this not because of an inherent relationship between the features, but because they tend to be grouped together in our stimulus set, possibly because some features tend to co-occur in real life. An example of the latter is our feature factor with high loadings of saturation and redness. Clearly, stimuli can be designed to have unsaturated red, so that the effects of both features can be dissociated. Indeed, an earlier study found that saturation is the main factor influencing preference (Valdez & Mehrabian, 1994), so it possible that saturation rather than redness is the feature responsible for the relationship of our color factor to beauty ratings.

Another limitation of the exploratory approach is that we performed many statistical tests. Although we took care to limit the number of tests by performing data reduction, and we applied corrections for multiple testing, we believe it is advisable to follow up our study with experiments in which the suggested features are varied systematically, controlling for the other features wherever this is possible.

A third limitation of our study is that we made pre-selections of the textures we showed to our participants. In the first study, we selected the most and least beautiful textures, based on a prior rating

study (see Appendix). This manipulation may have filtered out features that have inconsistent relationships to beauty ratings, so that we eliminated noise from our data, giving us enhanced power to demonstrate relationships between the remaining relevant features and beauty ratings. The disadvantage of this approach is that if the experiment would be repeated with a random selection of textures, this noise would not be filtered out, reducing the power to find the associations between features and beauty ratings. Hence, the correlations we report here should not be taken as absolute reflections of the relationships between features and ratings, but rather as indicative of qualitative relationships. A qualitative interpretation of the relationships is even more advisable for the direct correlations between features and ratings, shown in Table 3.1. Because the mentioned features have been pre-selected based on relationships between feature factors and the same beauty and roughness ratings, we are dealing with a circular analysis here, which may lead to inflated results (Kriegeskorte, Lindquist, Nichols, Poldrack, & Vul). Hence, we have reported these correlation coefficients only to indicate the direction of the relationships, not as an absolute measure of the association strength.

Future research should address the role that context plays in determining preferences. Numerous factors could play a role, such as the cultural or professional background of the subjects. Indeed, an initial report on socio-cultural influences on aesthetics ratings has appeared (Y. Zhang, Feick, & Price, 2006), pointing to the malleability of the aesthetic response. The spatial context may also play a role. In our experiments, textures were presented in isolation, always surrounded by a gray background. In real life, textures occur in complex environments. Results might be affected by the presence of such complex backgrounds.

Even though there is evidence that semantics provide a strong cue to preferences (Martindale, et al., 1990), future research into the affective processing of photographs and paintings could take into account the idea that the texture features present in such material may exert a substantial influence on beauty ratings, a possibility that has thus far been overlooked.

This study was designed as an exploratory study. Confirmation of the relationships we have reported is desirable, for example by selectively manipulating the features that we reported as important for beauty and roughness judgments. We would like to stress that our analyses were performed on average data, over groups of subjects. In reality, there is no such thing as an average observer, so it may be worthwhile to investigate inter-individual and cross-cultural differences.

Is beauty in the eye of the beholder?

Philosophers such as Plato (Plato, 2000) and Hutcheson (Hutcheson, 1973) debated about whether beauty is objective and inherent in the objects around us, or whether we impose beauty on the objects around us. As neuroscientists, we believe that beauty is computed by our brains, and is therefore imposed by us on the objects in our environment. Nevertheless, we have found links between stimulus features and beauty, lending support to the view that beauty is also inherent in the objects around us. Prior experience of a person with certain stimuli may influence his or her affective responses to similar stimuli encountered later in life. Our study has revealed that systematic affective responses to certain visual features exist in textures and across subjects. This must be a result of common factors in our ontogeny or phylogeny.

Palmer and Schloss (Palmer & Schloss, 2010) argue that our preferences for colour are based on prior associations of colours with reward outcome. We would like to extend this idea to all features that are relevant for beauty. We do not, however, accept their idea that such associations are mediated by objects, such as the blue sky or blue water. We believe that structures like the amygdala will associate reward outcome with simple features, such as colour, by default. For more complex input, such as faces or other objects, separate associations to reward outcome may be made. But this appears to only be worthwhile

when this outcome deviates from the sum of expected outcome to the different feature values. And we believe this occurs only for a limited range of stimuli.

Acknowledgments

We thank Remy Sijbom, Maarten Schotkamp, Erik de Breij, and Richard Sonnega for conducting the first study and assisting in its analysis. We thank Marieke Timmerman for suggesting multiple mediator models as a suitable analysis method, although this analysis was not part of the final manuscript. The research was supported by a grant from the European Commission, under contract #043157. The present work represents only the authors' view.

Appendix. Selection of textures and adjectives

Two pre-studies were conducted in preparation of the first semantic differential study, reported in the main text, to select the textures and adjectives for use in this study.

In a first phase, subjects ($n = 24$) rated a set of 300 textures for beauty. Based on the average rank order over subjects, the 20 most and least liked textures were selected, as well as 20 from the middle of the range. We previously determined that a selection of the most extreme textures is necessary to get reliable beauty ratings (supplementary materials, part I), and this procedure is likely to enhance our ability to detect influences on beauty ratings.

In the second phase, another group of subjects ($n=17$; 18-28 years) viewed the textures selected in the first phase, and wrote down any words (up to five) occurring to them. In addition, these subjects saw the textures (halved in size) in groups of three textures. Their task was to pick the one that did not belong to the others, and write down why it was different (the 'Minimum Context Card Form' of construct elicitation by triads of elements (Fransella & Bannister, 1977; Kelly, 1955)). A count was made of the occurrence of words, and similar words were grouped together to arrive at the words that were most often used. The results are displayed in table 3.2. The words occurring most often were selected for the first study reported in the main manuscript.

METHOD

Participants

12 male and 12 female subjects participated in the first part of the experiment. In the second part, a different set of 17 participants took part.

Stimuli

From a large database (available on request), taken from various sources, a pre-selection of 300 textures was made, based on criteria such as the absence of object outlines, elimination of very similar textures, and a random selection of what remained. The visual angle ranged from 3.27 to 31.89 degrees in height, and from 5.7 to 37.1 degrees in width.

Procedure

In the first phase, textures were presented one by one, and subjects were requested to move the slider, and to indicate their judgment by clicking at the desired location (right = beautiful; left = ugly/not beautiful), upon which the next texture would appear. They were asked to use the entire range of the slider, and to not necessarily regard the central point as being 'neutral'. In order to give a sense of the range of stimuli they would see, and to practice the procedure, some trials were performed by the subject before the actual start of the experiment. Subjects were asked to respond based on their first impression. Subjects performed the test individually.

In the second phase, subjects performed the test in groups of up to five subjects, being seated between two and three meters from the screen.

They took down their responses on paper, and the experiment leader paced the task according to the speed of the group. The 'word association round' always preceded the round in which triads of textures were presented. Both in the word generation task and in the triad task each picture was presented exactly once.

The texture selection round was performed in a completely dark room, except for the illumination provided by the screen. The adjective generation round was performed in a dimly lit room, to allow subjects to write down their responses.

Equipment and software

Experiments were run on a MacBook pro under Mac OS X v. 10.4.10 (Apple, Cupertino, California), using Matlab v7.4 (Mathworks, Natick, Massachusetts) with psychophysics toolbox extensions (Brainard, 1997). Stimuli were presented on a 30" Apple Cinema HD Display monitor.

RESULTS

The first study phase yielded a rank ordering of the 20 most and the 20 least liked textures, as well as 20 from the middle of the range. Four of each are displayed in figure 3.3.

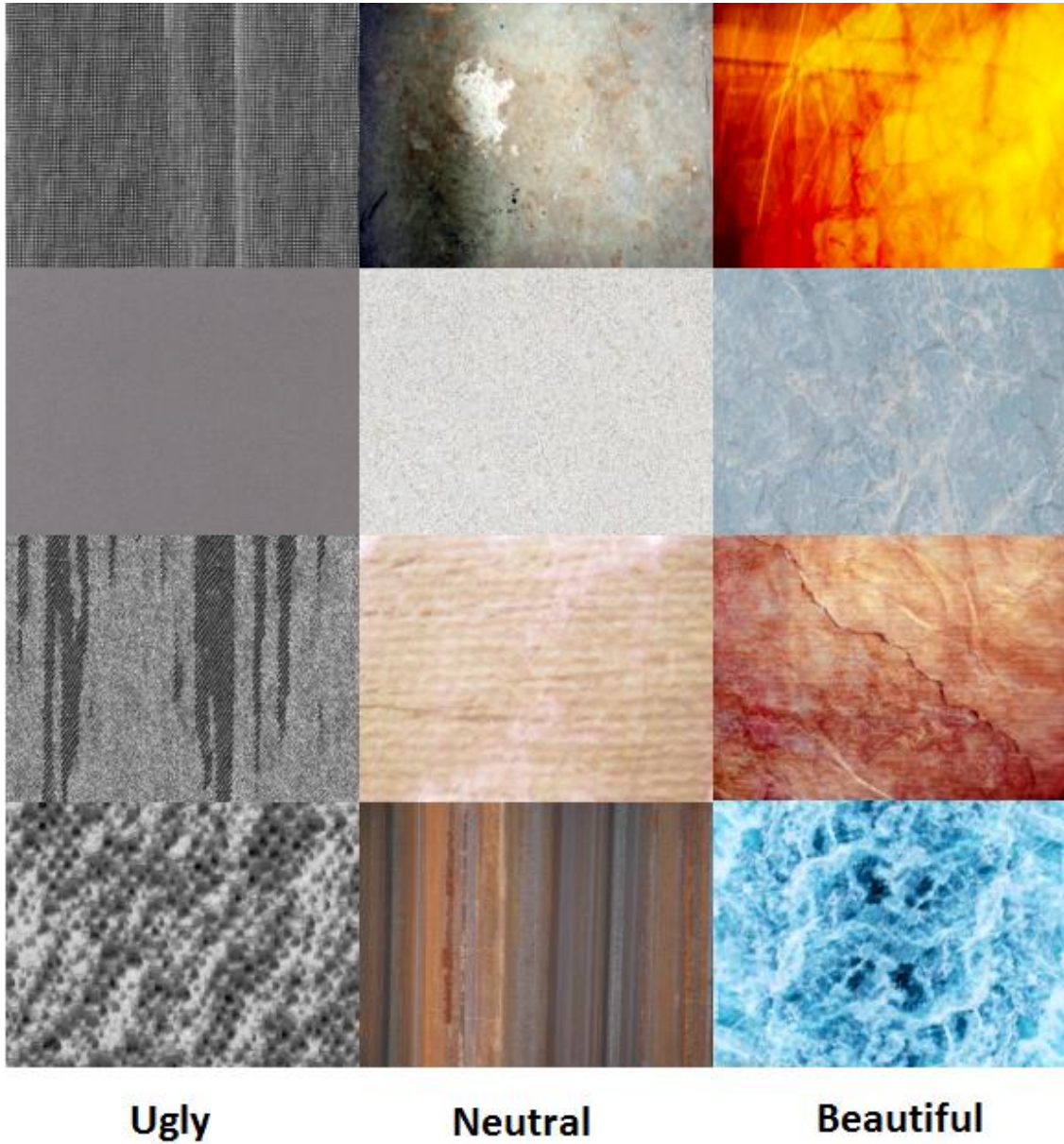


Figure 3.3. Examples of liked, disliked, and 'neutral' textures, based on their rank order in the texture selection phase.

The second study phase yielded a list of words, which is tabulated in Table 3.2, grouped according to a consensus judgment between four experimenters. For the most mentioned groups, one representative

adjective was chosen for use in the third phase. Words relating to contrast and luminance were not taken into the study, because it was thought they would relate too obviously to their computed counterparts.

Generated adjectives		
adjectives	adjectives	Word count
Ugly	<i>beautiful</i> , gorgeous	63
<i>Smooth</i> , flat, slender	<i>rough</i> , hefty, granular	82
<i>cold</i> , chilly, cool, not sunny	<i>warm</i> , sunny, cheerful, summertime, happy	172
<i>soft</i> , not hard	<i>hard</i>	40
Dark, unlit, night	light, bright	318
<i>boring</i>	<i>Exciting</i> , snazzy, snappy, touching, thrilling, interesting	22
not artistic	artistic, picturesque, skilful	7
not much color, black-white, faint, <i>colourless</i>	<i>colourful</i> , fierce colours, colour shades	235
<i>old</i> , outdated, antique	<i>young</i> , new	47
<i>fuzzy</i> , unclear, undefinable	not vague, <i>sharp</i> , clear	179
<i>artificial</i>	<i>natural</i>	78
irregular	regular	8
little contrast	a lot of contrast	37

Table 3.2. Words generated in the adjective generation phase. Words are grouped together according to similarity, as judged by the experimenters. The extremes of the relevant dimension are arranged in different columns, with a third column mentioning the number of times they were mentioned. Words selected for use in the actual study are italicized.

CONCLUSION

Textures were selected based on beauty ratings. There seems to be a trend for liked textures to be more colourful than disliked textures.

Participants generated many different words, which could be grouped into categories without much disagreement between experimenters. The words generated contained not only many descriptive words, like rough and hard, but also many subjective words, such as boring, artistic, beautiful, warm, and cheerful.

Based on the word counts and the beauty ratings to textures, a selection of textures and adjectives was made for use in the main study.

DISCUSSION

Rao and Lohse (Ravishankar Rao & Lohse, 1996) used a different technique to identify relevant dimensions for texture perception: Subjects grouped textures into categories of their own choice. The data were analyzed using multidimensional scaling and hierarchical cluster analysis. Based on this, they identified the dimensions of repetitiveness-irregularity, directionality, and simplicity-complexity as important for texture perception. It is striking that our subjects did not spontaneously generate words pertaining to these dimensions, except for regularity, which seems highly similar to repetitiveness. But even regularity was mentioned only eight times in our study. From the other side, it is striking that Rao and Lohse did not identify components relating to more subjective aspects, such as beauty, warmth, and naturalness.

What may underlie the differences between the adjectives we obtained, and the dimensions obtained by Rao and Lohse?

A first possibility is the difference in methodologies. We had subjects generate words, while Rao and Lohse had subjects classify textures, without an explicit reference to words or adjectives. For this categorization, subjects need not have the vocabulary to make a distinction, while for labeling they do. Possibly, subjects use more 'objective' criteria, in the sense of higher inter-subject agreement, for categorizing textures than for labeling them.

A second possibility is a difference in subject pools. We did not explicitly ask subjects for their studies, but as most were recruited from a psychology subject pool, they are likely to have studied psychology, which may bias the adjectives to be more subjective. We may have strengthened such a bias by recruiting subjects through an advertisement mentioning 'an emotional study'.

A third possibility lies in the different stimulus sets used: Rao and Lohse used thirty textures from the Brodatz album, which are limited in that they are all grey-scale pictures, and most of the repetitive textures have horizontal and/or vertical orientation. Colour or colourfulness might be an important factor eliciting more subjective qualifications, like beauty, as might be inferred from our main study, where both beauty and colourfulness judgments load highly on the same component. We used a much broader set of textures, which included Brodatz textures, but also a lot of other textures, obtained from commercial or other websites. From this large set, we had made a pre-selection based on beauty ratings, which is highly likely to have biased responses to those that are related to differences in beauty judgments. We think we have effectively filtered out the dimensions that are irrelevant for beauty, at least partly, which is good for our purpose of explaining beauty.

Chapter 4.

Neural correlates of visual aesthetics – beauty as the coalescence of stimulus and internal state

Richard H.A.H. Jacobs^{1,2}

Remco Renken^{1,2}

Frans W. Cornelissen^{1,2}

How do external stimuli and our internal state coalesce to create the distinctive aesthetic pleasures that give vibrance to human experience? Neuroaesthetics, the study of the neural representation of the human sense of aesthetics, has so far focused on the neural correlates of observing beautiful stimuli compared to neutral or ugly stimuli, or on neural correlates of judging for beauty as opposed to other judgments. Our group questioned whether this approach is sufficient. In our view, a brain region that assesses beauty should show beauty-level-dependent activation during the beauty judgment task, but not during other, unrelated tasks. In our study we therefore performed an fMRI experiment in which subjects judged visual textures for beauty, naturalness and roughness. Our focus was on finding brain activation related to the rated beauty level of the stimuli, which would take place exclusively during the beauty judgment task. An initial whole-brain analysis did not reveal such interactions, yet a number of the regions showing main effects of the judgment task or the beauty level of stimuli were nevertheless selectively sensitive to beauty level during the beauty task. Of the regions that were more highly activated during beauty judgements than roughness judgments, the frontomedian cortex and the amygdala demonstrated the hypothesized interaction effect, while the posterior cingulate cortex did not. The latter regions, which only showed a task effect, may play a supporting role in beauty assessments, such as attending to one's internal state rather than the external world. Most of the regions showing interaction effects of judgment and beauty level correspond to regions that have previously been implicated in aesthetics using different stimulus classes, but based on either task or beauty effects alone. The fact that we have now shown that task-stimulus interactions are also present during the aesthetic judgment of visual textures implies that these areas form a network that is specifically devoted to aesthetic assessment, irrespective of the stimulus type.

Keywords: Neuroaesthetics; functional magnetic resonance imaging; beauty; roughness; naturalness; visual textures; bottom-up; top-down; semantic differential; evaluative; descriptive; visuo-tactile; frontomedian cortex; amygdala; posterior cingulate cortex; supramarginal gyrus.

Affiliations:

1. Laboratory for Experimental Ophthalmology, School for Behavioral and Cognitive Neurosciences, University Medical Center Groningen, University of Groningen, PO Box 30001, 9700 RB Groningen, the Netherlands

2. BCN NeuroImaging Center, School for Behavioral and Cognitive Neurosciences, University Medical Center Groningen, University of Groningen, PO Box 30001, 9700 RB Groningen, the Netherlands

Introduction

How do external stimuli and internal state coalesce to create the distinctive aesthetic pleasures that give vibrance to human experience? The answer to this question can be found in the brain, that delicate machine that assumes different states reflecting our moods and intentions, and that processes the information impinging on our senses. Neuroaesthetics research is concerned with the neural basis of our aesthetic experiences, in particular the experience of beauty. Neuroimaging techniques make it possible to investigate brain activation associated with our processing of sensory information and with the ensuing experiences.

In recent years, several studies have been performed to investigate the neural correlates of human aesthetic experience. This research has taken two approaches: 1) The investigation of neural correlates of beauty level, i.e. brain regions that differentiate between beautiful and ugly stimuli that were presented to participants, and 2) The investigation of beauty judgment as opposed to other judgments.

However, we believe the most interesting question in this type of research is the following: where does the beauty assessment actually take place? Is it where the brain differentiates between the different beauty levels? This is unlikely. Beauty judgments are largely predictable from the features that are present in the stimuli. Because of this relationship between beauty and features, the observed brain activations may be caused by the processing of these features, rather than by the experience of beauty itself.

Studies examining the effects of stimulus beauty have reported many different brain regions, including the occipital and premotor cortex (Calvo-Merino, et al., 2008), the fusiform gyrus (Vartanian & Goel, 2004), the ventral tegmentum, the amygdala and the nucleus accumbens (Aharon, et al., 2001), and the orbitofrontal and motor cortex (Kawabata & Zeki, 2004). In the tactile domain (where pleasantness rather than beauty ratings were given), the orbitofrontal cortex, rostral anterior cingulate cortex, and amygdala (E. T. Rolls, et al., 2003) have been reported. These divergent findings may be explained by the processing of beauty-related features in the different stimuli, and may be less related to beauty aspects themselves. Instead, we could compare the activations related to different judgments, which we believe is a more plausible approach. We would certainly expect a brain region involved in beauty assessment to be more active during the judgment of beauty than during other types of judgment. The posterior cingulate and frontomedian cortex have been reported to be more highly activated during beauty judgements than during symmetry judgments (Jacobsen, et al., 2006). But we would also expect a beauty assessment to result in a response that differentiates between beautiful, neutral and ugly stimuli. In other words, we would expect an interaction between the type of judgment and beauty level in regions that are truly involved in making a beauty assessment. Brain regions merely differentiating between judgments – and not between beauty levels – may support the beauty assessment, but without actually performing the beauty assessment itself.

We identified three problems in the current literature on neuroaesthetics. The first is a focus on the main effects of judgment, which does not necessarily reflect the beauty assessment itself, as explained above.

The second problem is that the control task used as a baseline for the beauty assessment may not have been chosen adequately. In the only experiment we found that focused on differences between judgments (Jacobsen, et al., 2006), symmetry judgments were chosen as a baseline, on the grounds that symmetric stimuli are usually judged to be more beautiful. But by employing such a similar control task, the experimenter runs the risk of factoring out some of the processes that are relevant for making a beauty assessment. By choosing a more dissimilar task, while at the same time looking specifically at the interaction of judgment and beauty level, we believed that we would have a better chance of capturing the beauty assessment itself.

The third problem in the literature is that beauty level is confounded with features in the stimulus, as explained above. A related problem is that many different stimuli have been employed. The use of different

stimulus types may explain the divergent findings, because of the different features in the stimuli, or because of the different associations people have with the complex stimuli, such as paintings.

To address the above issues, we designed an experiment in which we first varied both the beauty level of stimuli and the type of judgment, in a single paradigm. Second, we employed a control task that is sufficiently different from a beauty judgement to make sure that we are not factoring out some crucial common elements. To this end, we employed a roughness judgment, which has been shown in a semantic differential study to be orthogonal to beauty judgments (Jacobs et al., 2011). Third, we employed visual textures as stimuli because they do not elicit many semantic associations. Moreover, these visual textures were individually selected for their beauty, so that the effects of beauty were enhanced. Due to individual differences in preferences, the effects of some (though probably not all) features would be levelled out. Fourth, by looking at interactions between beauty level and the type of judgment, we assumed we would capture brain regions involved in making beauty assessments per se, rather than regions responding merely to features that happen to be associated with beauty, or brain regions that merely support the making of beauty assessments, but without performing the actual assessment itself.

Method

Participants.

Ten men and eight women (age: 20-39), all right-handed, participated in the study. All had normal or corrected-to-normal visual acuity and gave their written informed consent according to procedures approved by the Medical Ethics Committee of the University Medical Center Groningen, the Netherlands.

Stimuli.

The stimuli were visual textures, which we defined as repetitive patterns in which no single object outline can be discerned. For current purposes, we take colour to be an integral part of textures. Textures were collected from various internet sources (<http://www.fundermax.at/>, <http://www.ux.uis.no/~tranden/brodatz.html>, <http://www.textureking.com/>, <http://inobsuro.com/textures/>, <http://textures.forrest.cz/>). Stimulus sizes were standardized, using cropping to reduce the size of large textures, and a texture growth algorithm to enlarge small textures. Example of textures are shown in Figure 4.1.

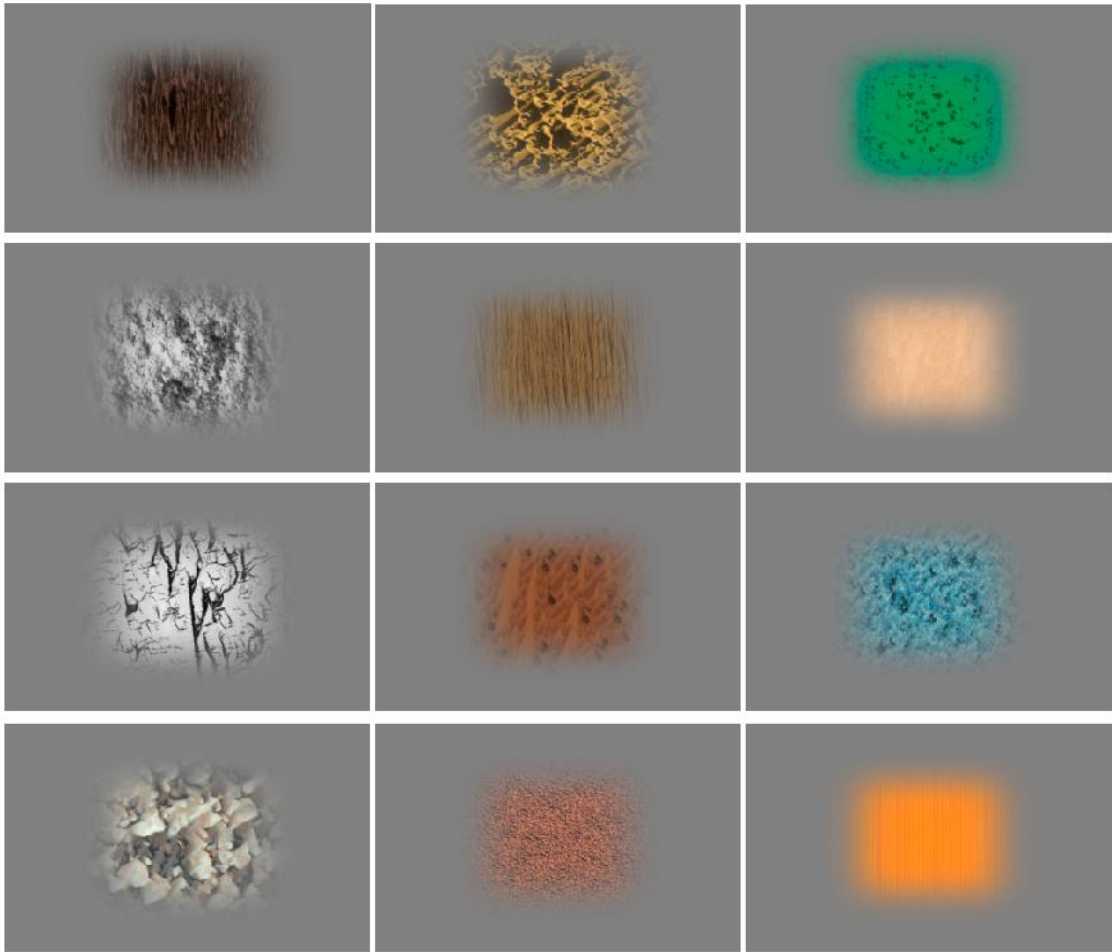


Figure 4.1. Example of textures used in the experiment. Textures were presented against a grey background. Computer-generated and photographed textures were used, some coloured and others in greyscale.

Stimulus presentation

In the initial texture selection procedure, stimuli were presented on a 30'' Apple Cinema HD Display monitor and were shown at a visual angle of about 22 x 22 degrees (viewing distance 70 cm), on a grey background (see figure 4.1) with a mean luminance of 55 cd/m².

In the fMRI scanner, stimuli were back-projected onto a translucent screen (44 x 34 cm) using a Barco LCD Projector G300 (Barco, Kortrijk, Belgium) set at a resolution of 800 x 600 pixels. The translucent screen subtended a visual angle of 32 x 25.5 degrees. Textures were presented at a size of about 13 x 13 degrees, on a grey background (see figure 4.1) having a mean luminance of 3260 cd/m². Stimuli were presented in Matlab (MathWorks, Natick, MA) with the Psychtoolbox (<http://psychtoolbox.org/>) extensions (Brainard, 1997; Pelli, 1997) using an Apple Macbook Pro (Apple, Cupertino, CA).

Texture selection

For each subject, the texture stimuli were selected from a collection of 436 textures based on a separate rating experiment. In this experiment, textures were presented one-by-one, and rated for beauty by moving a slider along a bar at the bottom of the screen. Based on the subject's judgment, the 12 textures judged least beautiful (negative valence) and the 12 judged most beautiful (positive valence) were selected, as well as 12 from the middle of the judgment range (neutral valence). These selected textures were used as stimuli in the functional magnetic resonance imaging (fMRI) experiment.

fMRI-procedure

In the fMRI experiment, subjects performed three runs. During each run they judged textures for their beauty, naturalness and roughness. At the beginning of a run a fixation period lasting 30 s was presented.

Judgments were grouped into blocks of six trials and interleaved in pseudo-random order within a run. Within each judgment block, textures with positive, neutral and negative valence were presented in random order. During an entire run, each texture was presented only once for each judgment condition. Hence, during each run, all 36 textures were presented once for each type of judgment (for a total of 108 trials per block). Each texture was presented for 4000 ms (ISI = 1000 ms), during which the subject could indicate his or her judgment by pressing one of three buttons on a fibre-optics response pad (Current Designs Inc., Philadelphia, USA). Depending on the judgment condition, the buttons' meaning corresponded to beautiful, neutral and ugly (beauty judgment), or rough, neutral and smooth (roughness judgment), or natural, neutral and artificial (naturalness judgment).

Scanning parameters.

The scanner was a 3 T Philips Intera (Best, the Netherlands) with a sense-8 head coil. It was used to acquire T1 anatomical volume images (256x256 matrix, 160 slices, voxel size 1x1x1 mm) and T2*-weighted echo-planar images with blood oxygenation level-dependent contrast (64x64 matrix, voxel size 3.5x3.5x4 mm (no gap), TR = 2500 ms, TE = 28 ms, Field of View 224x224). Each echo-planar image consisted of 40 slices, acquired in descending order, positioned to cover the whole brain, except the cerebellum.

Data analysis.

Analysis was performed in BrainVoyager version 1.8 (Brain Innovation B.V., Maastricht, the Netherlands). A 2 x 2 model was specified at the individual level, with judgment conditions "beauty-roughness" and "beauty-naturalness", and beauty levels "beautiful-neutral" and "beautiful-ugly". Every trial was modelled as an event lasting 4 s. Activation levels of all runs were Z-transformed before 2nd level analysis. A full-brain analysis was performed, with contrasts between the judgments and the beauty levels. Their interaction was also analysed. Activation to ugly-neutral stimuli and to roughness-naturalness judgments could be inferred by taking differences between the other contrasts.

Significance was thresholded at an alpha of 0.001 per voxel, with a minimum cluster size of 21 functional voxels (corresponding to 1029 mm³). This was done to achieve a corrected threshold of 0.05 for

falsely reporting a positive result, as determined by the AlphaSim-tool (B.D. Ward, <http://afni.nih.gov/afni/docpdf/AlphaSim.pdf>).

In addition to this full-brain analysis, region-of-interest analyses were performed on the regions showing effects of task (beauty versus roughness) and beauty level (beautiful versus ugly), where we looked for interaction effects between task and beauty level within these regions at a significance threshold of 0.05.

Results

The regions activated in our contrasts are shown in Table 4.1.

Contrasts between the judgments

Regions that were activated more strongly during beauty judgments than during roughness judgments included the frontomedian cortex, the posterior cingulate cortex, and the amygdala (see figure 4.2). Regions that were more active in the opposite contrast, roughness-beauty, involved the supramarginal gyrus, the frontal operculum and the fusiform gyrus. Activation related to naturalness judgments generally was not significantly different from either of the other judgments, with the exception of the supramarginal gyrus, where activation was lower for naturalness than for the other two judgments.

Contrasts between beauty levels

The secondary visual cortex (Brodmann area 18/19; middle occipital and fusiform gyrus) was more active to positively valenced textures than to negatively valenced ones. No regions responded more strongly to the negatively valenced textures, and contrasts involving the neutral textures yielded no activations.

Interactions between valence category and judgment condition

In the full-brain analysis, there were no brain regions displaying interaction effects at an uncorrected significance level of $p < 0.001$. Region-of-interest analyses in the regions displaying main effects of judgment showed that there were interaction effects in the amygdala ($t = -2.260$, $p = 0.024$) and the frontomedian cortex (ventral cluster $t = -2.227$, $p = 0.026$; dorsal cluster, $t = -2.50$, $p = 0.012$). Within the regions responding to beauty level, both the lateral cluster ($t = -2.707$, $p = 0.007$) and the medial fusiform cluster ($t = -2.899$, $p = 0.004$) showed significant interaction effects. These effects are visualized in figure 4.3, which also shows the effects of neutral stimuli and the naturalness judgments; it can be seen that the interactions between beauty level and type of judgment were qualitatively different for the regions responding to the main effect of judgment, when compared to the regions responding to the main effect of beauty level. The regions responding to the main effect of judgment showed stronger responsivity to beauty level during beauty judgments, and the differences were particularly pronounced for the beautiful stimuli. However, the regions responding to the effect of beauty level did not show such a clear pattern, with differences between the judgments being at least as pronounced for the ugly as for the beautiful and neutral stimuli.

Contrast	Talairach coordinates	Cluster size (mm ³)	Brodmann Area	Region	Interaction
beauty-roughness	-2, 63, 21	3043	10	frontomedian	$p < 0.05$
beauty-roughness	-2, 57, 38	1863	9	frontomedian	$p < 0.05$
beauty-roughness	-24, -2, -17	662		L amygdala	$p < 0.05$
beauty-roughness	-4, -49, 20	4806	30/31	posterior cingulate	<i>n.s.</i>
roughness-beauty	-45, 4, 22	1204	44	frontal operculum	<i>n.s.</i>
roughness-beauty	-50, -38, 40	5770	40	supramarginal gyrus	<i>n.s.</i>
roughness-beauty	-56, -58, -7	1166	37	occipitotemporal cortex	<i>n.s.</i>
positive-negative	-34, -44, -19	1924	cerebellum	culmen/fusiform gyrus	$p < 0.05$
positive-negative	-44, -75, -10	2708	18/19	visual cortex, middle occipital & fusiform gyrus	$p < 0.05$

Table 4.1. Activation clusters in the contrasts between the judgments and the different beauty levels of the stimuli, and their interactions.

The Talairach coordinates correspond to the centre-of-mass of the cluster. The cluster size is shown along with the Brodmann area and the name of the brain region. The last column indicates which clusters showed significant interaction effects in ROI analyses. *N.s.* = non-significant.

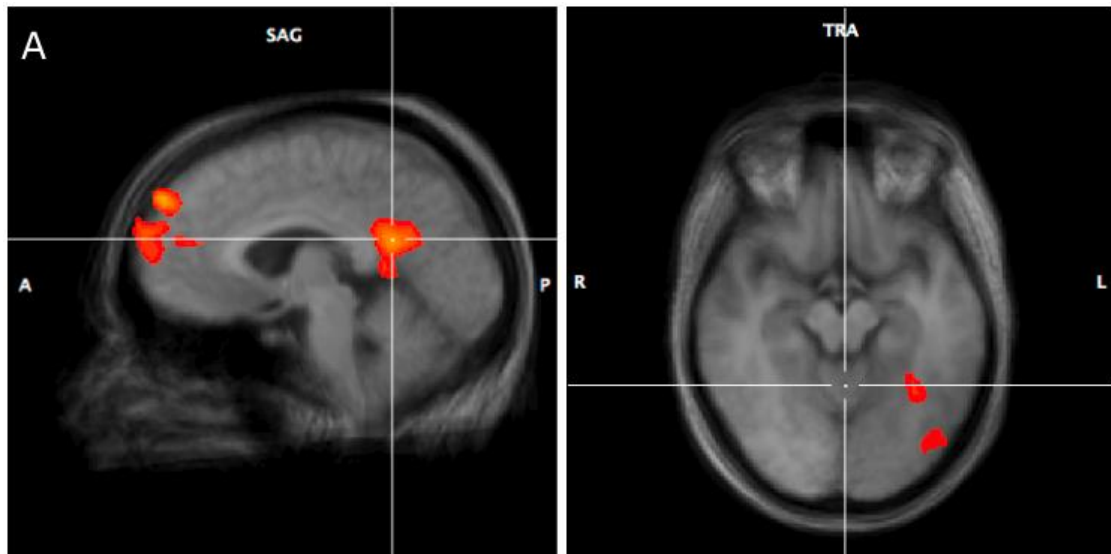


Figure 4.2. Examples of activation in the main contrasts.

A. Comparison of activation during beauty versus roughness judgments shows signal increase in the frontomedian and posterior cingulate cortices.

B. Comparison of activation for beautiful versus ugly stimuli shows signal increase in two clusters in the fusiform gyrus. Activation is presented for $p < .001$, uncorrected for multiple comparisons.

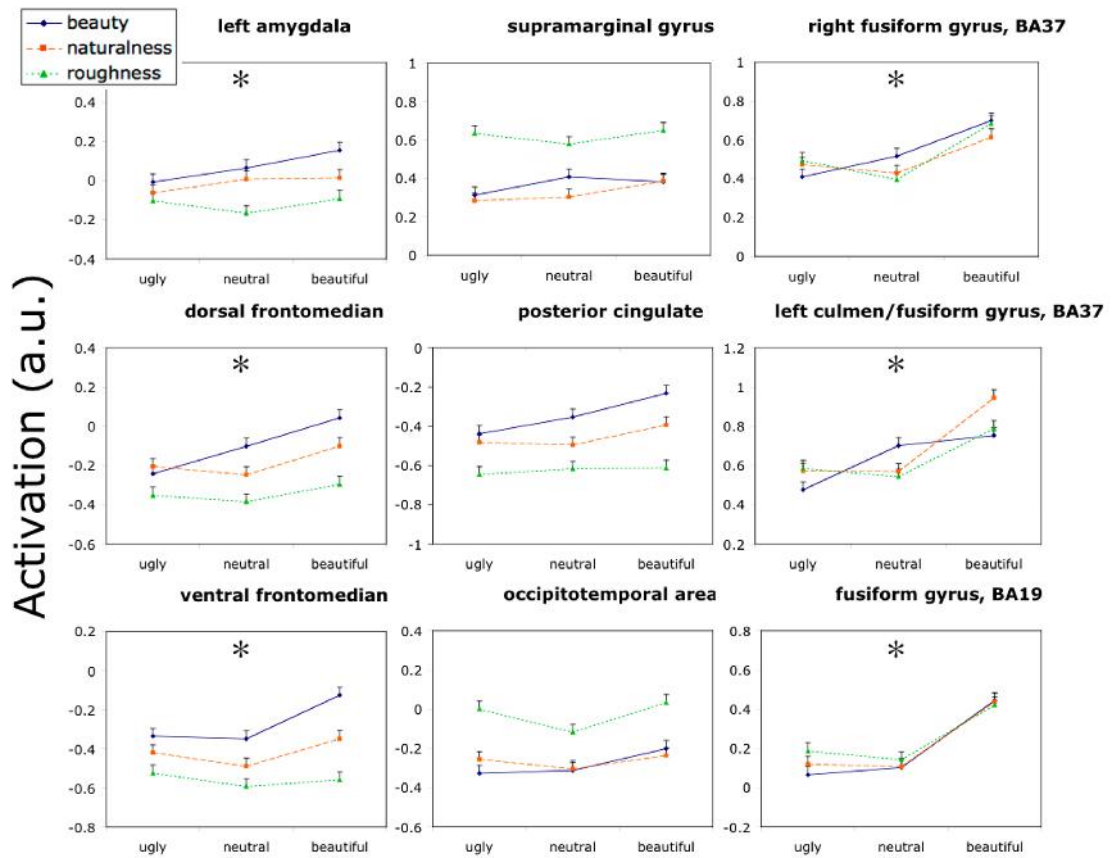


Figure 4.3. Activations in response to beautiful, neutral and ugly textures during beauty, naturalness and roughness judgments. Most regions-of-interest demonstrate significant interactions between beauty versus roughness judgments and beautiful (positive) versus ugly (negative) textures, as indicated by asterisks (*). Error bars indicate the standard error of the mean.

Discussion

We were interested in brain activation related to the evaluative and descriptive judgment dimensions, as exemplified by beauty judgments (evaluative) and roughness judgments (descriptive), and related to differences in level of beauty. We were particularly interested in the interaction between judgment and beauty level, as this appeared to us to be the strongest indication that a region is truly involved in making a beauty assessment.

Beauty levels

Contrasts between beautiful, neutral and ugly stimuli showed that the beautiful-ugly distinction was made only in two visual cortex clusters – regions that are distinct from the frontomedian and posterior cingulate cortices involved in making a beauty assessment. The coordinates (-44, -75, -10) of one of these clusters are an almost perfect match to those reported for preferred paintings in the fusiform gyri (-46, -74, -8, after conversion to Talairach coordinates) (Vartanian & Goel, 2004). Since this is a visual region, its activation in response to beautiful stimuli may be a consequence of increased attention to the beautiful textures. However, the region does not coincide with texture regions reported in a paradigm that focused on texture, as opposed to colour and shape (J. S. Cant & Goodale, 2007). We conjecture that this region is responding to some low-level features in the textures that are associated with higher beauty ratings. For example, the presence of low spatial frequencies leads to higher beauty judgments (Jacobs et al., 2011). Low frequencies are also characteristic of objects, as opposed to texture information, and the coordinates are close to the coordinates for a region that was more highly activated when attention was paid to object shape (J. S. Cant & Goodale, 2007).

Evaluative brain regions

The contrast between beauty and roughness judgments should reveal the evaluative brain regions. Our study has indicated that the frontomedian and the posterior cingulate cortex are the evaluative regions. This finding agrees with previous studies comparing evaluative to non-evaluative judgments (Jacobsen, et al., 2006; Zysset, Huber, Ferstl, & von Cramon, 2002). This agreement was especially striking because these other studies did not base their choice of judgments on semantic differential findings and the nature of the judgments (moral judgments) and the stimuli (sentences) was radically different in one them (Zysset, et al., 2002). This suggests a very general role for these regions in evaluative processing.

With regard to the posterior cingulate cortex, its role may not be the assessment of beauty itself. This is because interactions between judgment and beauty level – as described above for the orbitofrontal cortex – are more indicative of such a role, and such interactions were not found in this region. The posterior cingulate region may instead provide a more general supportive function, such as directing attention to the inner world, as opposed to the external world (i.e., self-reference, D. A. Gusnard, E. Akbudak, G. L. Shulman, & M. E. Raichle, 2001; Johnson et al., 2002; Kelley et al., 2002). In fact, pleasantness ratings have been used to investigate internally cued, self-reference conditions (D. A. Gusnard, et al., 2001). The frontomedian cortex, a brain region that often responds in a similar way as the posterior cingulate cortex, was sensitive not only to interaction between beauty and roughness judgments, but also to beautiful-versus-ugly stimuli. This pattern suggests that this region may truly be involved in assessing beauty, or evaluative aspects in general.

Descriptive brain regions

We assumed that the contrast between roughness and beauty judgments would reveal the regions that are recruited more for making descriptive judgments; our results indicated that these regions are the frontal operculum, the supramarginal gyrus, and the fusiform gyrus. However, the supramarginal gyrus did not meet the additional requirement of the naturalness judgments leading to intermediate activation. In most

regions, naturalness did not differ significantly from either of the other judgments, but in the supramarginal gyrus, naturalness judgments were associated with significantly less activation than the other judgments. Hence, the frontal operculum and the fusiform gyrus remain as candidate brain regions for processing descriptive judgments.

The supramarginal gyrus is generally recognized as secondary somatosensory cortex. As such it may not be surprising that it is involved in making roughness assessments. But its involvement in making roughness assessments of visually presented textures is surprising. Previous studies have reported visual cortical areas engaging in analysis of tactile stimuli (L. Merabet et al., 2004; L. B. Merabet et al., 2007; Sathian, 2005; Sathian & Zangaladze, 2002; Sathian, Zangaladze, Hoffman, & Grafton, 1997; M. Zhang, Weisser, Stilla, Prather, & Sathian, 2004), but to our knowledge the present study is the first report of a tactile region engaging in analysis of visual stimuli. We conjecture that this activation occurs when subjects imagine touching the visually presented stimulus and imagine the roughness sensations associated with it. However, this does not explain why activation during a naturalness judgment should be lower than during a beauty judgment. Figure 4.3 indicates that this is much smaller than the difference between roughness and the other judgments, so we should not place too much importance on the difference between beauty and naturalness judgments in this region.

Interactions between beauty level and judgment type

Interactions between judgment type and beauty level point to beauty assessments resulting in beauty outcomes. A full-brain analysis did not highlight any regions displaying such interaction effects. Region-of-interest analyses on the clusters that appeared in the main effects of beauty-versus-roughness judgments and beautiful-versus-ugly stimuli indicated that many of these regions indeed show interaction effects between these two contrasts. This means that these clusters may be involved in beauty assessments. The fusiform gyrus, the amygdala and the frontomedian cortex all showed interaction effects. For the amygdala and the frontomedian cortex, these interactions consisted of stronger responses to beauty level during the judgment of beauty. This pattern is highly suggestive of involvement in beauty assessments.

In line with the amygdala finding, the only other study that looked at both beauty judgment and beauty level (Di Dio, et al., 2007) reported that the right amygdala is more active to beautiful stimuli under explicit evaluation conditions. One other study reported that amygdala activation increased in response to positive names (e.g. Mother Teresa) when subjects evaluated positive aspects of famous people, and to negative names (e.g. Adolf Hitler) when they evaluated negative aspects of famous people (W. A. Cunningham, Van Bavel, & Johnsen, 2008). These findings provide further support for our contention that the amygdala is involved in making beauty assessments.

The semantic differential as a basis for functional neuro-imaging

If the other studies investigating evaluative judgments had employed semantic differential studies on their judgments, they might have found their judgments to be orthogonal. We believe that showing the distinctness of the judgments empirically adds to the interpretability of the findings. It also suggests generalizability over other judgments loading on the same components, such as warmth, interestingness and colourfulness for the evaluative dimension, even though such generalizability remains to be demonstrated. In fact, Jacobsen et al. (2006) may have chosen judgments loading on the same component, as they chose their symmetry and beauty judgment because they were correlated, and correlated judgments are likely to load on the same component. This highlights a way of further validating the semantic differential basis for distinguishing evaluative from non-evaluative processing, and distinguishing it from less empirically based

approaches: There are cases in which the semantic differential studies point to a judgment, such as colourfulness, as being evaluative in nature (Jacobs et al., submitted), even though this is contrary to intuition and the assumptions in the other approaches. It would be interesting to see if colourfulness judgments would be associated with brain activation patterns similar to beauty and other evaluative judgments, which the semantic differential approach predicts, or to roughness and other non-evaluative judgments, which other approaches would predict.

Another prediction of the semantic differential approach would be that naturalness judgments should lead to activations intermediate between beauty and roughness judgments; semantic differential studies show that naturalness judgments fall in between these other two judgments in judgment space (Jacobs et al., 2011). Although we generally did not find significant differences between naturalness and the other judgments in our whole-brain analysis, within our regions-of-interest, naturalness consistently fell in between the other judgments (see Figure 4.3). This suggests that brain activations follow the pattern of the semantic differential studies.

Conclusions

We used semantic differential studies as an empirical basis for distinguishing between evaluative and descriptive judgments. We looked for brain regions responding to this distinction between judgments. We chose beauty as a representative judgment for the evaluative judgments, and roughness as a representative for the descriptive judgments. Besides the effects of judgment, we also looked at the effects of beauty level, and in particular at its interaction with type of judgment. The frontomedian cortex and the amygdala appear to be selectively sensitive to beauty level during beauty judgments. Hence, these regions seem to compute a beauty outcome when attending to beauty, and may be directly involved in making beauty assessments. The fusiform gyrus was also sensitive to interactions between beauty level and type of judgment, but the pattern of these interactions is not commensurate with involvement in beauty assessments. The posterior cingulate cortex did not show an interaction with beauty level. Hence, this region appears to not be directly involved in making a beauty assessment itself. It may instead fulfil a supporting role, such as directing attention to the internal rather than the external world.

The frontal operculum and occipitotemporal area appeared responsive to the descriptive judgments, and may be directly or indirectly involved in making such judgments. These findings demonstrate the neural underpinnings of the judgment semantics. Another part of the fusiform gyrus distinguished between different beauty levels, but does not appear to make beauty assessments by itself.

By focusing on the interaction between beauty level and beauty judgments versus other judgments, we have narrowed down the regions that are potentially involved in making beauty assessments to the frontomedian cortex and the amygdala.

Acknowledgments

We thank Nikky van Bodegom and Anita Kuiper for operating the scanner. This study was supported by a grant from the European Commission, under contract #043157 (Syntex). This work represents only the authors' view.

Chapter 5.

Amygdalar guidance of feature-based attention during aesthetic judgments

Richard H.A.H. Jacobs^{1,2}

Remco Renken^{1,2}

André Aleman^{1,2}

Frans W. Cornelissen^{1,2}

Recent findings indicate that the amygdalae guide the eyes during emotional decision-making, but whether this guidance extends to non-spatial forms of attention is not known. Here, we show that amygdala activation increases when participants decide on the beauty of visual textures. As this decision requires selecting features that have similar values all over a given texture, our finding indicates that the amygdalar role reaches beyond the guidance of spatial attention to include top-down feature-based attention to emotional information.

Keywords: feature based attention, beauty, functional magnetic resonance imaging, texture perception, top-down

Affiliations:

1. Laboratory for Experimental Ophthalmology, School for Behavioral and Cognitive Neurosciences, University Medical Center Groningen, University of Groningen, PO Box 30001, 9700 RB Groningen, the Netherlands

2. BCN NeuroImaging Center, School for Behavioral and Cognitive Neurosciences, University Medical Center Groningen, University of Groningen, PO Box 30001, 9700 RB Groningen, the Netherlands

Introduction

The amygdalae are among the most heavily studied brain structures in neuroscience, and are commonly viewed as emotion processors. Despite decades of research, the precise function of the amygdala remains elusive, and is the subject of ongoing debate, as has recently been reviewed (Whalen & Phelps, 2009).

After initial reports that the amygdalae function as fear processors, more recent studies indicate a broader function, encompassing also the processing of other emotions. One of the most revealing findings in recent years indicates that amygdalar damage leads to disrupted scanning of expressive faces, but not to impaired emotion recognition per se (Adolphs, et al., 2005). Other studies have implicated the amygdala in orienting, eye movements, and attention (Anderson & Phelps, 2001; Bancaud, Talairach, Morel, & Bresson, 1966; J. M. Carlson, Reinke, & Habib, 2009; W. A. Cunningham, et al., 2008; Ohrmann et al., 2007; Van Reekum et al., 2007), usually directed at emotionally relevant information. Taken together, these findings suggested to us that the amygdala might play a key role in selecting visual information that is relevant for making emotional decisions. This idea was further strengthened by the presence of higher amygdala activation to explicitly emotional tasks than to other tasks, as was shown in a meta-analysis (Fusar-Poli et al., 2009). Such selection could occur through overt or covert shifts in spatial attention. Recent findings suggest that attention-attracting effects of expressive faces are based on low-level features.

Facial features, such as eye-whites and the white of exposed teeth in photographs of faces, or orthogonally oriented lines in schematic faces, or downward-pointing V-shapes, resembling a frown, have been shown to attract attention (M.G. Calvo & Marrero, 2008; M. G. Calvo & Nummenmaa, 2008b; Coelho, Cloete, & Wallis, 2010; Horstmann, Borgstedt, & Heumann, 2006; Larson, Aronoff, & Stearns, 2007). This appears in several measures, such as costs and benefits in search times, or in costs in time to identify a centrally presented facial expression flanked by other facial expressions. These results suggest that attention to emotional information is feature-based, although it is not clear whether it is the features per se, or the association of such features to emotional meaning, that cause such features to attract attention.

Combined with the finding that amygdalar activation to expressive faces is associated with the efficiency of finding expressive faces (Ohrmann, et al., 2007), these findings suggest that the amygdala may direct attention to these features. Hence, we speculated that the amygdalar function would involve not only spatial, but also feature-based attention, in particular to emotional aspects. Feature-based attention consists of attending to some features over others, even when they overlap spatially. A very simple example would be attending to the colour rather than the orientation of a bar, but there could be many types of features to which attention might be directed.

So far, no one has specifically addressed feature-based aspects of emotional attention in the brain, despite their obvious relevance. To investigate feature-based effects, faces may not be ideal, because the features that attract attention are also likely to be spatially separated. For example, the relatively orthogonal eyebrows indicative of an angry face are spatially separated from the more parallel lines formed by the mouth and the face outline of a happy face, and from the larger eye-whites associated with surprise and fear. Therefore, we opted for a different stimulus category, in which features are spatially overlapping, namely visual textures. Visual textures are visual patterns in which no clear object outline can be discerned. They tend to be highly repetitive, so that featural information is omni-present, and spatial aspects of attention are minimized. Textures are typically found in surfaces. See figure 5.1 for example textures. Visual textures offer an additional advantage in that they can be assumed to not be arousing, thereby minimizing the well-known effects of stimulus arousal on the amygdala. In this way, we could selectively investigate attentional effects, without contamination by bottom-up arousal effects.

To test whether the amygdala is involved in selecting emotionally relevant information, we employed different tasks to enforce participants to selectively attend to the different visual features necessary to make an emotionally tinged decision (beauty) versus two non-emotional decisions (naturalness, roughness), using identical stimuli. Beauty may be considered emotionally tinged, because beauty influences activity in emotional brain centers, such as the amygdala (Aharon, et al., 2001), and because emotions and beauty, unlike roughness, share a valence (positive-negative) dimension. Beauty and roughness judgments have been shown to be orthogonal, and hence maximally different, in judgment space (Jacobs et al., *submitted*). Naturalness was added as an additional non-emotional control judgment. Amygdalar activation was monitored during task performance in healthy participants using functional magnetic resonance imaging. We expected the amygdala to be more active during beauty judgment than during the other tasks.

Method

Participants

Ten men and eight women (20-39 years), all right-handed, participated. All participants had normal or corrected to normal visual acuity. Participants gave their informed written consent according to procedures approved by the Medical Ethics Committee of the University Medical Center Groningen, the Netherlands.

Stimuli.

Stimuli were visual textures, which we define as repetitive patterns in which no single object outline can be discerned. We take colour to be an integral part of textures. Textures were collected from various internet sources (<http://www.fundermax.at/>, <http://www.ux.uis.no/~tranden/brodatz.html>, <http://www.textureking.com/>, <http://inobscuro.com/textures/>, <http://textures.forrest.cz/>). Stimulus sizes were standardized, using cropping to reduce the size of large textures, and a texture growth algorithm to enlarge small textures. Example textures are shown in figure 5.1.

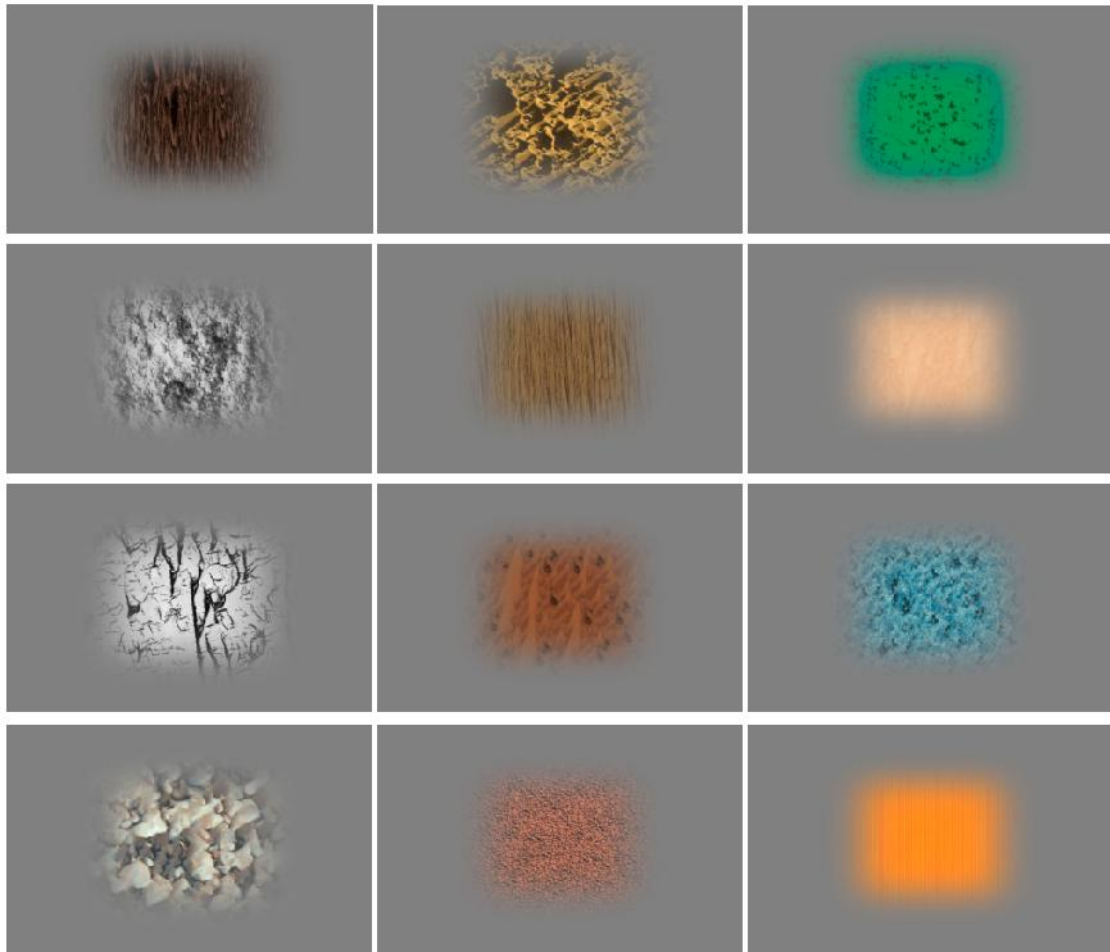


Figure 5.1. Example textures. Artificial and natural, coloured and grey-scale, complex and relatively simple, textures were included in our stimulus set. The bottom left picture is an example of a pebble texture after the growth algorithm has been applied to it. Textures were presented on a grey background, into which they gradually blended, to avoid sharp edges in the pictures.

Stimulus presentation

In the initial texture selection procedure, stimuli were presented on a 30'' Apple Cinema HD Display monitor and were shown at a visual angle of about 22 x 22 degrees (viewing distance 70 cm), on a grey background (see figure 5.1) having a mean luminance of 55 cd/m².

In the scanner, stimuli were back-projected onto a translucent screen (44 x 34 cm) using a Barco LCD Projector G300 (Barco, Kortrijk, Belgium) set at a resolution of 800 x 600 pixels. The translucent screen

subtends a visual angle of 32 x 25.5 degrees. Textures were presented at a size of about 13 x 13 degrees, on a grey background (see figure 5.1) having a mean luminance of 3260 cd/m².

Stimuli were presented within Matlab (MathWorks, Natick, MA) using the Psychtoolbox (<http://psychtoolbox.org/>) extensions (Brainard, 1997; Pelli, 1997) using an Apple Macbook Pro (Apple, Cupertino, CA).

Texture selection

Based on a rating experiment, for each individual 36 texture stimuli were selected from a collection of 436 textures. In this rating experiment, textures were presented one by one, on a 30'' monitor, and rated for beauty by moving a slider along a bar at the bottom of the screen. For each individual, the 12 textures judged least beautiful (negative valence) and the 12 textures judged most beautiful (positive valence) were selected, as well as 12 from the middle of the judgment range (neutral valence). These selected textures were used as stimuli in the functional magnetic resonance imaging (fMRI) experiment.

fMRI procedure

In the fMRI experiment, subjects performed three runs, in each of which they judged textures on one of three dimensions (beauty, naturalness, and roughness). At the beginning of a run a fixation period lasting 30 sec was presented.

Judgments were grouped in blocks of six trials and interleaved in pseudo-random order within a run. Within each judgment block, textures with positive, neutral, and negative valence were presented in random order, but over a run, each texture was presented only once for each judgment condition. Hence, during each run, all 36 textures were presented once for each type of judgment (for a total of 108 trials per block). Each texture was presented for 4000 msec (ISI = 1000 msec), during which the participants could indicate their judgment by pressing one of three buttons on a fiber-optics response pad (Current Designs Inc., Philadelphia, USA), using their right hand. Depending on the judgment condition, the buttons' meaning corresponded to beautiful, neutral, and ugly (beauty judgment), or rough, neutral and smooth (roughness judgment), or natural, neutral, and artificial (naturalness judgment). The correspondence between buttons and judgments was counterbalanced between participants, but the 'neutral' button was always in the middle.

Scanning parameters

A 3 T Philips Intera (Best, the Netherlands) with a sense-8 head coil was used to acquire T1 anatomical volume images (256x256 matrix, 160 slices, voxel size 1x1x1 mm) and T2*-weighted echo-planar images with blood oxygenation level-dependent contrast (64x64 matrix, voxel size 3.5x3.5x4 mm (no gap), TR = 2500 msec, TE = 28 msec, Field of View 224x224). Each echo-planar image consisted of 40 slices, acquired in descending order, positioned to cover the whole brain, except the cerebellum.

Data analysis

Analysis was performed in BrainVoyager (Brain Innovation B.V., Maastricht, the Netherlands). Preprocessing involved realignment of the functional scans, slice timing correction, coregistration with the anatomical image, and normalization of the anatomical images to a standard Talairach brain. Activation maps were smoothed with a kernel of 8 mm FWHM. Linear trends were removed, but no further temporal filtering was applied. At the individual level, a model with three judgments (beauty, naturalness, and roughness) and three covariates for valence (negative, neutral, positive, i.e. the rating on the beauty scale obtained prior to scanning) was built, with predictors for a BOLD-response for every stimulus, lasting for 4 sec. At the group level, an analysis of covariance was performed within anatomically defined regions of interest. A probabilistic amygdala-mask (Palmen, Durston, Nederveen, & Van Engeland, 2006) was thresholded at a probability of 0.4 to extract a left and right volume of interest. The resulting coordinates in MNI-space were transformed into Talairach space (using `mni2tal.m`, by M. Brett, <http://imaging.mrc-cbu.cam.ac.uk/downloads/MNI2tal/mni2tal.m>). Within these regions-of-interest, we looked for main effects of task while taking beauty level of the stimuli as a covariate. This analysis was followed up by planned contrasts between activity during beauty judgments and roughness and naturalness judgments, examined at a Bonferroni-corrected significance level of $0.05/4 = 0.0125$. Activations in other parts of the brain will be reported elsewhere. Activation levels of all runs were Z-transformed before group-analysis.

Results and discussion

Analysis of the functional data revealed a main effect of task in both the left ($F(2,9) = 9.60, p = 0.0005$) and the right ($F(2,128) = 4.3, p = 0.02$) amygdala. There was a marginal effect of the beauty level of the stimuli in the left ($F(2,128) = 2.98, p = 0.06$) amygdala, and no effect in the right ($F(2,128) = 0.22, p = 0.81$) amygdala. There were no interaction effects between beauty level and task in the left ($F(4,128) = 0.86, p = 0.49$) or the right ($F(4,128) = 0.72, p = 0.58$) amygdala. Direct contrasts between beauty and roughness, and between beauty and naturalness, revealed increased activation of the amygdala during the judgment of texture beauty relative to the judgments of roughness and naturalness (figure 5.2), in both hemispheres (all $p < .0001$).

These results highlight a key involvement of the amygdala in the assessment of beauty. Although the amygdala has been implicated in the rapid, unconscious, presumably bottom-up, detection of biologically relevant stimuli (Dolan & Vuilleumier, 2003; Killgore & Yurgelun-Todd, 2004; Öhman, 2005; Pasley, Mayes, & Schultz, 2004; P. J. Whalen et al., 2004; M. A. Williams, Morris, McGlone, Abbott, & Mattingley, 2004), our results imply that this amygdalar involvement acts in a top-down fashion, in this case triggered by task instructions of beauty versus roughness and naturalness judgments for identical stimuli. Other studies that used diverse procedures such as mood induction (Ramel et al., 2007; Wang, LaBar, & McCarthy, 2006), focusing on different emotional aspects of stimuli (W. A. Cunningham, et al., 2008), or the attentional blink (Anderson & Phelps, 2001; Lim, Padmala, & Pessoa, 2009), report amygdalar activation, all in support of an amygdalar role in top-down, attentional processing. In all these studies, emotional stimuli were used, and the top-down effects may have been modulatory effects on already present bottom-up effects. For future studies, we suggest that non-arousing and neutral stimuli, as our textures may be assumed to be, should be considered for selectively investigating top-down effects (different tasks, moods, etc.), to avoid potential interference by bottom-up effects. It is our impression that such an approach has not been pursued thus far, because of an implicit assumption that top-down influences would only modulate already present bottom-up effects.

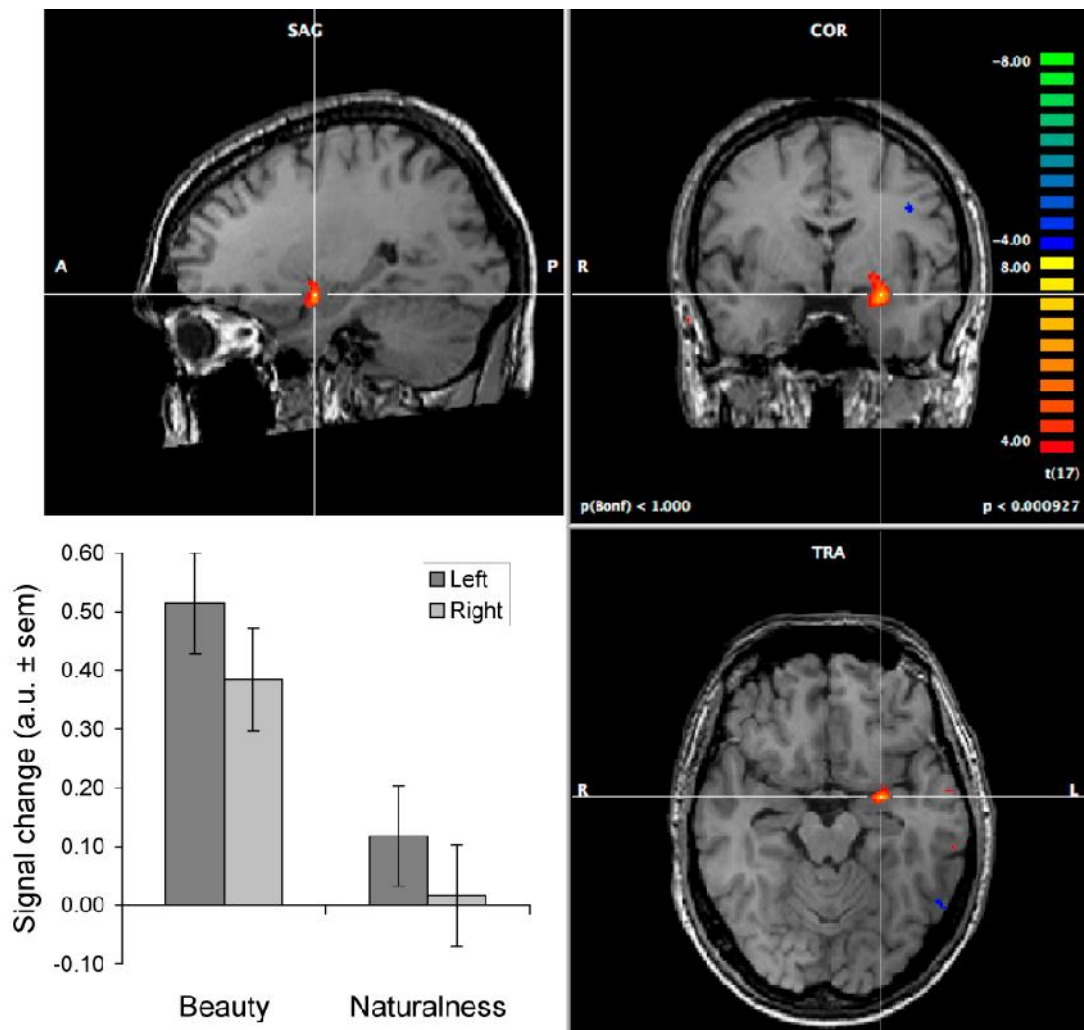


Figure 5.2. Selectively increased activation of the amygdalae during the judgment of beauty. This increase in activation is relative to the judgment of texture roughness. The activation of the left amygdala is centered around Talairach coordinates $-25, -3, -15$. A region-of-interest analysis was performed, separately on the left and right amygdalae, contrasting both beauty and naturalness judgments to roughness judgments (the baseline). This yielded highly significant effects for beauty compared to both roughness and naturalness, in both hemispheres (all $p < 0.0001$), but not between naturalness and roughness.

Beyond demonstrating top-down effects, our result suggests that in this emotionally tinged task, the top-down involvement is related to the guidance of feature-based attention. In visual textures, feature values are similar all over the stimulus, thus obviating the use of eye-movements and spatial attention shifts. Only at a very fine scale, one could focus on, e.g., a bright element versus its neighbouring dark element. Hence, attending to specific features in textures likely requires non-spatial, feature-based attention. Eye tracking indicates that people make shorter fixations and attend more to colour information during beauty judgments

than during roughness judgments (Jacobs, Renken, Thumfart, et al., 2010). Moreover, beauty and roughness judgments correlate with the values of different features such as colour information for beauty and uniformity measures for roughness (Jacobs, Haak et al., submitted). Consequently, our fMRI-finding suggests a role for the amygdalae in the top-down guidance of feature-based attention during emotional decision-making.

This finding extends work, mentioned in the introduction, indicating that the amygdalae are involved in guiding spatial attention. Together with our new finding, these relations with spatial attention confirm our idea that the amygdalae have a key role in selecting aspects of the environment relevant for emotional decision-making by guiding both spatial and non-spatial, feature-based, forms of attention.

Recent studies cast substantial doubts on amygdalar automaticity, as amygdala activation appears to be related to those instances in which masked information is nevertheless consciously perceived (Pessoa, Japee, Sturman, & Ungerleider, 2006), and the rapid detection of emotional information appears to survive amygdala damage (Tsuchiya, Moradi, Felsen, Yamazaki, & Adolphs, 2009). Consequently, in our view, many of the traditional findings related to amygdalar activation may actually be contingent upon its role in the guidance of spatial and feature-based attention, rather than on the bottom-up perception of emotions. In particular in the absence of an engaging non-emotional task or goal, traditional stimuli such as faces may trigger an evaluation for emotions, thereby recruiting the putative amygdalar selective attention mechanisms to a larger extent than less emotional stimuli.

While an attentional role for the amygdala has been proposed before, such accounts thus far (Vuilleumier, Armony, Driver, & Dolan, 2001) appear to focus entirely on stimulus-driven spatial attention-grabbing mechanisms that are activated by emotional stimuli. There have been studies reporting top-down (task or mood driven) effects on the amygdala, without an obvious spatial component (Fusar-Poli, et al., 2009). These studies employed emotional stimuli, however, and therefore attention may have only modulated already present bottom-up effects. Besides, most of these studies fail to interpret these effects in terms of selective attention. Hence, we believe our study to be the first to present a case for top-down attentional effects in the absence of any bottom-up emotional effects, and also the first to make a strong case for an amygdalar role in the guidance of feature-based attention during emotional decision-making.

In summary, we find that amygdala activation increases when participants decide on the beauty compared to the roughness or naturalness of visual textures, implying involvement in –top-down– feature-based attention. Like other studies reporting top-down effects, emotional information had to be selected from the environment, and in our view such results are consistent with the amygdala’s top-down role in guiding attention to emotional information. Our finding extends the amygdala’s known role in guiding the eyes, and indicates that the amygdalae guide both spatial and non-spatial forms of attention during emotional decision-making in a top-down manner.

Acknowledgments

This study was supported by a grant from the European Commission, under contract #043157 (Syntex). We thank Anita Kuiper and Nikky van Bodegom for operating the scanner. This work represents only the authors’ view.

Chapter 6.

Different Judgments about Visual Textures Invoke Different Eye Movement Patterns

Richard H.A.H. Jacobs^{1,2}

Remco Renken^{1,2}

Stefan Thumfart³

Frans W. Cornelissen^{1,2}

Top-down influences on the guidance of the eyes are generally modeled as modulating influences on bottom-up salience maps. Interested in task-driven influences on how, rather than where, the eyes are guided, we expected differences in eye movement parameters accompanying beauty and roughness judgments about visual textures. Participants judged textures for beauty and roughness, while their gaze-behavior was recorded. Eye movement parameters differed between the judgments, showing task effects on how people look at images. Similarity in the spatial distribution of attention suggests that differences in the guidance of attention are non-spatial, possibly feature-based. During the beauty judgment, participants fixated on patches that were richer in color information, further supporting the idea that differences in the guidance of attention are feature-based. A finding of shorter fixation durations during beauty judgments may indicate that extraction of the relevant features is easier during this judgment. This finding is consistent with a more ambient scanning mode during this judgment. The differences in eye movement parameters during different judgments about highly repetitive stimuli highlight the need for models of eye guidance to go beyond salience maps, to include the temporal dynamics of eye guidance.

Keywords: Scanning modes, textures, beauty, roughness, top-down, features

Affiliations:

1. Laboratory for Experimental Ophthalmology, School for Behavioral and Cognitive Neurosciences, University Medical Center Groningen, University of Groningen, PO Box 30001, 9700 RB Groningen, the Netherlands

2. BCN NeuroImaging Center, School for Behavioral and Cognitive Neurosciences, University Medical Center Groningen, University of Groningen, PO Box 30001, 9700 RB Groningen, the Netherlands

3. Machine Vision Group, Profactor GmbH, Im Stadtgut A2, A-4407, Steyr-Gleink, Austria

Introduction

Background

In his seminal work, Buswell (Buswell, 1935) demonstrated that fixation locations on scenes differ according to the questions the observer had to answer. This finding has been confirmed many times (DeAngelus & Pelz, 2009; Lipps & Pelz, 2004; Rothkopf, Ballard, & Hayhoe, 2007; Underwood, Foulsham, & Humphrey, 2009; Yarbus, 1973). As Buswell's questions related to information that was present in different parts of the pictures, his finding may not appear too surprising, yet it was the first formal demonstration of task effects on the guidance of the eyes.

Our interest in task-dependent differences in the guidance of eye movements was raised when we found that judging visual textures for beauty lead to higher activation of the amygdala than judging the same textures for roughness (Jacobs, Renken, Aleman, & Cornelissen, 2010; Jacobs, Renken, & Cornelissen, 2009). The amygdala has been linked to orienting behavior (Bancaud, et al., 1966), to spatial attention to emotional information (Adolphs, et al., 2005; J. M. Carlson, et al., 2009; Ohrmann, et al., 2007), to emotional effects on the attentional blink (Anderson & Phelps, 2001; Lim, et al., 2009) and to emotional judgments (Fusar-Poli, et al., 2009). Together, these findings suggest that the guidance of visual attention may differ between an emotionally tinted task – judging for beauty – and a non-emotional, descriptive task – judging for roughness.

Although attention can be directed to peripheral parts of a visual scene, there is a tight coupling between attention and eye movements. For example, evidence suggests that a shift in spatial attention is required for shifts in eye movements to occur (Hoffman & Subramaniam, 1995; Shepherd, Findlay, & Hockey, 1986). Hence, eye movements can be used as a proxy for the allocation of spatial visual attention.

Models of eye guidance generally focus on salience maps that are derived from bottom-up visual information (e.g., Vincent, Troscianko, & Gilchrist, 2007), and that are modulated by task and other context effects (Kanan, Tong, Zhang, & Cottrell, 2009; Navalpakkam & Itti, 2005; Torralba, Oliva, Castelhana, & Henderson, 2006). However, other eye movement parameters, such as total saccade distance, are generally not considered (with the exception of studies looking at scan paths, see e.g. Groner & Menz (1985)). Here, we assume the existence of separate bottom-up and top-down influences on eye guidance, although both are still contested (Ballard & Hayhoe, 2009; Parkhurst & Niebur, 2003). We are interested in the influence of different instructions on how people look, and less so in where they look. Differences might be found in eye movement parameters such as average fixation duration, the number of fixations/saccades, the length of saccades, and other measures derived from these measures.

When paintings or other real-world scenes are used as stimuli, finding differences in such parameters is relatively trivial, as they may be contingent on the placement of objects that are relevant for the task at hand. To minimize such spatial effects on the way participants look around, we used visual textures as stimuli. Texture stimuli contain repetitive elements, so that re-directing spatial attention does not lead to focusing on substantially different information. Assuming that eye movements do occur, as they do for fractals (Parkhurst, Law, & Niebur, 2002) and visual noise (R. Groner & Menz, 1985), differences in eye movement parameters during different judgments about visual textures would constitute evidence for the presence of task effects on the non-spatial guidance of eye movements. However, it is not a priori evident that eye movements will occur to texture stimuli in the first place, as visual noise is less repetitive than visual textures, and salient features that attract bottom-up attention might arise in visual noise purely by chance.

For the tasks, we selected beauty and roughness judgments. Previous work has shown that these judgments are orthogonal in judgment space (Jacobs et al., 2010), which indicates that they are maximally different. This enhances our chance of finding an influence of these judgments.

For the current paper, we define a visual texture as a repetitive visual pattern that does not contain clearly recognizable object outlines. Typically, surfaces contain texture. We regard color as an integral part of texture information.

Tasks could influence eye movements based on differences in the rate of feature extraction, assuming that the different judgments are based on different features. Beauty and roughness judgments are partly based on different features (Jacobs, Haak, et al., 2010). Different tasks could even result in the deployment of entirely different scanning modes, for example in ambient versus focal scanning modes (Unema, Pannasch, Joos, & Velichkovsky, 2005).

Besides eye movement parameters, tasks also influence pupil size. In particular, increased effort or cognitive load leads to increases in pupil size (Beatty, 1982). We are not aware of reports about other task effects on pupil size, in particular ones contrasting emotionally tinted versus more neutral tasks. Nevertheless, effects are quite conceivable. Pupil size increases when observers view more interesting stimuli (Hess & Polt, 1960). Assuming that beautiful stimuli might also be considered more interesting, one would expect beauty and pupil size to correlate. One may ask whether this correlation occurs during explicit evaluation for beauty, or during evaluation for another aspect, such as roughness, or during both. Hence, we looked for a relationship between pupil size, averaged over the time of stimulus presence, and judgment, separately within the beauty and roughness judgment condition. We looked separately at explicit effects (correlating roughness ratings with pupil size during the roughness task, and correlating beauty ratings with pupil size during the beauty task) and at implicit effects (correlating roughness ratings with pupil size during the beauty task, and correlating beauty ratings with pupil size during the roughness task). The correlations with beauty were our primary interest here, and the correlations with roughness ratings were added for completeness.

Hypothesis

Judgments of visual textures for beauty or roughness are associated with different eye-movement behavior. These differences are related to non-spatial aspects of attention, and will occur in parameters such as average fixation duration, number of fixations, and total distance traveled by the eyes. We have, however, no prior expectations about the direction of such effects. We also expect feature values to differ between fixated locations in the two judgment conditions.

Moreover, during the observation of highly repetitive visual stimuli, eye movements do not result in different information impinging on the retina. Hence, we expect no differences in the spatial allocation of attention, as indexed by the spatial distribution of eye movements.

In addition, we expect task-dependent correlations between beauty and pupil size.

Methods

Participants

Twelve observers (8 males, of whom 1 left-handed; age range 23-36) participated in this study.

Equipment and Software

Experiments were written in Matlab, using the Psychophysics and EyeLink Toolbox extensions (Brainard, 1997; Cornelissen, Peters, & Palmer, 2002); see <http://psycho toolbox.org/>).

An EyeLink 1000 System (SR Research, Canada) was used for eye tracking. The participants' left eyes were tracked at 500 Hz. We used the manufacturer's software for calibration, validation, drift-correction, and determining saccade and fixation parameters. Participants had their viewing position stabilized by a head and chin rest.

Stimuli were presented on a 41 by 31 cm CRT-monitor (LaCie, Paris, France). Experiments were conducted in a room that was dark, except for the illumination provided by the screen.

Stimuli

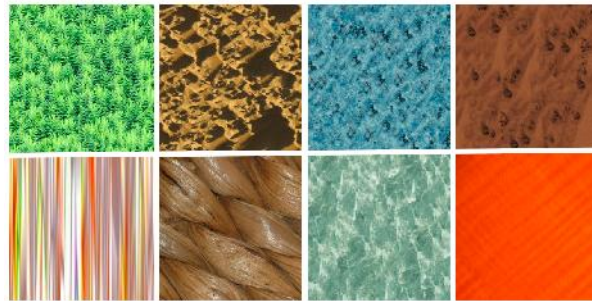


Figure 6.1. Example textures, used in the experiment. Both computer-generated and natural textures were used, and the set included both colored and gray-scaled pictures.

Texture images had a size of 1280 by 1024 pixels. A texture growth algorithm (Ashikhmin, 2001) was applied to textures that originally were smaller than this. This growth algorithm does not significantly affect feature values (Jacobs, Haak, et al., 2010). When presented, textures filled the entire screen. The visual angle of the stimuli was 39 by 29 degrees. A total of 292 stimuli were presented. We aimed at using a diverse set of texture stimuli. The stimulus set consisted of textures taken from a standard set (Brodatz, 1966), with additional textures gathered from diverse internet-sources (the set is available on request). Both colored and gray-scaled pictures were included. Figure 6.1 shows thumbnails of some of the textures used in the experiments.

Procedure

After signing an informed consent form, participants completed four blocks of trials of judging visual textures. A block typically lasted about 15-20 minutes, and blocks were separated by substantial pauses. No more than two blocks of trials were assessed on a single day. Textures were judged for beauty (B) and for roughness (R), in separate blocks of trails. The order of blocks was either R-B-B-R or B-R-R-B. A single block consisted of 146 trials.

Before starting a block of trials, the participant was instructed to judge the visual textures either on beauty or on roughness. A few test trials were performed before the first block of trials. Following calibration of the eye tracker, the experiment was started. The participant self-initiated a trial by pressing

the spacebar on the computer's keyboard. A trial started with the presentation of a fixation dot which was used to drift-correct the eye-tracker calibration. Next, the fixation dot disappeared and a visual texture was presented for 3500 ms. After disappearance of the texture the fixation dot reappeared, and participants had to indicate their judgment by pressing one of the keys on the numerical part of the keyboard. Key 1 indicated "least beautiful" or "least rough", while key 9 indicated "most beautiful" or "most rough". There was no time limit for making a judgment. The space bar could be pressed to indicate an absence of a judgment. To indicate that the response was registered, the fixation dot increased in size. Following this, the participant initiated the next trial.

Analysis

Criteria for detecting saccades were standard settings for the Eyelink. A saccade was defined by a velocity of at least 30°/s, and an acceleration of at least 8000°/s², each lasting at least 4 ms. Fixations and saccades starting before the onset of the texture stimulus, or ending after the offset of the texture stimulus were excluded from the analysis.

Per participant and judgment condition, for each texture, the number of fixations, blinks, and saccades were counted, and average fixation duration, cumulative saccade distance (over saccades within a trial), average saccade velocity, average saccade duration, and average pupil size (during the time that stimuli were presented) were computed. In addition, total fixation duration over all trials in a condition was determined. Next, differences in these parameters for the two different conditions were expressed as a contrast, according to the formula:

$$P = 100\% \times \frac{V(Beauty) - V(Roughness)}{V(Beauty) + V(Roughness)} \quad (1)$$

where V(condition) represents the value of the parameter under study. P can in principle range from -1 to +1. For each participant, the resulting values were averaged over all stimuli. Kolmogorov-Smirnov tests were performed to check for deviations from normality of the distributions of these parameters. Deviations from 0 were statistically tested, over participants. One-sample, two-tailed t-tests were performed in SPSS, for all parameters. No correction for multiple testing was performed on these tests, as the parameters are interrelated, and our conclusions are based on the differences as a group, and not so much on the individual parameters.

Fixation contrast maps (Wooding, 2002) were computed as follows. First, for each individual participant and within each judgment condition, we computed for each stimulus the total amount of time spent fixating each screen location. These values were spatially smoothed with a Gaussian kernel with a standard deviation of 30 pixels. Next, per stimulus a fixation contrast map was computed according to Formula 1, where V(condition) represents the fixation map for a particular judgment condition. Next, the obtained contrast maps were averaged over stimuli. Finally, these maps were averaged over participants, and a familywise-error-corrected non-parametric test (Nichols & Holmes, 2002) was applied to test for differences in maximum dwell time over the screen.

Correlations between beauty and roughness ratings on the one hand, and pupil size on the other, were computed. This was done both for the pupil size during the judgment (explicit effects of beauty and roughness on pupil size), and for the pupil size during the other judgment (to assess implicit effects of beauty and roughness on pupil size). These correlations were computed per participant. Then, after checking for normality using Kolmogorov-Smirnov tests, one-sample t-tests were conducted to ascertain whether these correlations were significantly different from 0, over participants. We also report some correlations between feature values and ratings and pupil sizes. Considering the amount of features we computed, correction for multiple comparisons would leave none of these relations significant. Hence, we report them without statistical testing, for confirmation in future experiments.

Feature Computation

The texture features most strongly associated with beauty and roughness decisions were determined as follows. First, we computed the correlations between a set of 188 computationally derived features on the one hand, and the beauty and roughness ratings on the other hand. Computed features are based on Gray-Level Co-occurrence Matrices (Haralick, et al., 1973), a set of features related to psychological judgments (Tamura, et al., 1978), Neighborhood Gray-Tone Difference Matrices (Amadasun & King, 1989), the Fourier spectrum (Tuceryan & Jain, 1998), Gabor energy features (M. Kim, Park, & Koo, 2005), and features expressing the presence of colors, brightness, and saturation (Datta, et al., 2006).

The Tamura features are based on psychological evaluations, and comprise coarseness, contrast, directionality, line-likeness, regularity, and roughness. The Gray Level Co-occurrence Matrices indicate how often particular gray levels co-occur at a certain distance. For our purposes, we computed them for distances of 1, 2, 4, and 8 pixels. These matrices are used to compute statistical properties like entropy, energy, homogeneity, et cetera. A Neighborhood Gray Tone Difference Matrix is a vector containing, for each gray-level, a sum of the differences in gray-tone with all the surrounding pixels, for each pixel with that gray-tone. The size of the neighbourhood is variable, and we computed matrices for sizes of 3 by 3 and 5 by 5 pixels. Based on these matrices, the features coarseness, contrast, busyness, complexity, and strength are computed.

Fourier features are based on the spatial frequencies in the brightness variations. The extent to which a certain spatial frequency is present is expressed as its energy or power. First, a two-dimensional image is transformed into the frequency domain using the fast Fourier transform to obtain the Fourier spectrum. Each component of the spectrum is represented by a complex number that describes a frequency in the two-dimensional image by means of amplitude and phase. The component coordinates in the spectrum determine the frequencies' wavelength and direction. The spatial frequency with highest wavelength (uniform signal, i.e. average brightness) is represented in the centre of the spectrum, while high frequencies can be found on the outside. The average energy of circular bands around the average brightness is computed for different radii. Also, the energy of wedges with their peak at the average brightness is computed, yielding a measure of the orientation of the image. In this way, 12 circular energy, and 24 wedge energy features were computed, each reflecting the presence of information at a different spatial frequency (circular rings) and orientation (wedges). In addition, a number of features summarizing their distribution were computed.

Like Fourier features, Gabor features capture the spatial frequencies in pictures, but they preserve some spatial information. The human visual system is known to contain cells that work as Gabor filters. Gabor 'energy', over the entire texture, was computed for 4 spatial frequencies, in six orientations. Average saturation and intensity were based on HSV color space. The presence of the colors red, green, yellow, cyan, blue, and magenta, was computed by partitioning HSV color space into six sectors, and counting the relative frequency of pixels within each sector. The sector frequency was normalized to the average image value and saturation. As we extensively described relations between visual texture features and judgments elsewhere (Jacobs, Haak, et al., 2010; Thumfart et al., 2008), we here restrict ourselves to simply reporting the features correlating most strongly to beauty and roughness judgments.

Features around fixations

To support our idea that differences in eye guidance between the two judgments reflect differences in feature-base attention, we extracted patches around fixations from the textures, and computed the 188 feature values for each of these patches. We then computed average feature values per stimulus, over all fixations. Next, we computed for each stimulus a difference in feature values, according to formula (1), but with absolute values in the denominator, to deal with negative values. Then we computed the means for the 188 feature differences, over subjects. We sorted the resulting (absolute value of) averages, and compared these to permuted data. Our 1000 permutations consisted of switching the feature values between roughness and beauty fixations for randomly selected textures. We then followed the same procedure as with the real data, so that we got 1000 examples of ordered features. We then looked up till what point the real data stayed in the top 5% of the permuted data. Those features were considered to be significantly different between judgments, and the direction of the difference was determined.

Results

Observations

Participants responded well, skipping roughness judgment on 1.2% of the stimuli, and beauty judgment on 1.6 % of stimuli.

Observers did make eye movements. On average, 8.0 fixations (and as fixations alternate with saccades, a similar number of saccades) were made in the 3500 ms period that textures were presented. Over all participants, 26 trials were encountered in which no fixations (and hence, also no, or maximally one, saccade) fell completely within the stimulus duration. Such trials did not contribute to average durations computed over all trials, and derived measures, but they did contribute to the counts of saccades and fixations.

Frequency plots of fixation durations during beauty and roughness judgments are displayed in figure 6.2. There are more short fixations (< 400 ms) during beauty judgments. For longer fixation durations, the numbers are similar for both judgment types. The distributions of fixation durations per observer were skewed to the right (peak shifted to the left). The most frequent fixation duration was between 200 and 300 ms, although there was an observer with most fixation durations at 700-800 ms (not shown). As pointed out by others, for different experiments (Pelz, Canosa, Lipps, Babcock, & Rao, 2003; Velichkovsky, Dornhoefer, Pannasch, & Unema, 2000), fixation durations under 200 ms were not uncommon.

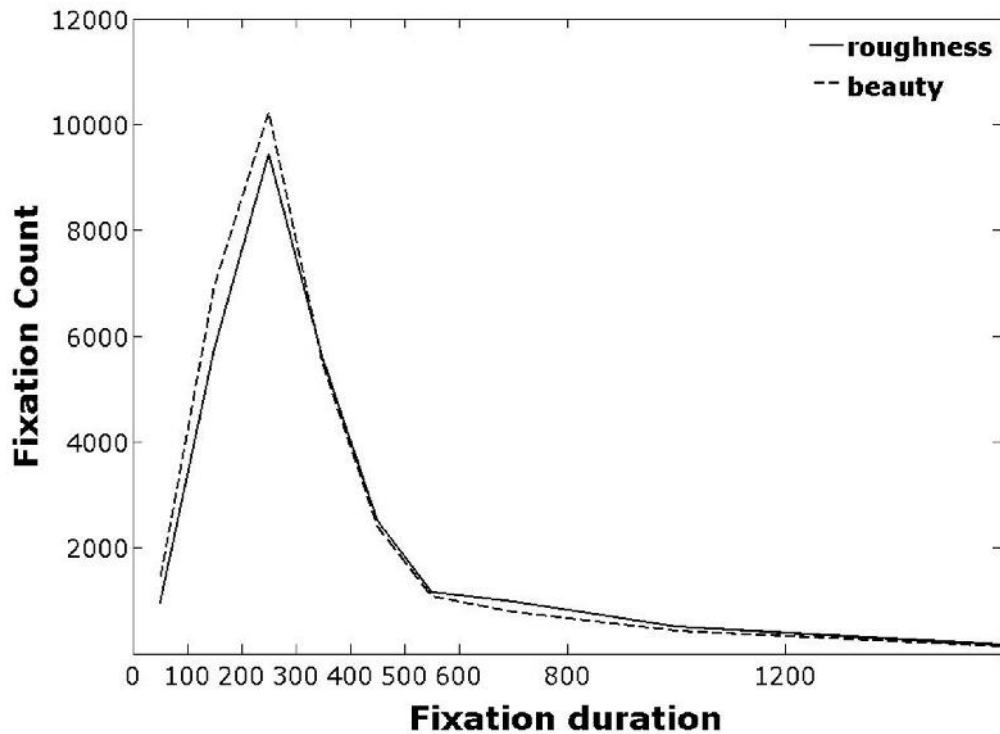


Figure 6.2. Distribution of fixation durations for the beauty and roughness judgments, integrated over all participants.

Spatial distribution of gaze

Figure 6.3 shows a map indicating the relative amount of time spent at each location for the two judgment conditions. During beauty judgments, on average participants spend about 8% more of their time (cumulative fixation duration) just above the center of the screen, while they spend on average about 3% more of their time below the screen center during roughness judgments. Although suggestive, these differences were not statistically significant ($p = 0.89$ for the maximum, and $p = 0.12$ for the minimum, FWE-corrected). There were few fixations in the periphery, resulting in 0% differences there, between the judgments.

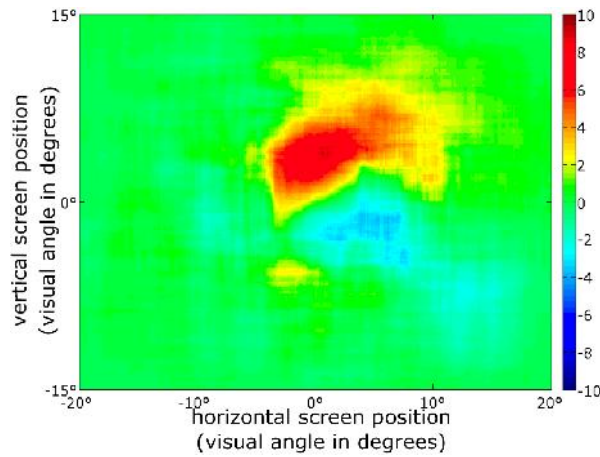


Figure 6.3. Dwell time contrast map. Red indicates locations on the screen where participants dwelled longer during beauty judgments, blue locations where participants dwelled longer during roughness judgments. Effects are non-significant ($p = 0.12$ for the maximum, and $p = 0.89$ for the minimum, FWE-corrected).

Eye movement parameters

Kolmogorov-Smirnov tests on the eye movement parameters, as computed using Formula (1) did not reveal significant deviations from normality (all $p > .76$). Figure 6.4 shows changes in eye-movement parameters. Average fixation duration was higher during the roughness judgments compared to the beauty judgments ($t(11) = -4.27$, $p = 0.001$). Both number of saccades ($t(11) = 2.49$, $p = 0.03$) and the distance covered by the saccades (or cumulative saccade amplitude; $p = 0.02$) are significantly higher during the beauty judgments. This suggests observers scanned coarser and more globally during beauty compared to roughness judgments. There was no difference in average saccade duration ($t(11) = .997$, $p = 0.35$), and average saccade velocity was higher during beauty judgments ($t(11) = 2.30$, $p = 0.04$).

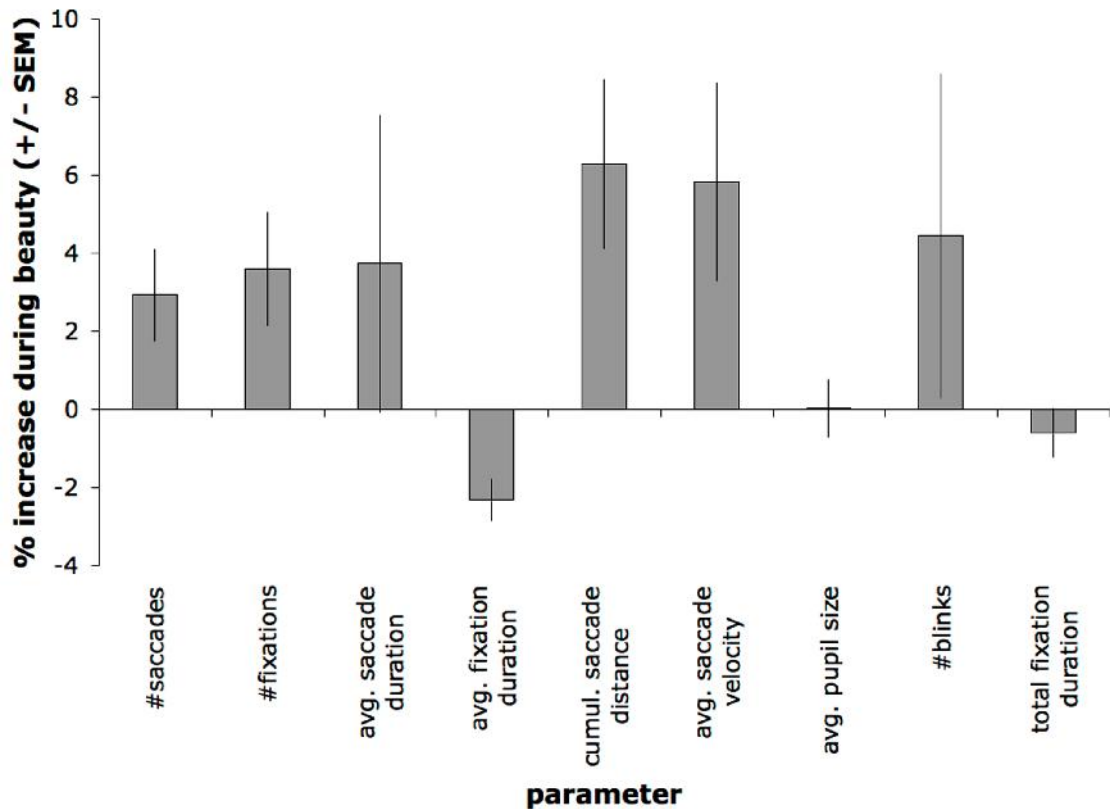


Figure 6.4. Eye movement parameters. Increases during beauty compared to roughness judgments, expressed as a percentage of their average. Cumul. = cumulative, avg. = average.

Pupil size

Kolmogorov-Smirnov tests on the correlations between pupil size and ratings did not reveal any significant deviations from normality (all $p > .8$).

No differences were found in the average pupil size ($t(11) = 0.03$, $p = 0.98$) nor in the number of blinks ($t(11) = 1.07$, $p = 0.31$), between the judgment conditions.

There was no correlation between pupil size and beauty rating, neither during the explicit rating of beauty ($r = 0.02$, $t(11) = 0$, $p = 1$), nor during the implicit rating of beauty (i.e. between pupil size during the roughness judgment and the beauty rating) ($r = -0.01$, $t(11) = .192$, $p = .851$).

There was a correlation between pupil size and rated roughness, both during the (explicit) rating of roughness ($r = 0.13$, $t(11) = 8.07$, $p = .000$), and during the (implicit) rating of beauty ($r = 0.11$, $t(11) = 5.83$, $p < .001$).

Feature correlations

The features correlating most strongly to mean beauty ratings were average saturation ($r(10) = 0.47$) and the yellowness of the texture ($r(10) = 0.37$), and a coarseness-measure based on the Neighborhood Gray-Tone Difference Matrices ($r(10) = 0.33$).

The features correlating most strongly to roughness ratings were entropy-measures (for a range of distances) based on the Gray-Level Co-occurrence Matrices (all correlations in the range of 0.6 to 0.7). We note also a positive correlation between average pupil size and average saturation, during both beauty ($r(10) = 0.24$) and roughness judgments ($r(10) = 0.22$).

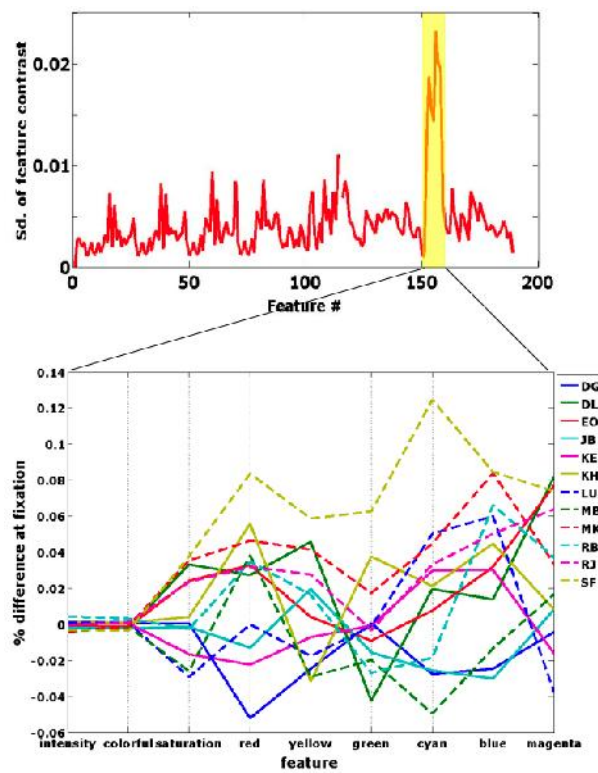


Figure 6.5. Feature differences, computed according to Formula (1), between fixations during beauty and fixations during roughness. The top shows the standard deviation over subjects for all features. The color features are numbered 150-158 (highlighted in yellow). The bottom graph shows the feature differences per subject for the color features.

Fixations on different features

We found that the colors blue, magenta, red and cyan had higher values around fixations during the beauty judgment than during roughness judgments. More striking than the differences in average feature values between judgments, were the standard deviations over subjects (figure 6.5, top). The color features showed much higher standard deviations than the other features. Looking at the individual participants' averages (figure 6.5, bottom), it appears that some participants looked more at all colors during the beauty judgment, while others looked at some colors at the expense of other colors. One participant, DG, looked less at some colors, possibly indicating that he was in fact judging for ugliness rather than beauty.

Discussion

We examined differences in eye movement parameters between beauty and roughness judgments to visual textures, because previous findings of differential engagement of the amygdala in these judgments suggested such a possibility.

We found that several eye-movement parameters differed between roughness judgments and beauty judgments, even though identical stimuli were shown. As this is a task effect, it is a top-down effect. Although this classification does little more than rephrasing the finding, it brings forward the possibility that other forms of top-down effects on eye movements may exist. For example, mood might also have an influence on the guidance of eye movements, and indeed such influences have already been reported (Wadlinger & Isaacowitz, 2006).

Although we demonstrated the presence of task effects on eye movements in our texture stimuli, it remains to be shown what the relevant dimensions are along which these tasks differ. We chose beauty and roughness judgments, because we found that these loaded strongly on orthogonal dimensions in a judgment space, derived from a range of judgments that people made about visual textures (Jacobs, Haak, et al., 2010). We interpreted these dimensions as an evaluative dimension on the one hand, on which judgments such as beauty, elegance, warmth, and colorfulness loaded strongly, and a descriptive dimension on the other, with high loadings of roughness, age, and complexity. We chose judgments from these orthogonal dimensions to maximize the possibility of finding effects. Now that we indeed found effects these may arise from this distinction, but other differences between the tasks may also account for the different findings. To confirm our idea that the evaluative-descriptive distinction is the relevant one, replications with other judgments, such as complexity (descriptive) and elegance, warmth, interestingness, or colorfulness (evaluative) would be in order. One can think of other differences between the tasks, such as difficulty in feature extraction, a possibility that we entertain below. Another possibility would be the implicit tactile nature of a roughness judgment, likely requiring a visuo-tactile transformation of the information. But even if such differences exist, these may generalize to all judgments differing along the evaluative-descriptive dimension.

As the differences in eye guidance between the two tasks were not related to differences in the spatial location of the relevant information, these differences are strong evidence for non-spatial, possibly feature-based, differences in attention. In particular, the longer average fixation durations during the roughness judgments can readily be interpreted as reflecting differences in feature-based attention. A longer fixation during roughness judgments likely reflects additional time needed to extract the relevant information. Longer fixation durations have already been shown to be related to tougher discriminability of the information at the fixated location (Cornelissen, Bruin, & Kooijman, 2005; Hooge & Erkelens, 1996), to

more elements around a fixation location (Salthouse & Ellis, 1980), to search for detailed information, as compared to free viewing (Buswell, 1935), to time spent searching (Over, Hooge, Vlaskamp, & Erkelens, 2007), and to non-expertise (Antes, Chang, Lenzen, & Mullis, 1985). All these findings corroborate the notion that more difficult feature extraction leads to longer fixation times. Also, the nature of the information upon which the judgments are based suggests that simpler features are used for beauty (e.g., color information, a first-order feature) than for roughness (e.g., entropy information; a third-order feature) assessments. Shorter fixations and larger saccades have been associated with higher spatial frequencies (M. T. Groner, Groner, & von Mühlenen, 2008), suggesting that attention may have been directed at different spatial frequencies in our stimuli, under the different task instructions. Closely related to our current findings, fixation durations are longer when attending to location than when attending to color (Hayhoe, Bensinger, & Ballard, 1998), again suggesting that color is a relatively easy feature to extract.

In the previous paragraph, we argue that our findings should be interpreted in terms of feature-based attention differing between two different judgments. We should point out, however, that it is also possible that beauty and roughness judgments are based on the same features, and that differences occur only in the processing subsequent to the extraction of the features. Longer fixations could then be the result of higher processing load during the judgment of roughness. However, pupil size, an index for processing load, did not differ between the judgments. Hence, it is unlikely that processing load differs between the judgments, and differences in the extraction of features remain as an alternative. Also, one may question to what extent it is possible to separate feature extraction from processing further downstream. Importantly, we showed that feature values for some color features are, overall, higher around fixations during beauty judgments than during roughness judgments, although there is individual variability in the colors that are attended. Behavioral results here, and in other data from our group (Jacobs, Haak, et al., 2010), indicate that color information is important for determining beauty. These results support the idea that people attend to different features, depending on what is relevant for the task at hand. The results also suggest that (most) people attend predominantly to the beautiful, colored, parts of a stimulus, when judging for beauty. It would be interesting to see in future experiments if this changes when people judge for ugliness.

A parsimonious explanation for longer fixation durations during roughness judgments may be the following: sensory evidence for the presence of certain features at a fixated location needs to build up and exceed some recognition threshold. If this build-up is slower or the threshold is higher for the roughness features than for the beauty features, this would lead to longer fixation durations during roughness judgments. This procedure repeats, until sufficient information is gathered from different parts of the stimulus, until a decision has been reached.

It is not clear how models of eye guidance based on salience maps can explain our findings. In these models, longer fixations are translated into a higher salience for the fixated region. Hence, longer fixations during roughness judgments would have to be translated into higher salience for the fixated regions. But as the information in our textures is highly repetitive, the computation of salience would increase all over the stimulus. If fixation durations are based on the relative salience of a fixated region with respect to the salience of the surroundings, the resulting duration would not be higher at all, and the modeling would fail. In addition, the models that incorporate task effects only deal with search tasks with pre-defined targets (Navalpakkam & Itti, 2005; Torralba, et al., 2006). In the case of beauty judgments, there is no pre-defined search target, although it would be possible to translate such a task into a search for relevant features. It seems that our findings relate better to a window of attention. This window of attention is larger during beauty judgments. The window of attention tends to narrow for more difficult tasks (Ahissar & Hochstein, 2000), suggesting that the roughness judgment or the extraction of the relevant features for this judgment is more difficult. In terms of ambient versus focal modes of information processing (Unema, et al., 2005), our findings mean that beauty judgments are associated with a more ambient (short fixations, long saccades), and roughness judgments with a more focal (long fixations, short saccades), mode of processing. We note that the saccade durations were not significantly different between our judgments, however, although numerically in the right direction. We do not endorse the notions of ambient processing relying on the

dorsal visual pathway and focal processing relying on a ventral visual pathway, as is often claimed in connection with the ambient-focal distinction (Unema, et al., 2005). Models need to go beyond the computation of salience maps, and incorporate eye movement parameters separately. Recently, reinforcement learning has been applied to model the deployment of human attention and eye gaze (Ballard & Hayhoe, 2009). As this approach includes not only where, but also when people look, this seems to us a much better framework for modeling data of the type we provided.

The finding of higher amygdala activation during beauty judgments than during roughness judgments (Jacobs, Renken, Aleman, & Cornelissen, 2010) that inspired our current investigation, may underlie the enforcement of the different scanning modes found here. The experiments were nearly identical, except that in one case brain activity was measured, while in the current experiment eye movements were monitored. Hence, the different findings related to the different judgments are likely to be associated, certainly when one considers reports of amygdalar involvement in attention (Anderson & Phelps, 2001; J. M. Carlson, et al., 2009; Jacobs, Renken, Aleman, et al., 2010) and eye movements (Adolphs, et al., 2005; Bancaud, et al., 1966; Ohrmann, et al., 2007; Van Reekum, et al., 2007).

One separate issue that deserves discussion is that we did not find effects of stimulus beauty on pupil size, despite reports in the literature pointing to such effects in the presence of emotional stimuli. For example, sounds, such as baby's crying and laughter (Partala & Surakka, 2003) and visual stimuli that are selectively interesting to the different sexes, such as opposite sex semi-nudes and pictures of mothers and babies (Hess & Polt, 1960), increase pupil size. Those effects may reflect arousal elicited by the stimuli. As our stimuli were clearly not very arousing, this may account for the absence of an effect of beauty on pupil size. Moreover, beauty itself may not be a very arousing aspect to judge on, compared to evidently emotional judgments. In line with our results, the valence of written words does not seem to influence pupil size (Silk et al., 2009). The original Hess and Polt finding has been interpreted as reflecting relationships between positive or pleasurable emotions and pupil size, even in textbooks (Mather, 2006), but this interpretation appears to be unwarranted.

There were no influences of judgment task on pupil size. Rated roughness was related to pupil size, with rougher-looking textures eliciting pupil dilation. So, a relationship with rated roughness is established here, independent of whether this roughness was explicitly rated. This relationship may be based on (a combination of) features.

In consideration of the many features we computed, some of which are interrelated, and none of which we manipulated systematically, we cannot draw any hard conclusions with regard to relations of dependent variables to those features. The correlations between features and some dependent variables were reported for confirmation in future experiments, although we believe that the correlation of several color features (saturation, yellowness) with beauty judgments is no coincidence, and also a correlation between entropy measures and roughness judgments makes sense to us.

Conclusions

We found task-driven differences in eye movement parameters between beauty and roughness judgments of identical texture stimuli. As the spatial distribution of dwell times does not differ between these judgments, the differences in the eye movement patterns must result from differences in non-spatial, hence feature-based, attention. Average fixation duration, the number of fixations and saccades, and the average saccade duration differed between the two judgments. This points to differences in how people scan their environment, depending on their current goals. These differences in how people scan their environment cannot be explained by differences in placement of the relevant information, as would be possible when paintings or photographs were used as stimuli. Rather, we believe these differences should be interpreted as reflecting differences in non-spatial, feature-based attention (repetition in the paragraph), related to a higher difficulty in extracting the relevant information during the roughness judgment.

So far, models of attention and eye guidance focus on the guidance of the eyes to salient information, often taking the observer's task into account. Our findings indicate that models of eye guidance need to go beyond spatial salience maps, and need to incorporate top-down effects on eye movement parameters other than location of fixation, for example by modeling effects of feature complexity on fixation duration.

People's fixation locations are a good index of what they are currently thinking about. We have shown that more subtle indices of eye movements may provide additional, valuable information about stimulus processing, such as the difficulty of extracting features for the assessment of certain higher-order qualities, such as beauty and roughness of textures. The eyes are a window to the soul, as an English proverb goes. As we have shown, this may be true, in more ways than hitherto acknowledged.

Acknowledgments

This study was supported by grants from the European Commission, under contracts #043157 (Syntax), #043261 (Percept), and #033816 (GazeCom) to Frans W. Cornelissen, and by the Groningen graduate school of Behavioral and Cognitive Neuroscience. We thank Jan Bernard C. Marsman for explanation of the eye tracking procedure. This work represents only the authors' view.

Chapter 7.

The amygdala, top-down effects, and selective attention

Richard H.A.H. Jacobs^{1,2}

Remco Renken^{1,2}

Andre Aleman^{1,2}

Frans W. Cornelissen^{1,2}

While the amygdalar role in fear conditioning is well established, it also appears to be involved in a wide spectrum of other functions concerning emotional information. For example, the amygdala is involved in guiding spatial attention to emotional information, and it gets activated differentially during different tasks. Here, we propose feature-based attention as the basis for these seemingly disparate functions. Feature-based attention usually precedes spatial attention, and performing different tasks usually requires attending to different features. Although to date, no experiments have specifically tested the amygdalar role in feature-based attention, studies showing that the amygdala responds to simple elements, and findings of amygdalar involvement in non-spatial forms of attention hint at such a role. We propose that the amygdala is involved in guiding feature-based attention, a hypothesis that results in testable predictions. Our hypothesis builds on earlier proposals that the amygdala is involved in guiding attention and assessing biological relevance, but is more specific and can account for failures to find amygdalar activation when attention is guided by spatial cues.

Keywords: amygdala, feature-based attention, selective attention, top-down, orienting, conditioning

Affiliations:

1. Laboratory for Experimental Ophthalmology, School for Behavioral and Cognitive Neurosciences, University Medical Center Groningen, University of Groningen, PO Box 30001, 9700 RB Groningen, the Netherlands

2. BCN NeuroImaging Center, School for Behavioral and Cognitive Neurosciences, University Medical Center Groningen, University of Groningen, PO Box 30001, 9700 RB Groningen, the Netherlands

Introduction

The amygdala is a group of nuclei in the medial temporal lobe, located just anterior to the hippocampus. It is generally considered to be an emotion processor (J. E. LeDoux, 1992; Sergerie, Chochol, & Armony, 2008). Whereas animal experiments have established a crucial role for the amygdala in fear conditioning (e.g., Davis, 1992; Fanselow & LeDoux, 1999; Knight, Smith, Cheng, Stein, & Helmstetter, 2004; J. E. LeDoux, Cicchetti, Xagoraris, & Romanski, 1990), human neuroimaging (e.g., Breiter et al., 1996) and patient (Calder, 1996) studies have shown that the amygdala responds more strongly to emotional expressive faces than to neutral faces (but see Fitzgerald, Angstadt, Jelsone, Nathan, & Phan, 2006; Van Der Gaag, Minderaa, & Keyzers, 2007). In general, it is concluded that the function of the amygdala is related to the processing of incoming emotional information and to the execution of emotional responses such as an increased heart rate, increased startle responses, freezing (Davis, 1992) and increased skin conductance (L. M. Williams et al., 2001). In addition, the amygdala is often characterized as automatic,

unconscious, and fast (Dolan & Vuilleumier, 2003; Öhman, Carlsson, Lundqvist, & Ingvar, 2007). These characteristics emphasize the bottom-up processing of stimuli. At the same time, many reports indicate that the magnitude of the amygdalar activation depends on the task performed by the observer, implying that the amygdala exerts top-down influences on perception. Besides being implicated in bottom-up and top-down processing, the amygdala has been implicated in selective spatial attention.

In the present exposé, we will first review the evidence for these functions and properties of the amygdala and conclude that none of the currently existing theories about the amygdala can coherently explain all these, seemingly widely different, functions and properties. Next, we will present our new hypothesis that the unifying mechanism that does explain the diversity in amygdalar roles is selective – feature-based – attention. Several lines of evidence support this new hypothesis and we will review these. First, the amygdala differentially activates according to the task performed by an observer. Second, the amygdala is responsible for directing the eyes as well as spatial attention to emotionally tinged information. From these findings, we deduce that the amygdala is not actually involved in spatial attention per se, but in a process that precedes it (Hopf, et al., 2004), namely feature-based attention. Although this hypothesis is novel and has not yet been directly tested, it is supported by a substantial body of evidence showing that the amygdala responds to features and is involved in non-spatial aspects of attention. A question emanating from this hypothesis is what features the amygdala is sensitive to. Existing work implies that the amygdala can quite flexibly select the features that are relevant for the task at hand. In particular, the amygdala may be active while an observer learns to select the appropriate features to respond to. Thus, the well-known amygdalar role in fear conditioning may be one instance of a more general one in learning the relevance of features for current purposes. In the next sections we will elaborate these thoughts and generate a number of new predictions.

Automatic processing

The amygdala is thought to respond to stimuli of which we are unaware. This idea is based on the results of experiments in which participants are very briefly shown facial expressions that are immediately followed by another stimulus, called a mask. The brief presentations in combination with the mask supposedly prevent participants from becoming aware of the faces and their expressions. In such experiments, the amygdala still differentiates expressive from neutral faces (J. S. Morris, Öhman, & Dolan, 1998; Whalen et al., 1998), as it usually does for faces presented for longer durations. Unawareness is often associated with automaticity (e.g., Posner & Snyder, 1975).

However, the arguments for amygdalar involvement in the processing of emotional stimuli of which observers are unaware is contradicted by recent demonstrations that the amygdala is only activated in people who report being aware of the stimuli (Pessoa, 2005; Pessoa, et al., 2006; Pessoa, Padmala, & Morland, 2005). Moreover, the rapid detection of fearful stimuli survives amygdala damage (Tsuchiya, et al., 2009). Hence, these more recent results raise doubts about the earlier claims of amygdalar processing of stimuli that did not reach conscious awareness.

Still, even if the amygdala would respond to stimuli of which we are unaware, this does not imply that the processing involved is automatic. While it was originally thought that automatic processes were characterized by being involuntary, unintentional, autonomous, effortless, and occurring outside of awareness, such characteristics can be dissociated from each other (Bargh, 1992). Hence, an amygdalar response to stimuli of which we are unaware does not directly imply that processing of these stimuli is not amenable to volitional, top-down, influences. More importantly, the amygdala also responds to consciously perceived stimuli and the processing of this information is likely to be amenable to top-down influences.

Building on earlier proposals of a subcortical route serving a ‘quick and dirty’ assessment of stimuli for their significance (J. LeDoux, 1998; Liddell et al., 2005), occasionally a subcortical route to the amygdala has been proposed to mediate unconscious processing of stimuli (Jolij & Lamme, 2005; J. Morris, Öhman, & Dolan, 1999). A parallel cortical route is responsible for the conscious processing of stimuli, and also feeds into the amygdala (J. LeDoux, 1998). However, strong evidence that the subcortical route processes stimuli of which we remain unconscious is lacking and it may not even be faster than the cortical processing routes (Adolphs, 2008).

Besides the claims for automaticity, there are claims suggesting that the amygdala is mainly involved in the bottom-up processing of emotional stimuli (e.g., P. Wright et al., 2008). Neuroimaging experiments focusing on the amygdala seem to rely mainly on facial expressions and emotional scenes (e.g. from the International Affective Picture System picture set (Lang, Bradley, & Cuthbert, 2005)) to get it activated. Usually the focus is on the processing of these pictures, and not on the task observers have to perform. If tasks are varied, one task merely serves as a control for the other, usually emotionally tinged, task. Attentional aspects are rarely if ever varied in neuroimaging experiments focusing on the amygdala. Those that do will be mentioned in this review.

To conclude this section, the evidence that the amygdala processes stimuli of which we are not aware is far from compelling. Moreover, even if some stimulus aspects were to influence amygdalar activation outside of awareness, this does not exclude an amygdalar involvement in more controlled stimulus processing. Hence, both the view that the amygdala is an –automatic-- processor, and the related view – which seems to be implicitly present in the literature – that the amygdala is mainly concerned with the bottom-up processing of stimuli, do not stand in the way of our upcoming proposal that the amygdala is involved in attentional processing, which is often equated with controlled processing (Posner & Snyder, 1975).

Top-down effects

We will refer to a differential activation of the amygdala caused by different tasks as task effects. Task effects are usually cast in terms of top-down activation. Top-down activation refers to the effects of a pre-existing mind/brain state on perception. Dror and Fraser-MacKenzie (2008) define it as follows: “Top-down influences include, among other things, contextual information, expectation, what we already know, hope, motivation, and state of mind”. In the case of different tasks, the brain has been configured differently as a consequence of the instructions given to the participant. Brain states will also change in relation to changes in someone’s mood (a temporary condition, or state, as in state anxiety). In addition, different personalities and disorders may be associated with different brain states (more permanent, often called trait, as in trait anxiety). Although such permanent differences between persons are not necessarily the result of differences in top-down activation, we include them as tentative additional evidence for top-down effects.

Evidence for top-down effects on amygdalar activation comes from a study employing different tasks, without perceptual input. Mental imagery of expressive faces appears to enhance amygdalar activation compared to mental imagery of neutral faces (S. E. Kim et al., 2007). The amygdalar response to seeing food is also enhanced in a state of hunger, as a recent meta-analysis concluded (Van der Laan, De Ridder, Viergever, & Smeets, 2010). In addition, many studies report that the amygdalar activation depends on the task performed by the observer. Given the presumed role of the amygdala in emotional processing (J. LeDoux, 1998), these effects are usually attributed to the emotional nature of the task. However, different meta-analyses have come to contradictory conclusions. Specifically, Fusar-Poli and colleagues (Fusar-Poli, et al., 2009) concluded that emotional tasks are associated with more amygdala activation, while Costafreda and colleagues (Costafreda, Brammer, David, & Fu, 2007) concluded that emotional tasks are associated with less amygdala activation. Table 1 lists studies comparing the effects of different tasks upon amygdalar activation. Most of the studies compare at least one emotional task to one non-emotional task. We included several studies that do not report an amygdalar activation despite comparing emotional to non-

emotional tasks. Such null findings may be underrepresented due to the publication bias that favours non-null effects, and because we presumably were less likely to find such null effects in studies focusing on other findings.

The table shows that there is substantial evidence that the amygdala is involved in task-dependent or top-down processing, even though emotional tasks do not consistently increase or decrease the amygdalar activation when compared to the non-emotional tasks. Nevertheless, some consistent effects can be found in the reported studies.

One quite consistent result comes from reappraisal studies (grouped together as a single entry in table 1). In such studies, observers are shown negative emotional and neutral pictures. One condition typically consists of the observers watching the pictures passively, without a particular instruction. The other – emotional – condition typically consists of re-interpreting the negative emotional scenes in either a neutral or a positive manner (e.g., by thinking ‘this child is crying for joy’). With few exceptions (Harenski & Hamann, 2006; Kalisch, Wiech, Critchley, & Dolan, 2006; Urry et al., 2006) these reappraisal studies report attenuated amygdalar responses during the emotional (suppression) task (Beauregard, Levesque, & Bourgouin, 2001; Eippert et al., 2007; Goldin, McRae, Ramel, & Gross, 2008; Herwig et al., 2007; Johnstone, van Reekum, Urry, Kalin, & Davidson, 2007; Lévesque et al., 2003; Modinos, Ormel, & Aleman, 2010; Ochsner, Bunge, Gross, & Gabrieli, 2002; Ochsner et al., 2004; K.L. Phan et al., 2005; Ray et al., 2005; Wager, Davidson, Hughes, Lindquist, & Ochsner, 2008). In some of these studies, observers were also asked to enhance or prolong the feelings induced by the negative stimuli. Under these circumstances, amygdalar activation increases (Schaefer et al., 2002; Urry, et al., 2006).

Studies other than those reappraisal studies usually report enhanced amygdalar activation during the assessment of an emotional aspect (e.g., determining the expression of a face) in comparison to a non-emotional aspect (e.g., estimating the age of the same face) (see table 1). Stated in terms of the emotionality of the task, these findings seem to contradict each other. However, the reappraisal findings and the other task effects are consistent with the amygdala becoming more active when the observer emphasizes the emotional quality of a stimulus. Emphasizing aspects of stimuli is exactly what is called selective attention.

There is one possible exception to this pattern, however. Some studies that compare the classification of facial expressions to the classification of faces on the basis of gender find stronger amygdala activation during the gender classification task. Of the three studies that report increased amygdala activation in the non-emotional task (Keightley et al., 2003; Lieberman et al., 2007; Taylor, Phan, Decker, & Liberzon, 2003), two compared expression identification to gender identification (Keightley, et al., 2003; Lieberman, et al., 2007). There are also null effects regarding differences between gender and expression judgment, but these may be due to lack of power. The number of null effects is not substantial enough to attribute the non-null effects to chance. From this, it can be deduced that gender judgments are as potent as expression judgments in activating the amygdala. This implies that it is not emotionality as such that activates the amygdala, but some related factor.

Thus far, we have focused entirely on task effects, i.e. differential amygdalar activation due to differences in task requirements. But as stated at the beginning of the paragraph, top-down effects can be seen broader, encompassing also effects of temporary states such as mood. The situation is less clear for more permanent states such as mood disorders and personalities, which may theoretically be based on differences in bottom-up processing. Even though one may contest that mood disorders and personality are examples of top-down processing, we include them as tentative evidence for top-down factors influencing amygdalar activation, in table 2. Tables 1 and 2, together with some studies reported at the start of this section, suggest that amygdalar function is influenced by top-down effects such as the task being performed and the mood of the participant.

Reference	Tasks	Effect on amygdala	Emo effect
Bleich-Cohen et al. (2006)	Identify emotion, versus identify gender of faces	No task effect	o
Wright et al. (2008)	Rate pleasantness versus rate frequency (on television)	No task effect or interaction	o
Jacobsen et al. (2006)	Beauty versus symmetry judgment of block patterns	No task effect	o
Wright & Liu (2006)	Match faces on identity and on expression	No main effect of task, but left amygdala habituates to expression matching, not to identity matching	o
Winston et al. (2005)	Trustworthiness ratings versus age estimation	No task effect	o
Winston et al. (2003)	Choose more emotional versus more masculine face (both 2AFC)	No task effect	o
Lange et al. (2003)	Passive viewing versus gender decision versus emotion judgment of faces	Amygdala responds to fearful versus neutral faces during passive viewing, but not during gender or emotion judgments	-
Chatterjee et al. (2009)	Judging beauty versus facial identity	No task effect	o
Gusnard et al. (2001)	Decide pleasant or unpleasant, vs. indoors or outdoors	Amygdala not mentioned	o
Taylor et al. (2003)	Passive viewing versus pleasantness rating	Weaker activation in right amygdala during rating than during passive viewing	-
Hariri et al. (2000)	Matching facial expressions versus labeling facial expressions	amygdala up during matching of fearful/angry faces, down during labeling of fear and anger. Compared to matching geometric figures.	/
Hariri et al. (2003)	Matching of IAPS picture to IAPS (identical or emotionally congruent??) target, vs. matching the label natural or artificial to IAPS target, vs. matching geometric shapes	Higher activation during matching than during labeling	/
Liberzon et al. (2000)	Rate disgust on 5-point scale vs. rate recognition on 3-point scale (of negative and neutral IAPS pictures)	right amygdala activity to negative-neutral stimuli significantly greater during rating condition	+
Phan et al. (2004)	Rate emotional intensity vs. rate extent of self-relatedness of IAPS pictures	left amygdala more active during evaluation of emotional intensity	+
Habel et al. (Habel et al., 2007)	Matching emotion label to face (2 AFC; 5 emotions used) vs. matching closest age decade to face	stronger left amygdala activation during explicit emotion recognition; task difficulty mentioned as a possible explanation	+
Cunningham et al. (2004)	Good-bad judgments vs. abstract concrete judgments (about words describing socially relevant concepts)	Right amygdala more activated during good-bad judgments	+
Cunningham et al. (2008)	Judge overall (positive and negative) aspects of famous people (stimulus = their written name), vs. judge positivity, vs. judge negativity	Amygdala more activated to the aspect that was evaluated for	+
Keightley et al. (2003)	Gender discrimination vs. Expression identification + People count (2 or less vs. more than 2) vs. positive-negative scene evaluation	Amygdala more activated during gender discrimination and scene evaluation	- +
Gorno-Tempini et al. (2001)	Judgments of disgust vs. judgments of happiness vs. gender decision	Left amygdala more activated during judgment of disgust than during judgment of happiness	o
Kim et al. (2004)	Negative versus positive (written verbal) cueing of surprised faces	Left ventral amygdala more activated to negatively cued faces	/
Lieberman et al. (2007)	Matching affect label to affective face, matching affective face to affective face, matching gender of expressive face to gender of expressive face	Amygdala activation lower during affect labeling than during affect matching or gender tasks	-/o
Fichtenholtz et al. (2004)	Counting circles vs. counting emotional scenes in a stream of pictures	No task effect	o
Reappraisal studies (see text)	Reappraising a negative scene as neutral or positive, versus watching passively	Lowered amygdala activation during reappraisal	--/o

Table 7.1. Studies comparing emotional to non-emotional tasks. The last column indicates whether the emotional task lead to more amygdala activation (+), to less amygdala activation (-), no reported difference (o), or to effects that are not interpretable in terms of the emotionality of the task (/).

Paper	Groups	Effect
Carlson et al. (2010)	Individuals differing in anger expression	Higher anger expression was associated with higher amygdala response to masked fearful faces and decreased amygdala response to unmasked fearful faces
Dickie & Armony (2008)	Individuals differing in trait anxiety (regressor) and sex	Higher trait anxiety associated with a higher amygdala response to non-attended (but within-focus) fearful faces, only in women
Sehlmeyer et al. (2011)	Individuals differing in trait anxiety (regressor)	High trait-anxious subjects exhibited sustained amygdala activation during the extinction of fear conditioned responses
Most et al. (2006)	Individuals differing in harm avoidance (regressor)	High harm-avoidant individuals showed high amygdala activation when attending to non-specific items (e.g., look for the building or the landscape), compared to specific attention or low harm-avoidant individuals
Modinos et al. (2010)	Low vs. high psychosis-proneness	Amygdala response to negative pictures attenuated only in the low psychosis-prone participants
Herpertz et al. (2001)	Borderline vs. healthy controls	Amygdala activated to negative-neutral IAPS pictures, only in the borderline patients, not in the control group
Donegan et al. (2003)	Borderline vs. healthy controls	Borderline patients showed greater amygdala activation to emotional faces (vs. fixation) compared to healthy controls
Canli et al. (2002)	Extraversion (regressor) & borderline (regressor)	Amygdalar activation to happy (not angry, fearful, or sad) facial expressions correlated with extraversion scores. No correlations with neuroticism scores
Canli et al. (2001)	Extraversion (regressor) & borderline (regressor)	Amygdalar activation to positive (vs. negative) pictures correlated with extraversion; amygdalar activation to negative (vs. positive) pictures correlated with neuroticism scores
Haas et al. (2007)	Neuroticism (regressor)	Amygdalar activation during trials of high emotional conflict correlated positively with neuroticism scores
Wang et al. (2006)	Happy vs. sad mood	Amygdala activation to sad distractor faces and scenes (in an oddball task) was enhanced after viewing sad movie clips (sad mood induction) compared to happy mood induction
Chen et al. (2006)	Manic vs. depressed state	The brain response to sad faces was enhanced in the manics during the color rating, and attenuated during the expression rating, compared to both healthy controls and depressed patients.

Table 7.2 (continued on next page). Amygdalar involvement in top-down effect. Included are studies comparing different patient groups, studies looking at the effects of personality variables, and a study comparing different moods.

Paper	Groups	Effect
Sheline et al. (2001)	Depressed subjects vs. healthy controls	Depressed show increased amygdala response to masked fearful & happy faces vs. neutral faces
Somerville et al. (2004)	Individuals differing in state anxiety	Higher state anxiety associated with lower signal change to happy vs. neutral faces
Thomas et al. (2001)	Children with generalized anxiety disorder vs. children with major depressive disorder vs. healthy children	Anxiety: stronger amygdalar response to fearful vs. neutral facial expressions; Depression: blunted amygdalar response to fearful vs. neutral expressions
Bishop et al. (2004)	Low vs. high-anxious participants	low-anxious participants showed a reduced amygdala response to unattended versus attended fearful faces. High-anxious participants had an increased amygdala response to fearful vs. neutral faces regardless of attentional focus
Shin et al. (2005)	PTSD patients	PTSD show exaggerated amygdala responses to fearful vs. happy facial expressions, with diminished habituation of this contrast in the right amygdala
Etkin et al. (2004)	Trait anxiety (regressor)	Amygdalar activation to masked fearful vs. neutral faces reflects individual's trait anxiety level
Donegan et al. (2003)	Borderline patients	Borderline patients showed greater left amygdalar response to facial expressions of emotion (compared to fixation)
Straube et al. (2006)	Spider phobics vs. healthy controls	Healthy controls show no differential activation to mushrooms vs spiders. Spider phobics show enhanced left amygdala activation to spiders during the matching of geometric figures in the foreground, and enhanced bilateral amygdala activation to spiders during identification
Ashwin et al. (2007)	Asperger adults vs. healthy controls	Higher amygdala activation in the control group, for faces expressing high, low, or no fear. Activation increased with increasing fear, but not in Asperger
McClure et al. (2007)	Pediatric generalized anxiety disorder vs. healthy controls	Patients but not controls showed greater activation to fearful faces than to happy faces
Straube et al. (2004)	Social phobics vs. healthy controls	amygdala more strongly activated in phobics, in the 'implicit' (photographic or schematic face?) task, not during question "angry or neutral?"
Fakra et al. (2008)	Schizophrenia patients vs. healthy controls	groups had similar activation in the labeling condition; during matching, schizophrenics failed to activate bilateral amygdala
Gur et al. (2002)	Schizophrenia patients vs. healthy controls	Schizophrenics have lower amygdala activation than controls during positive-negative decision about faces (but not during age judgment)
Wright et al. (2003)	Small animal phobics vs. healthy controls	No group difference to expressive faces
Fu et al. (2007)	Unmedicated, acute major depression vs. healthy controls	Attenuated response to happy faces in patients
Cremers et al. (2010)	Neuroticism (regressor)	Enhanced connectivity between dorsomedial prefrontal cortex and amygdala during perception of fearful and angry faces is stronger for neurotic individuals

Table 7.2 (continued). Amygdalar involvement in top-down effect. Included are studies comparing

different patient groups, studies looking at the effects of personality variables, and a study comparing different moods.

To summarize this section, different tasks performed on identical stimuli can result in differential activation of the amygdala. Focusing attention on emotional aspects of the stimuli usually enhances amygdalar activation, even though other, related factors may more accurately capture what the amygdala responds to. The mood of the participant may also act as a top-down influence.

Selective attention as an explanation for task effects

Selective attention involves the differential processing of different stimuli (Dayan et al., 2000) or stimulus aspects. Evidence indicates that task effects in the amygdala can be explained by selective attention. One study (Van Reekum, et al., 2007) reports that the re-appraisal effects on the amygdala, alluded to above, can for a large part be explained by eye movements. The study found that participants' eyes tended to fixate on the non-emotional parts of images during re-appraisal, and that eye movements explained 35% of the variability in amygdala activation (Van Reekum, et al., 2007). The other indication comes from studies on SM, a patient diagnosed with bilateral amygdala damage. SM has problems identifying facial expressions and these problems are based on a deficit in focusing on the parts of the face that are relevant for identifying the expressions, i.e. the eyes and the mouth (Adolphs, et al., 2005).

The above studies point towards a relationship between amygdalar function and eye movements. In addition, autistic individuals' fixations on the eye region of faces are positively correlated to amygdala activation (Dalton et al., 2005). However, the relationship must be indirect, as SM could direct her eyes to the eyes and mouth in a face when explicitly instructed to focus on these parts, indicating a normal ability to generate eye movements. Intriguingly, in such explicit instruction conditions, the inability to recognize facial expressions also disappeared. This indicates that the deficit is not related to the bottom-up perception of emotionally relevant information, but rather must be related to directing attention and the eyes to the relevant information necessary for facial expression recognition. As eye movements are usually preceded by shifts in spatial attention (Deubel & Schneider, 1996; Kowler, Anderson, Doshier, & Blaser, 1995; Montagnini & Castet, 2007; Moore & Fallah, 2001), and the ability to generate eye movements appears to remain intact after amygdala damage, this implies that the amygdala must be involved in directing selective attention to the emotionally relevant parts of faces.

Further support for a role in directing attention comes from amygdalar stimulation in the cat, which results in attentional responses, characterized by an arrest of spontaneous activities, contralateral searching, pupil dilation, and pricking and directional movement of the ears (Ursin & Kaada, 1960). In humans, activation of the right amygdala to briefly presented masked fearful – but not angry or happy – faces, is positively correlated to the speed of finding negative schematic faces among other faces, and in deciding that there is no deviating (all neutral) expression (Ohmann, et al., 2007). This further supports the idea of an amygdalar role in spatial attention.

Two studies point out that this amygdalar role in selective attention depends on the availability of information in the periphery of the visual field. First, an investigation of SM, the patient with the bilateral selective amygdala damage, showed that when information in the periphery of the visual field is continuously blotted out the patient fixated the eye region of faces in a similar way as healthy controls who underwent the same procedure (Kennedy & Adolphs, 2010). Second, Gamer and Buchel (2009), using neuroimaging, found that in a task that required classifying expressions, amygdalar activation predicted a gaze shift towards the eye region of faces. This effect was particularly pronounced for fearful faces, for which the eye region is most diagnostic (Smith, Cottrell, Gosselin, & Schyns, 2005). This effect did not occur when faces were presented at a position where the eyes were already fixating. Hence, the amygdala appears to be involved in reorienting in order to bring relevant information into the focus of attention. In the case of faces, this reorienting could be based directly on the featural information, or on the –spatial– location of elements relative to other parts of the face, or on both.

To conclude this section, the amygdala appears to be involved in reorienting to relevant information. This leaves open the question what type of information triggers amygdalar involvement and what information is used to guide attention. Is the information spatial in nature, or is it non-spatial, such as particular visual features, elements or objects that are present in a scene? In the next section, we will first lay out the evidence for amygdalar involvement in non-spatial forms of attention.

The amygdala and non-spatial attention

Evidence for an amygdalar role in non-spatial forms of attention comes from olfactory studies, as well as from studies in which either the visual information to be attended overlaps spatially or in which the to-be-attended information is only defined spatially. In primates, olfactory orienting in the form of sniffing does not have a spatial component. Yet, amygdalar activation appears to be related to sniffing, rather than to olfactory perception per se. In the words of Ganzha (Ganzha, 1986): "The amplitude of bursts of olfactory rhythm corresponded to the vigor with which the odor was inhaled [...] The above rhythm occurred not only during olfactory stimulation, but also accompanied deep rhinal inhaling and sniffing movements without the breathing in of odoriferous substances, when the receptors of the nasal cavity [were] just stimulated by room air". Stimulation of the amygdala also leads to sniffing behaviour in cats (Ursin & Kaada, 1960). Therefore, it seems that the amygdala is involved in some form of non-spatial orienting. The relationship between sniffing behaviour and amygdalar activation is evidence for feature-based attention, without a clear spatial attention component.

In the visual modality, evidence for an amygdalar involvement in non-spatial forms of attention comes from studies where the information to be attended overlaps spatially. For example, in participants that are phobic for spiders, the amygdala shows a trend towards being more active when attending to spiders than to birds, compared to when these stimuli are presented superimposed on each other (Alpers et al., 2009). Moreover, compared to healthy control participants, patients with amygdalar damage respond differently to emotional pictures presented in the attentional blink paradigm (Lim, et al., 2009). In this paradigm, a rapid stream of stimuli is presented at a single location, and the observer's task is to identify or indicate the presence of some prespecified targets in the stream. Typically, observers miss a target more often when it shortly (200-500 ms) follows a previous target than when it is the first target, or compared to when it follows a first target after a longer lag. In normal observers, this 'blinking' of attention is attenuated when the second target is emotional in nature, and enhanced when the first target is emotional in nature. Patients with amygdalar damage appear not to be susceptible to these emotional effects in the attentional blink paradigm (Lim, et al., 2009). This implies that the drawing of attention by emotional stimuli relies on the amygdala.

There is also evidence that the amygdalar involvement is not triggered by purely spatial information. Above, we mentioned that it is hard to dissociate feature-based attention from spatial attention, as the former (almost) always precedes the latter. However, it is possible to contrast feature-based spatial attention to spatial-based spatial attention. Without using these terms, some neuroimaging studies have investigated one or both of these forms of attention. These studies find amygdalar activation in the feature-based variant, but not in the spatial-based variant.

The amygdala does not activate when to-be-attended stimuli are only indicated by means of a spatial instruction. Vuilleumier et al. instructed participants to match either top and bottom stimuli or left and right stimuli in displays where faces or houses could appear on the indicated positions. They found no modulation of the amygdalar response to expressive faces by the allocation of attention to the location of the faces, as compared to attending to the location of the houses (Vuilleumier et al., 2001). Neither does a cue that moves over a face like a typical scan path and that has to be followed result in more amygdalar activation than an atypical scan path, in which there is less focusing on the eyes and mouth, (J. S. Morris, et al., 1998), even though fixations on the eyes and mouth may be expected to lead to more amygdalar

activation, based on the above mentioned findings with patient SM. Moreover, attentional cues that predict the appearance of an angry face activate both the amygdala and the spatial attention network (a combination of frontal and parietal regions). In contrast, cues that are exclusively spatial only activate the spatial attention network (Mohanty, Egner, Monti, & Mesulam, 2009). Hence, this is evidence that cues that indicate what type of visual information to search for do activate the amygdala, whereas spatial cues do not.

Additional evidence for the guidance of non-spatial attention comes from an experiment that employed visual textures. In visual textures, by definition, the visual information tends to be rather evenly distributed over the stimulus, and consequently, shifts in spatial attention do not result in the perception of different information. In a neuroimaging study, visual textures were presented to observers who judged these stimuli for beauty, naturalness, and roughness. The study found that the amygdala was more active during the beauty judgement than during the other two judgments (Jacobs et al., 2011). This suggests that the need to attend to emotionally relevant visual information, such as presumably also occurs during beauty judgments, recruits the amygdala.

To conclude this section, there is compelling evidence for an amygdalar role in non-spatial forms of attention. A requirement to attend to spatially defined information fails to activate the amygdala. It does, however, activate when observers have to attend to non-spatially restricted olfactory or visual information. In the next section, we will evaluate the evidence that this is feature information, and that the amygdala is active when attention is guided towards features.

The amygdala and feature-based attention

We define features as quantifiable aspects of a stimulus or part of a stimulus. Examples are contrast energy in certain spatial frequencies, element orientation and size, and the degree to which certain colours are present. Features are thus not countable, as they are continuous, and reflect to what extent a certain stimulus aspect is present¹. In our view, this is also what distinguishes features from elements. Elements, such as bars, dots, eye brows or noses, are countable, and can be either present or absent. Elements can be more or less salient, depending on the difference in the feature values of the element and its surround. We define feature-based attention as attending to one feature, or a group of features, rather than others, irrespective of their location. Features may therefore be spatially overlapping. For example, one can attend to the orientation rather than the shape or the colour of a bar. In our view, attention is guided by features, not elements. For example, when searching for a red bar we will look for the feature “red” in the display. When an observer wants to find an element, such as a horizontal bar amidst vertical bars, his brain translates the instruction for searching for an element into a search for a diagnostic feature, in this case orientation, or a feature contrast.

Evidence showing that the amygdala is responsive to relatively simple features is accumulating. In a search paradigm that employed stimuli that contained schematic faces, Santos et al. (2010) found that the amygdala activated similarly when the targets were faces containing coloured (rather than black) eye brows and mouth, and when targets were happy or angry faces (rather than neutral). The visual texture study of Jacobs et al. (2011) mentioned earlier, also implied that when participants needed to attend to different features when performing different tasks, this affected amygdalar activation.

¹ We note that the literature often refers to elements, such as parts of faces, or bars, or units (‘textons’) in a texture or landscape, as features (e.g., Morgan, 2011). Luckily, this confusion is not too detrimental as in many cases where the literature refers to features – and where we would consider the term elements more appropriate – , these “features” will nevertheless have feature values that deviate from the surrounding feature values.

Searching for emotional faces may also engage the amygdala. Emotional faces can often be found faster than neutral faces, and these search advantages have been theoretically related to amygdalar function (M. G. Calvo & Nummenmaa, 2008a; Juth, Lundqvist, Karlsson, & Ohman, 2005). However, such search advantages can be accounted for by the presence of simple features in the stimuli (M. G. Calvo & Nummenmaa, 2008a; Juth, et al., 2005), such as the white of the teeth in some emotional face photographs (M. G. Calvo & Nummenmaa, 2008a), or orthogonal orientations (Coelho, et al., 2010) in angry schematic faces. Indeed, presenting only the eye region appears to be just as effective as presenting the whole face for producing a threat superiority effect (Fox & Damjanovic, 2006).

Based on fear conditioning experiments, it has been known for quite a long time that the amygdala can respond to simple features such as light flashes or simple tones, if these stimuli have been paired to shocks or other aversive stimuli (e.g., Davis, 1992). These conditioning studies have typically been performed in rats or other lab animals. Using neuroimaging, the amygdala has been found to activate in humans observing relatively simple elements, such as downward-pointing Vs (Larson, Aronoff, Sarinopoulos, & Zhu, 2009), and sharp as opposed to curved objects (Bar & Neta, 2007). The amygdala also responds to eye whites, but not to their negative (eye blacks, P. J. Whalen, et al., 2004), as well as to the spatial frequencies present in faces (Vuilleumier, et al., 2003). Indirect evidence that the amygdala is responsive to relatively simple features comes from a study showing that contrast sensitivity is enhanced after the presentation of fearful, as compared to neutral, faces, an influence that is presumably mediated by the amygdala (Phelps, Ling, & Carrasco, 2006).

To conclude this section, the amygdala responds to features as well as to elements which can be distinguished based on features. The amygdalar involvement in spatial forms of attention may be the result of non-spatial, feature-based forms of attention, as in search tasks spatial attention normally follows feature-based attention (i.e., searching for a target is followed by focusing on the target) (Hopf, et al., 2004). In view of the evidence for an amygdalar role in feature based attention, it may well be the case that the top-down effects on amygdalar activation are all the result of differences in feature-based attention. But what are the features that the amygdala is sensitive too? This issue is addressed in the next section.

Fixed features vs. Relevant features

We mentioned studies in which the amygdala responded to fairly simple elements such as angular objects, downward-pointing “V”s, and eye whites. This suggests that the amygdala simply responds to certain features, irrespective of their emotional meaning or relevance. On the other hand, such features have all been linked to negative emotions. For angular objects, their association with discomfort or harm is obvious (Bar & Neta, 2007), while downward pointing “V”s resemble certain aspects of a frowning face (Larson, et al., 2009). Larger eye whites are diagnostic of fearful faces (P.J. Whalen et al., 2004). So in all these cases, an association with fear and/or potential harm is present. This kind of amygdalar activation would be in line with the prevalent view of the amygdala as an emotion processor, in particular of negative emotions. Also, the stronger activation of the amygdala during beauty, as compared to roughness, judgments (Jacobs et al., 2011) is consistent with an amygdalar role in emotion processing – only this time including positive emotions.

The search advantage for emotional faces, mentioned above, seems to rely on salient elements present in the faces, such as the presence of visible teeth in natural faces (M. G. Calvo & Nummenmaa, 2008a), or the presence of orthogonally oriented versus parallel lines in schematic faces (Coelho, et al., 2010; Horstmann, et al., 2006). The variety of features to which the amygdala responds suggests that it is able to flexibly guide attention to the relevant, emotional, aspects of the stimuli, at least when the task allows to discriminate targets and distracters based on simple cues. The fact that the distractor faces in search tasks are typically homogeneous facilitates such easy discriminations (M. G. Calvo & Nummenmaa, 2008a; Juth,

et al., 2005), although the effect was recently demonstrated to extend to conditions with heterogeneous distractor faces (Pinkham, Griffin, Baron, Sasson, & Gur, 2010). A flexible adaptation to the relevant features by the amygdala would accommodate findings of search advantages for stimuli that had little opportunity to shape the evolution of our brain's functionality, such as guns (Blanchette, 2006; Brosch & Sharma, 2005). Findings of search advantages for fear relevant stimuli such as snakes and spiders, but also cats, among flowers and mushrooms (Lipp, Derakshan, Waters, & Logies, 2004), might all reflect a learning of diagnostic features by the amygdala. Inputs to the amygdala appear to originate from low-level sensory cortices as well as polymodal association cortex (Yaniv, Desmedt, Jaffard, & Richter-Levin, 2004), allowing for attention to features of differing levels of complexity. We suggest that simple features, such as the blueness of a stimulus, always provide input to the amygdala for determination of the importance of this cue. Given the abundance of such cues, the importance attached to it will be relatively low, but may still be reflected in judgments such as beauty ratings. For many objects, their associated importance will merely be a weighted sum of the importance attached to its features. Representations of such objects need not provide input to the amygdala beyond that already provided by their features. However, other objects may prove to be highly important to detect, even though the values for the simple features do not indicate this. In such cases, a combination of features has to be found that fairly uniquely represents this object, for association with a rated importance. The input to the amygdala is then 'escalated' to incorporate this more complex feature. With this view we deviate from Palmer & Schloss's (Palmer & Schloss, 2010) proposal that preferences for colours (i.e., features) are mediated by objects.

The finding by Santos et al. (2010) that the amygdala responds as strongly to target faces defined by a blue or red mouth and eye brows as to similar target faces, but defined by a happy or sad/negative expression, indicates that it is not emotionality per se to which the amygdala reacts. Furthermore, the fact that the amygdala often gets more activated during gender decisions than to expression decisions about faces, mentioned above, suggests that there are factors other than emotionality per se at work. As someone's gender seems at least as relevant to human beings as someone's expression, relevance in general may be what drives the amygdala. A general role in –biological– relevance detection has been stressed by others (Sander, Grafman, & Zalla, 2003).

Evidence that the amygdala responds to relevant information comes from studies showing that emotionally neutral but task relevant stimuli will activate the amygdala (Kiehl, Laurens, Duty, Forster, & Liddle, 2001; Laurens, Kiehl, & Liddle, 2005; Ousdal et al., 2008). Emotional stimuli, whether they are conditioned stimuli or expressive faces, are a subset of the class of relevant stimuli. The responsiveness of the amygdala to task instructions suggests that the relevance is not restricted to biologically relevant stimuli. Such a role could explain why gender judgments evoke higher or similar amygdala activation, compared to expression judgments. In our view, positing a general role for the amygdala in relevance detection is too broad. The complete nervous system is involved in filtering relevant information, not just the amygdala. So, to be meaningful the proposed amygdalar role needs to be more specific. In the next section, we propose that a flexible adaptation specifically to relevant features may distinguish the amygdalar role from the more rigid sensory cortices.

To conclude this section, features do not activate the amygdala in a fixed manner. Emotional relevance of the features does not appear to be a prerequisite for amygdalar activation either. Rather, a feature's momentary relevance appears to determine the activity of the amygdala.

Learning what is relevant

We could leave the story as it is at this point, and conclude that the amygdalar role in feature-based attention may underlie both its differential activation under different task instructions and its involvement in spatial search. However, we believe there is one final connection that can be made, namely with the well-known amygdalar role in conditioning.

The conditioning literature suggests a flexible role for the amygdala in detecting features that personal experience has taught are important. Rolls (1999, p. 48) has proposed that the amygdala is involved in relatively slow types of learning, involving multiple trials, as compared to the more flexible orbitofrontal cortex.

Many of the neuroimaging studies reported here indicate that the amygdala adjusts flexibly depending on the task at hand. Because such neuroimaging studies involve many trials, the tasks may involve a learning of the features that are relevant for performing the task. Consequently, the amygdala may become involved during the learning of the task. The amygdalar role in conditioning supports this possibility. Animal experiments by Gallagher and Holland (Gallagher & Schoenbaum, 1999; Holland & Gallagher, 1999) suggest that it is the unpredictability of a cue that drives the amygdalar response, rather than a learned consistent negative prediction, and similarly Knight et al. (Knight, et al., 2004) report that the amygdala is particularly activated when relationships between stimuli change. Neuroimaging studies show that the amygdala responds more strongly to fearful faces than to angry faces, presumably because the fearful faces are more ambiguous regarding the source of threat (Whalen, 1998). Pursuing this line of thought, Adams et al. (2003) showed that the amygdala responds more strongly to fearful faces with direct gaze and angry faces with averted gaze rather than to fearful faces with averted gaze and angry faces with direct gaze, presumably because angry faces with direct gaze indicate more clearly that the threat is directed at the observer, and fearful faces with averted gaze should indicate more clearly where in the environment threat is to be expected (Adams, et al., 2003). The amygdalar involvement in resolving ambiguity (Brand, Grabenhorst, Starcke, Vandekerckhove, & Markowitsch, 2007), in assessing trustworthiness (Todorov & Engell, 2008), and in novelty detection, fits with the proposed role in learning to attend to relevant features. However, the conditioning literature suggests that the amygdala is necessary both for the acquisition and the expression of conditioned fear (Wilensky, Schafe, Kristensen, & LeDoux, 2006). So it seems that the amygdala will be responsive to novel and ambivalent stimuli initially, and retain its responsiveness to stimuli and stimulus features that have proven to be relevant.

To conclude this section, it seems that the amygdala is involved in learning the relevance of features. Once learned, it retains responsiveness to the features if they prove to be relevant, but it loses responsiveness if features turn out to be irrelevant. Hence, the amygdala can flexibly adjust to the momentary relevance of features. That being said, the amygdala may be slower than some other regions, such as the orbitofrontal cortex, in adapting to fast changes in relevance.

Connecting input to output

As we indicated at the start of our paper, most neuroimaging experiments stress the perceptual influences on amygdalar activation. This may be a consequence of the passive nature of the experiments, where the observers of the stimuli lie motionless, only moving their fingers for pressing buttons to indicate their decisions. In focusing on amygdalar guidance of attention, we put more emphasis on the output of the amygdala, to guide perception and attention.

To be sure, the amygdala is a central perceptual node where information from olfactory, visual, auditory, and tactile (Romanski, Clugnet, Bordi, & LeDoux, 1993; Zald & Pardo, 1997) modalities converges. However, from animal studies it is clear that the amygdala also plays a key role in organized defence reactions. Via output connections to the hypothalamus and brainstem regions, it exerts effects on fear potentiated startle responses, freezing behaviour, and other fear-related behaviours (Davis, 1992). The evidence reviewed above indicates that it also exerts an effect on spatial attention and eye movements. These effects on spatial attention are thought to rely on projections from the amygdala back to visual areas (Adolphs, 2004; Vuilleumier, Richardson, Armony, Driver, & Dolan, 2004), or on projections from the amygdala to orbitofrontal or basal forebrain areas (Vuilleumier, 2005), or on projections from the amygdala to the cingulate gyrus (Baluch & Itti, 2011). The animal literature indicates that lesioning the amygdalar

output to subcortical areas interferes with orienting/search behaviour, although no pathway to a single brainstem structure seems solely responsible for this (Ursin & Kaada, 1960b). Hence, the amygdalar influences on attention may not rely on direct projections to the cortex, but on widespread connections to subcortical areas, which may in turn influence cortical responsiveness.

Summary

We have reviewed evidence that the amygdala is involved in top-down effects and that it is critical for guiding spatial attention. We provided evidence arguing that the amygdala is in fact guiding feature-based attention. Recapitulating the arguments of the previous chapters:

We argued that the evidence that the amygdala processes stimuli of which we are not aware is far from compelling. Moreover, even if some stimulus aspects were to influence amygdalar activation outside of awareness, this does not exclude an amygdalar involvement in more controlled stimulus processing. Hence, both the view that the amygdala is an –automatic-- processor, and the related view – which seems to be implicitly present in the literature – that the amygdala is mainly concerned with the bottom-up processing of stimuli, do not stand in the way of our proposal that the amygdala is involved in attentional processing, which is generally equated with controlled processing.

Next, we reviewed how different tasks performed on identical stimuli can result in differential activation of the amygdala. Focusing attention on emotional aspects of the stimuli usually enhances amygdalar activation, even though other, related factors may more accurately capture what the amygdala responds to than the emotion itself.

Next, we indicated how the amygdala appears to be involved in reorienting attention in order to select relevant information – such as the eye region in faces – and bring it into the focus of attention. This role can also – indirectly – explain its involvement in guiding eye-movements to such information. This left open the question what type of information triggers amygdalar involvement and what information is used to guide attention.

We found that there is compelling evidence for an amygdalar role in non-spatial forms of attention. A requirement to attend to spatially defined information fails to activate the amygdala. It does, however, activate when observers have to attend to non-spatially restricted olfactory or visual information.

Next, we reviewed evidence that indicates that the amygdala responds to features as well as to elements which can be distinguished based on features. As feature-based attention tends to precede a re-focusing of spatial attention (Hopf, et al., 2004), the amygdalar involvement in spatial forms of attention may be the result of non-spatial, feature-based forms of attention, as in search tasks spatial attention normally follows feature-based attention (i.e., searching for a target is followed by focusing on the target). In view of the evidence for an amygdalar role in feature based attention, it may well be the case that the top-down effects on amygdalar activation are all the result of differences in feature-based attention.

Moreover, we found that features do not activate the amygdala in a fixed manner. Emotional relevance of the features per se does not appear to be a prerequisite for amygdalar activation either. Rather, a feature's momentary relevance appears to determine the activity of the amygdala.

Finally, we argued that it seems that the amygdala is involved in learning the relevance of features. Once learned, it retains responsiveness to the features if they prove to be relevant, but it loses responsiveness if features turn out to be irrelevant.

We started our review by asking how task effects on amygdalar activation can be explained. We provided compelling evidence that the amygdala is involved in re-focusing the eyes and spatial attention to emotionally relevant parts of faces. Next, we showed that the amygdala appears also to be involved in non-spatial forms of attention. Based on this evidence, we proposed an amygdalar role in feature-based attention. This proposal was supported by a variety of findings showing that the amygdala is involved in non-spatial forms of attention, and that it responds to relatively simple elements and features such as orthogonally oriented lines, low spatial frequencies, eye whites, and simple tones and light flashes. By way of its involvement in feature-based attention, the amygdala may influence spatial attention, which in search tasks often follows the localization of relevant features in the periphery of the visual field.

In summary, we propose that the amygdala learns the features that are relevant for the task at hand, and subsequently guides responses (orienting, attention) to those features that have proven to be relevant. In our view, this proposal is able to explain or at least accommodate (nearly) all the major behavioural and neurological findings about the amygdala. We will now compare this theory to previous theories, discuss non-trivial and testable predictions for future experimentation, and address some open questions.

Comparison to previous theories

There have been earlier theories which postulated that the amygdala is involved in selective attention. We will compare our theory with two of them. One theory restricts the amygdalar attentional role to reacting to bottom-up, stimulus-driven processing, reserving top-down influences for the spatial attention network (Vuilleumier, 2005). As we have shown, the amygdala does not only respond to stimuli in a bottom-up way, but it also exerts top-down, attentional effects. Consequently, a strict separation between top-down spatial effects and bottom-up emotional effects cannot be maintained. Tasks influence feature-based attention, thereby mixing up bottom-up salience effects and top-down goals.

Another proposal sees a role for the amygdala in exerting top-down influences on perception, and this proposal sees attention as a two-stage process, apparently similar to our proposal for separate stages for feature-based detection and spatial attention guidance (Compton, 2003). Despite its superficial resemblance, the latter proposal struggles with the absence of attentional effects on the amygdala when faces are matched, compared to when houses are matched, in conditions where the to-be-attended stimuli are indicated by their spatial position (Vuilleumier, et al., 2001). This proposal sees other experiments which do find amygdalar activation related to attention (Pessoa, McKenna, Gutierrez, & Ungerleider, 2002) as confounded by the different task demands. We take the stance that different tasks promote focusing on different features, thereby enhancing amygdalar activation.

Predictions

Our present hypothesis postulates that the amygdala is involved specifically in feature-based attention and that other, apparently spatial functions are a consequence of this role.

The amygdala should be involved when searching for a target defined by features such as its colour or orientation. If, however, the target is indicated not by a feature but by a spatial cue, the amygdala should not be activated in the search. Patients with amygdalar damage should have difficulty finding targets defined by features other than its location. Many experiments have investigated selective attention using neuroimaging techniques, but apart from Mohanty et al. (Mohanty, et al., 2009) the amygdala is hardly ever mentioned. These experiments typically do not compare feature-based attention with spatial attention. We call for more experiments that do. Monhanty et al. found amygdalar activation with cues indicative of fearful faces. We predict that any cue that indicates what kind of stimulus to expect will lead to higher amygdala activation than spatial cues. We also predict a large degree of flexibility regarding the nature of

the features. We expect that the amygdala is in fact able to guide attention to whatever feature is relevant for the task at hand.

Another issue is related to the changes in amygdalar activation over the course of multiple trials. If learning feature relevance is the driving factor underlying amygdalar activation, one would predict high amygdalar activation in the early experimental phases. This period of increased activation would be prolonged as the complexity, diversity or ambiguity of stimuli increases. The strong amygdalar response to faces may be a consequence of face stimuli being relatively complex. Alternatively, as the amygdala appears to be involved also in the expression of learned responses, it may continue to respond to relevant items after this learning phase.

Open questions

Is there still a role for the amygdala in small scale spatial attention?

In our section on non-spatial attention, we referred to studies employing spatially overlapping stimuli, or rapidly alternating stimuli in the center of attention (the attentional blink), or visual textures (in which features overlap spatially). We argued that as the sought-for information was spatially overlapping with the irrelevant information, amygdalar activations to such stimuli indicated that it is involved in non-spatial forms of attention. One could raise the objection that spatial attention may operate at a small spatial scale. When faces are presented in the attentional blink paradigm, for example, an observer can still reorient spatially to the elements within the face, such as the eyes, the nose, and the mouth. Similarly, when viewing visual textures an observer may reallocate his attention from dark to bright, or from blue to red parts of the image, and this has in fact been shown to occur (Jacobs, Renken, Thumfart, et al., 2010). Attention then still has a spatial component in these cases. One counterargument could be that stimuli in the attentional blink paradigm are presented very briefly, for only up till 100 milliseconds per stimulus. Also in the study of Alpers et al., the spatially overlapping stimuli were presented for only 200 milliseconds. These durations seem too short to allow for saccades. However, covert attention may shift faster than overt eye movements, and a (small) saccade might be initiated within this time window. So we cannot completely rule out a spatial component to attention in these cases, and maybe the amygdala is responsible for that. At this scale, spatial attention and feature-based attention may be extremely hard to dissociate from each other, given the tight coupling between the two, at least in visual search (Hopf, et al., 2004). In fact, in some ways, the amygdala may serve as an interface between feature-based and spatial attention. We already mentioned a study that only found amygdalar activation when attention had to be reoriented to the eye region of faces, but not when the faces were presented so that the task-relevant eye region was already fixated to start with (Gamer & Buchel, 2009), supporting this possibility. Still, we think that the other evidence we put forward, in particular the studies implicating the amygdala in feature-based as opposed to spatial-based reorienting, speaks strongly in favour of an amygdalar role in feature-based attention, possibly as the basis for spatial reorienting.

Is orienting to elements in faces based on spatial attention?

We mentioned that orienting to the elements in faces can in principle be based on orienting to features, as well as on orienting based on the well learned fixed spatial relationships between the elements. Taking Adolphs' finding that patient SM would not orient to the eye region of faces when performing an emotion classification task, but would orient to the same eye region when explicitly instructed to do so, we are inclined to interpret this pattern in line with our hypothesis. I.e., we believe that a request to perform an

emotional task has to be transformed in a search for the relevant features, by our brain. SM could not do that, and as a consequence failed to focus on the appropriate elements. When explicitly instructed to focus on the eyes, we are forced to take the position that this is not based on feature-based attention, but on spatial attention. So, we predict that the amygdala is not necessary when the observer is asked to look at an element or a region which can be found based on its fixed spatial relationship to other elements. When spatial relationships are not fixed, the amygdala will be required. Also if the request is not to focus on an element, but to perform some task based on the information that is present in the features in the element, the amygdala will be required.

Conclusion

We propose that the amygdala learns the features that are relevant for the task at hand, and subsequently guides responses (orienting, attention) to those features that have proven to be relevant. In our view, this proposal is able to explain or at least accommodate (nearly) all the major behavioural and neurological findings about the amygdala. The theory results in non-trivial and testable predictions for future experimentation.

8. Conclusions

I started this thesis with the aim of getting a grip on the processes involved in the perception of beauty. This objective has been met at the behavioural and the neural level.

At the behavioural level, beauty judgments were found to resemble judgments of elegance, warmth, interestingness, colourfulness, and ‘feeling’. Judgments of complexity, age, and roughness were found to be independent of all these judgments. Beauty appeared to depend to a fair extent on visual texture features such as average intensity, intensity variation, saturation/redness, low spatial frequencies, and diagonal orientation of elements.

At the neural level, the fusiform cortex showed activation correlating with the beauty level of the observed stimuli. This activation may be related to some of the features that correlate with beauty. The frontomedian cortex and the amygdala came up as regions that responded more strongly to beauty level during a beauty judgment than during a roughness judgment, and are therefore strong candidates for regions that actually do make a beauty assessment. Our most important finding was that the amygdala was activated more strongly during beauty judgments than during roughness and naturalness judgments. The literature shows that the amygdala is involved in selective attention. As we presented stimuli containing repetitive stimuli, in which features were very similar all over the stimulus, re-focusing attention on another part of the stimulus would hardly lead to the perception of new information. Hence, effects of spatial attention were minimized. In consideration of the reliance of the different judgments on different features, the higher activation of the amygdala during beauty judgments is then very likely to result from differences in feature-based attention. In consideration of the amygdalar involvement in emotional processing, and of the more emotionally tinged nature of a beauty judgment, the amygdalar role may be restricted to guiding attention to emotionally relevant information.

To further investigate the hypothesized role for the amygdala in feature-based attention, I examined eye movement parameters of observers judging visual textures for beauty and roughness. I found that fixations lasted longer during roughness judgments, suggesting that it took longer to extract the features that are relevant for arriving at roughness judgments. On average, observers also looked at more colored patches in textures while they were making beauty judgments than when they were making roughness judgments. These two findings both suggest important differences in feature-based attention during the two judgments.

Overall then, it seems that beauty and roughness assessments are characterized by differences in the deployment of feature-based attention, and that these differences are mediated by the amygdala.

Additional conclusions

As cognitive scientists we are taught that many words, such as ‘attention’, do not refer to a single concept, and that we should be careful to distinguish the different senses in which the word is used. Following this practice, it may be easy to lose sight of the inter-relatedness of some senses in which the word attention is used. For me, and I suspect for most readers, it took some time and effort before I could see how top-down attention could be related to feature-based attention. The lesson to be learned is that we should not assume words in everyday language use to refer to a single concept, but at the same time it may be fruitful to hypothesize such terms to refer to concepts that are at least somewhat related.

Relevance for the medical sciences

The questions posed in this thesis are all about aesthetics and its relation to stimulus features and the underlying neural substrates. These questions and answers are mainly relevant for neuroscientists, psychologists, people working in the arts, and material designers. Yet this thesis is written for a Ph.D. in the medical sciences. So a natural question to ask is: What is the relevance of this thesis to the medical sciences?

A large part of this thesis deals with the function of the amygdala, and as such, it is directly relevant for patients with a dysfunctioning amygdala. The clinical literature abounds with mood and other disorders which are hypothesized to result from amygdala dysfunction. A better understanding of the amygdala may aide in understanding deviant processing mechanisms accompanying these disorders. In fact, the idea that the amygdala is connected with top-down influences in perception, as reflected in processing biases for emotional information, has been readily embraced by the clinical literature (e.g., see the studies reporting on task effects reported in table 7.2). Nevertheless, the evidence for top-down influences in perception so far comes mainly from patient groups showing deviant amygdalar activations to emotional stimuli, in experiments manipulating the emotional content of stimuli, in a bottom-up fashion. I hope this thesis will lead the way to more investigations where the selective attention and/or tasks are manipulated, to investigate top-down processes and attention in patient groups and healthy participants.

Texture perception has been implicated in several neurologic and psychiatric disorders, such as dyslexia, autism, schizophrenia, and visual agnosia. Insight in the processing of textures may lead to a better understanding of processing mechanisms in such disorders. There are no case reports about specific disturbances in the assessment of beauty of textures. As textures are thought to be processed in brain regions that are anatomically separated from regions processing shapes (Arcizet, Jouffrais, & Girard, 2008; Beason-Held, et al., 1998; J.S. Cant, et al., 2009; J. S. Cant & Goodale, 2007; Cavina-Pratesi, et al., 2010a, 2010b; Peuskens, et al., 2004; Puce, et al., 1996; Stilla & Sathian, 2007), specific disturbance of texture input to beauty assessment regions may be expected. Possibly, such cases are not serious enough to warrant medical attention.

To my knowledge, there are not even case reports about selective disturbance of beauty assessments. It may be the case that beauty assessment relies on broader processing mechanisms, that are also involved in emotion processing, so that usually only the emotional impairment would be noted. A disorder that comes close to a disorder in beauty perception is anhedonia. Anhedonia is a disorder in experiencing pleasure, and occurs mainly as a symptom in schizophrenia. A recent study showed that schizophrenics have a diminished sensitivity to feature changes in works of art (Y. Chen, Norton, & McBain, 2008). The work presented in this thesis furthers our understanding of beauty, and anhedonia is likely to result from a failure of these same, or closely related, mechanisms. Hence, our work may aide in the understanding and ultimately the treatment of anhedonia, through interventions aimed directly at the working of the amygdala, or probably wiser, through behavioural interventions indirectly remedying amygdalar function. For example, by devising ways to guide attention to beautiful or emotionally/biologically relevant information.

Art and beauty may in general have healing powers (Sheppard, 1994). The effects of relaxation, as opposed to stress, on human development (Perry & Szalavitz, 2007), on the immune response (Bartolomucci, 2007; Ben-Eliyahu, Yirmiya, Liebeskind, Taylor, & Gale, 1991), and on recovery after illness or injury (Holden lund, 1988) are beneficial. Assuming that beautiful stimuli are relaxing, surrounding patients with beautiful stimuli may aid in their recovery, and raising our children in beautiful environments may promote their health and growth. Textures may be an important source for healthy development, since classic studies by Harlow have shown how monkeys' mothering behavior benefits from being raised by a clothed (i.e., textured), as opposed to a wire frame, puppet mother (Harlow, Harlow, Dodsworth, & Arling, 1966). An understanding of what stimulus characteristics are generally found beautiful may certainly help in promoting healthy development.

Future directions

Many questions are left unanswered. For example, we examined aesthetic responses to visual textures against a grey background. One may ask to what extent our results generalize to other spatial contexts, and to what extent our results remain valid for real-life decisions, such as what clothes to buy, or how to decorate our walls. We also restricted ourselves to the visual domain, and it would be interesting to see whether preferences for textures in the visual domain agree with preferences in the tactile domain. It may be wise to ask for pleasantness, rather than beauty, when examining preferences in the tactile domain. The next question then is to what extent visual and tactile processing converge (in the brain) when judging textures for pleasantness, roughness, and other judgments. Alternatively, does visual information maybe project directly to the tactile domain, when making roughness judgments? Another question is to what extent all our findings about roughness and beauty generalize to the other evaluative and descriptive judgments, to which they are related according to our results. Our finding that many judgments can be summarized by these two dimensions does not imply that all evaluative judgments are the same. There are likely to be differences between elegance and beauty, and between roughness and complexity. It would be highly controversial to conclude that our use of all these words is redundant. Finally, it would be interesting to confirm the relationships between visual texture features and beauty ratings we found by selectively manipulating the feature dimensions we found to be relevant. In practice, this will be impossible as many features are related, but one can try dissociating the features as much as possible. While pursuing this approach, it may be interesting to see if variables that affect our appreciation of music (developing over time, and in that sense one-dimensional) do also affect our appreciation of visual textures (which are spatial and two-dimensional).

9. Summary

To summarize this thesis, the main goal was to understand beauty. The first aim was to investigate whether observers showed consistency in their beauty judgments about visual textures. I showed that this was the case, although it is necessary to select the most and least beautiful textures to demonstrate this. The second aim was to establish the relationship of beauty judgments to other judgments about the same stimuli. I found that beauty judgments were highly related to other evaluative judgments, such as elegance, warmth, interestingness judgments, and also colourfulness judgments. These judgments as a group were unrelated to another group of roughness, complexity, and age judgments about the same visual textures. The latter judgments were also highly interrelated, and naturalness judgments occupied an intermediate position between these groups of judgments. From then on, I compared responses related to the beauty judgments to responses related to the roughness judgments. My third aim was to relate beauty judgments to visual texture features. I found that low spatial frequencies, colour information, and diagonally oriented elements were important factors in determining the beauty of textures. My fourth aim was to elucidate brain responses related to beauty assessments, by looking for brain regions that responded to the difference between beautiful and ugly visual textures during the beauty judgment, but not during other judgments. I found that the frontomedian cortex and the amygdala showed exactly this pattern, and conclude that these regions are involved in making beauty assessments. Other regions that were previously implicated in the assessment of beauty seem to be only indirectly involved in assessing beauty. For example, the posterior cingulate cortex may be involved in directing attention to the inner mental world, while the fusiform cortex may be responsive to features which happen to be judged as beautiful. For the amygdala, I believe its involvement in beauty assessments may lie in guiding attention to emotionally tinged features. This belief is based on evidence from various sources that the amygdala is crucial for guiding attention to emotional,

or more generally relevant, information. Because of my use of visual textures, which contain homogeneously distributed feature values, I believe we provided evidence that the amygdala is involved in feature based attention, and that its supposed role in guiding spatial attention is only secondary to this primary role. To get an idea of attentional differences between beauty and roughness judgments, I then performed an eye tracking study, comparing eye movement parameters during these judgments about visual textures. I found that fixations were longer during roughness than during beauty judgments, and that the eyes jumped around more during beauty than during roughness judgments. This pattern I interpreted to reflect differences in feature based attention, with feature extraction for a roughness assessment taking more time per fixation than feature extraction for a beauty assessment. Examination of the texture patches around the fixations revealed that in particular coloured patches tended to be fixated more during beauty judgments than during roughness judgments. Finally, I reviewed the evidence for an amygdalar involvement in guiding feature-based attention. The amygdalar involvement in selective attention, its involvement in studies where attention has to be paid to features and/or emotional information, and its non-involvement in studies where attention is guided in other (spatial) ways, all point to exactly such a role. The amygdala may be involved in guiding feature based attention in general, but it is likely that it is mainly involved in guiding attention to emotionally or otherwise relevant features in particular. In consideration of the well established role of the amygdala in fear conditioning, and its higher activation to ambiguous as compared to non-ambiguous stimuli, the amygdala may be particularly involved in learning to select the relevant features, in a relatively flexible way.

10. Samenvatting (Nederlands)

In dit proefschrift onderzoek ik hoe we de schoonheid van visuele texturen bepalen. Eerst stel ik vast dat er een zekere consistentie is in welke texturen mensen mooi vinden. Vervolgens onderzoek ik de relaties tussen verschillende beoordelingen over texturen, en vind dat de beoordelingen grotendeels in twee groepen vallen, namelijk een groep van beschrijvende en een groep van evaluatieve beoordelingen. Deze groepen beoordelingen zijn onafhankelijk van elkaar, zodat een ruwheidsbeoordeling een goede controle vormt voor de schoonheidsbeoordelingen waarin we geïnteresseerd zijn. Mooie texturen blijken relatief laag-frequente patronen te bevatten, gekleurd te zijn, en vooral een diagonale orientatie van elementen te hebben. Kijkende naar hersenactivatie die gepaard gaat met schoonheidsbeoordelingen, blijken vooral de frontomediane cortex en de amygdala sterk te reageren op de schoonheid van texturen, en dan met name tijdens het maken van schoonheidsbeoordelingen. Dit wijst erop dat deze hersengebieden een belangrijke rol spelen in het bepalen van schoonheid. Gezien de rol van de amygdala in het sturen van de ogen en de selectieve aandacht, denken we dat de rol van de amygdala bestaat uit het richten van de aandacht op kenmerken die bepalend zijn voor schoonheid. Een aantal andere hersengebieden die enkel gevoelig zijn voor het soort beoordeling dat gemaakt wordt, of voor de mate van schoonheid, zijn waarschijnlijk slechts indirect betrokken bij het bepalen van schoonheid. Op basis van ons vermoeden dat de amygdala ervoor zorgt dat we op bepaalde kenmerken letten die met schoonheid samenhangen, verwachtten we verschillen in het richten van de ogen tijdens schoonheids- en ruwheidsbeoordelingen. Inderdaad vonden we dat fixaties langer duurden tijdens ruwheidsbeoordelingen, en dat de ogen meer bewogen werden tijdens schoonheidsbeoordelingen. Ook fixeerden mensen op meer gekleurde delen van de texturen tijdens schoonheidsbeoordelingen. Dit wijst erop dat de aandacht op verschillende kenmerken gericht wordt, afhankelijk van de gevraagde beoordeling. Uit een literatuurstudie blijkt het aannemelijk te zijn dat de amygdala waarschijnlijk inderdaad verantwoordelijk is voor het richten van de aandacht op bepaalde kenmerken.

Full publications by the author

Brascamp, J.W., Van Ee, R., Noest, A.J., Jacobs, R.H.A.H., & Van den Berg, A.V. (2006). The time course of binocular rivalry reveals a fundamental role of noise. *Journal of Vision*, 6(11), 1244-1256.

Jacobs, R.H.A.H., Renken, R., Thumfart, S., & Cornelissen, F.W. (2010). Different judgments about visual textures invoke different eye movement patterns. *Journal of Eye Movement Research*, 3 (4), 1-13.

Jacobs, R.H.A.H. (2011). Can disordered texture perception account for Capgras delusion? (in preparation).

Thumfart, S., Jacobs, R.H.A.H., Lughofer, E., Eitzinger, C., Cornelissen, F.W., Groissboeck, W., & Richter, R. (2011). Modelling human aesthetic perception of visual textures. Accepted for publication in *ACM Transactions on Applied Perception*.

Thumfart, S., Jacobs, R.H.A.H., Haak, K.V., Cornelissen, F.W., Scharinger, J., & Eitzinger, C. (2008). Feature based prediction of perceived and aesthetic properties of visual textures. *Proceedings Materials & Sensations*, pp. 55-58, Pau, Oct. 2008.

Thumfart, S., Jacobs, R.H.A.H., Cornelissen, F.W., & Eitzinger, C. (2008). A feature based approach towards predicting the perceived and aesthetic properties of visual textures. 32nd Workshop of the Austrian Association for Pattern Recognition, pp. 211-222, Linz, May 26th-27th 2008.

Publication status of chapters, at the time of printing this thesis

Chapter 2, "Consistency in beauty ratings to visual textures", is under revision as a supplement to chapter 3.

Chapter 3, "Aesthetics by numbers - deriving perceived texture qualities from computed visual texture properties", is under revision for publication in Plos One.

Chapter 4, "Neural correlates of visual aesthetics - beauty as the coalescence of stimulus and internal state", is under (minor) revision for publication in Plos One.

Chapter 5, "Amygdalar guidance of feature-based attention during aesthetic judgments", is under review at Neuropsychology

Chapter 6, "Different judgments about visual textures invoke different eye movement patterns", is published in the *Journal of Eye Movement Research*

Chapter 7, "The amygdala, top-down effects, and selective attention", is under revision for publication in *Neuroscience and Biobehavioral Reviews*.

Acknowledgments

I would like to thank some colleagues in particular for their contribution to the research presented in this thesis. First of all, the supervision by Frans Cornelissen, Remco Renken, and Andre Aleman was indispensable. Remco was involved in the project mainly for help in the statistical analyses, but he also provided valuable comments on my writings. In this regard, he was particularly good at bringing one central issue to the foreground, while minimizing stress on other, subsidiary questions. Frans also had a major impact on my writing. It took me some time to fully grasp the importance of some subtleties in the writing process, and maybe I still do not fully grasp them, but I am convinced I will benefit from the lessons learned in Groningen. He also pushed me to connect my finding about amygdalar activation during the beauty judgments with literature concerning amygdalar involvement in guiding eye movements. In this way, he taught me to look ‘beyond the length of my nose’, as a Dutch saying goes, and I am convinced that this will help me in writing down future papers in ways that are more appealing to a broad audience. More generally, he offered us insights into the mechanisms of forming a scientific project, and occasionally he gave us a glimpse into negotiations about a co-authorship in exchange for assistance in someone else’s project. Such insights are indispensable if one wants to pursue a career in science, as I intend to do. Most importantly, Frans also had the initial idea for the research project described here, and he acquired the grant. Without the grant, this whole research project would not have been possible. In general, Frans was very supportive and accessible. Few other Ph.D. students will get supervision that is intensive as I and my colleagues got. Andre Aleman gave some useful feedback on some of my manuscripts, and he gave me useful information about some research topics that interest me. I collaborated quite intensively with some partners in our European projects. In particular, Stefan Thumfart was invaluable for the texture feature computations. We have written many manuscripts together by now. I thank Brian Henson and Tom Childs for demonstrating their Kansei engineering approach to me, from which we took parts to use in our semantic differential studies, described here in chapter 3. Finally, I thank Anneke Hooymans who, together with Andre Aleman was the promotor for my Ph.D. thesis. In the background, she had an essential role in guiding this research project.

I would also like to thank my direct colleagues in the Laboratory for Experimental Ophthalmology, and some other colleagues at the Neuroimaging Center in Groningen. Foremost, I have to thank Jan Bernard Marsman. He was my direct colleague throughout my Ph.D. project. He was invaluable for his help concerning network issues, and also concerning the installation of certain not-so-easy-to-install programs. He also introduced me to the basics of BrainVoyager. Moreover, he agreed to be the paranimf during my defense, just as I was a paranimf during his. Second, I have to thank Koen Haak. He started his Ph.D. training a year after me, and he worked on the same project as I did. He was keen on getting a better grip on the analysis techniques that I used, thereby pushing me to get a better grip on mediator analyses. Although these mediator analyses did not make it into my papers, nor into my thesis, I spent a lot of time mastering them, and this will certainly be useful in the future. In this regard, I also have to thank Marieke Timmerman for suggesting the use of mediator analyses for answering the questions I was asking. Third, I have to thank Aditya Hernowo. Although his work was quite unrelated to mine, we always had a good working relationship. Fourth, I have to thank Erik Groenewold. He was a good colleague during the first three years of my Ph.D. training. I thank Katharina Goerlich for fulfilling the role of second paranimf during my defence. I have to thank Luca Nanetti for his help on installing BrainVoyager on my computer, and for explaining some aspects of BrainVoyager to me. I have to thank Dave Langers for some help in interpreting my principal components analyses. Next, I have to thank the students who helped me acquire and analyze the data of the behavioural experiments: Remy Sijbom, Maarten Schotkamp, Erik de Breij, and Richard Sonnega. Many thanks also to the MRI scanner operators, Nikky van Bodegom and Anita Kuiper. The secretaries, Tinie Alma, Hedwig van Oosten, and Evelyn Kuypers were very helpful in various ways. Finally, I have to thank the European Commission for funding the research project Syntex, and our research

school, BCN, for funding the research presented in this thesis. The Professor Mulderstichting provided support for this thesis.

Epilogue

The thesis is finished. Now it is time to look back. Besides the scientific work written down during my time as a Ph.D. student, a Ph.D. is also a time of personal development. This personal development consists of the development of skills, such as writing skills, but also of social life, and of increased insight into the mechanisms of the scientific community.

To start with the social part, I found myself in the welcoming environment of the NeuroImaging Center in Groningen. Besides the support of my direct colleagues from the Laboratory of Experimental Ophthalmology, Jan Bernard Marsman, Koen Haak, Aditya Hernowo, Ronald van den Berg, Marije van Beilen, Erik Groenewold, Charmaine Pietersen, Tony Vladusic, Angela Martinez, and supervisors Remco Renken, Andre Aleman, and Frans Cornelissen, there were many occasions of social interaction with colleagues from the other departments residing at the Center. In particular, I would like to mention Ramona Demenescu, Katharina Goerlich, Anne Marthe Meppelink, Luca Nanetti, Dave Langers, Shippoo, Harma Meffert, Marc Thioux, Johan Lambregs, Jojanneke Bastiaansen, Lisette van der Meer, Piray Atsak, Ozlem Korucuoglu, Nynke Groenewold, Linda Geerligs, Gemma Modinos, Ans Vercammen, Marleen Schippers, and Ana Amaral. They employed many activities, varying from having a drink or playing pool in the bars and cafes of Groningen, to visiting the liberation festival and the Queen's Day market, to visiting Rock Werchter, to swimming at the Paterswoldsemeer, to a weekend at the island of Schiermonnikoog, to picnicks and dinners, to a retreat, and to participation in a Frisbee tournament. All these activities ensured a nice and comfortable stay in that town in the far north of the Netherlands, Groningen. I have to say that I lost a lot of my nerdiness. My social life there was richer than ever before, and I will strive for an even richer social life in the future.

I came to the Ph.D. position with some expectations and intentions. For example, after reading many contradictory statements surrounding the concept of 'attention', I had resolved myself to not use that word and stick to more concrete descriptions, so that the different meanings of the word attention could not be confused. Related to this, I had formed the opinion that it was not very fruitful, rather confusing, to speak about some central, unobservable concepts, like that of attention. I thought it wise to stick to generalizations along relevant stimulus and task dimensions in the discussion of findings. Another idea I had was that research projects were set up after careful consideration of the existing scientific literature, and after lots of discussions to get to the bottom of certain ideas. A more practical expectation that I had, was that most of the time in research would be invested in the analysis of data, or maybe in the preparation of experiments. Writing seemed to me like a straightforward activity, in which you would discuss your findings in the context of related findings. After grouping the relevant information, and making a rough outline of your story, the rest would just be a filling-in exercise that could be accomplished in about two months, and I expected to be able to do all the writing just in the evenings and maybe some weekends. All those expectations were proven wrong, and not just a little bit. At least, that is how it appears to me. I will mention a few things that struck me as odd.

One thing that struck me, was how in our research project there was a profound misunderstanding about one of the core concepts in the project, as became apparent during the kick-off meeting of our project. This was the case for the word 'feelings', which was interpreted as the basic emotions in part of the project (where these emotions were supposed to be measured from the face of the observer), while in other parts of the project clearly something else was meant, referring to words like elegance and other judgments. At times I had the feeling that there was misunderstanding about yet an additional meaning, naming feeling in the sense of touch sensations. To me it was stunning that such misunderstandings were not resolved during the formation of the project, or during the decision about whether to fund it. Maybe one cannot always avoid misunderstandings between different collaborating parties. Misunderstandings are bound to occur when communicating, and during the writing of the proposal researchers may be too focused on obtaining

the grant to be critical of terminology. But I have the feeling that institutions handing out research grants should take a better look at the consistent use of terms in the research proposals. Behaviourism once started to avoid inconsistent terminology. We should retain the good parts of that movement.

Another issue in our project which initially struck me as odd was the plan of measuring facial expressions via automated encoding of videotapes of observers' facial expressions. The advantage of such a technique is obviously that it is nonintrusive, while more established alternatives, such as electromyography, require sticking electrodes to someone's skin. However, the party involved in the project for developing this technique readily admitted, beforehand, that electromyography was more sensitive than their automated expression analysis. The expression analysis worked in itself, let there be no misunderstanding about that. But the expressions displayed by observers in our experiments were too weak for the algorithm to work. In such a case, I would have started with the established technique, and then see if the new technique is able to add something useful to this existing technique. However, our project obtained a grant from a call for a research project 'measuring the impossible', and this was often used in defence of seemingly curious aims of the project. Although I was stunned that research projects could be started like this, in the end I think we manoeuvred around the obstacles satisfactorily. What I learned is that these research projects rely on the participating researchers to iron out the rough spots as the project goes along. And that is exactly what happened. And I should mention that, if the technique of analyzing facial expressions automatically had worked, I would probably not have criticized the proposal about this aspect. Judgment is easy in retrospect.

Regarding the writing of papers, my idea that this could be done in just a couple of months appeared wrong. I think writing took up more than half of my time in the research project, and I later heard from others that this is not exceptional at all. The manuscript about our finding of the amygdala activating during beauty judgment was re-written so many times that I felt quite frustrated at times. I found that even after one has prepared the article for submission, writing a pre-submission enquiry can still take several weeks, and after that, re-writing the manuscript based on the pre-submission enquiry will take still more time. All this has a purpose. Ideas develop as one goes along. But at times it is very frustrating to see how slow progress can be in the writing part of things, and I often wondered whether it wouldn't have been more productive to do some extra experiments, at the expense of being less concise in the wording. But another intention I had was to rely on the experience of my supervisors, to learn as much as possible from them, and I persevered in optimizing my writing.

The aspect of writing that I underestimated most was the importance of phrasing. When writing essays or papers during my studies, I always focused on finding the relevant literature, organizing the material, and then writing everything together. That usually resulted in few comments from the teachers who judged the manuscript, and in good grades. I thought that was all there is to it. But I was wrong again. Most of the time actually goes into the subtleties of language. A phrasing like 'we failed to find ...' will be regarded as a statement that is negative, suggesting that you did something wrong. In such cases, a more neutral or positive formulation has to be found. Also, I had a tendency to just mention some related findings after each other, expecting the reader to see the connection. It takes some time to see that in many cases, the connections are not obvious. Usually, instead of mentioning three findings in three sentences, it is necessary to first say why you are going to mention them, and after presenting them, to explicitly draw a conclusion. Et voila, the sentences have become a paragraph. In the beginning of the Ph.D. project, I think I had a kind of neglect for such subtleties. At times I really doubted whether the re-formulations were bringing us forward. In the beginning (before I discovered the 'track changes'-option in Word) I often only realized when I had gone through half of my manuscript, that about every sentence in it had been re-written. If the changes are so subtle, is it worth investing time and effort in them? My doubts reached their pinnacle when I showed the twelfth version of an abstract to a colleague, who asked why I didn't write it in some other words. That was exactly how I had written the abstract in the first version. I proceeded by showing five of my colleagues both the first and the twelfth version, asking for their opinion. It appeared that two colleagues were undecided, two preferred the first version, and one preferred the twelfth version.

Of course, this led to even more re-formulations. Only very gradually I came to see the benefits of the re-formulations. I think my initial neglect is partly the result of reading lots of papers, in which you try to ignore the subtleties of formulations, and focus on the content. Ignoring things leads to disliking them, which is probably how I developed a total neglect for the importance of formulations. During the Ph.D. project, this blind spot has been filled in a bit. More than the gradual development of ideas, re-formulating sentences has cost a lot of time in my Ph.D. project, but it will help me in future writings, where the art of phrasing will become more natural to me. In the end, I think it was very fortunate that I had supervisors who are quite skilled in phrasing, so that I had the opportunity to develop this hitherto neglected skill. I believe writing is one of the core activities for a scientist, and poor formulations could pose a serious hindrance for someone pursuing a scientific career.

My ideas of sticking to the relevant task and stimulus dimensions when discussing your results proved to be a bit naive. In my first version of the paper about the amygdala being more active during beauty than during other judgments, I simply interpreted the finding as a top-down effect, and I linked the findings to other top-down effects in the literature. I found that my co-authors didn't like that approach at all. It simply wasn't attractive enough. And believe it or not, science needs to be attractive. My co-authors brought some papers to my attention, linking amygdalar activation to eye movements. This puzzled me. I didn't do eye movements. Not even spatial attention. Where did they get the idea that this was at all relevant to the task effects I had found? But after thinking about it for a while, I realized that the task effects could be related to the spatial attention effects, something that was probably obvious to my supervisors. Along the way, I got rid of my intention to not ever use the word 'attention'. From the idea of an amygdalar role in spatial attention and in top-down attention, the ideas about an amygdalar role in feature-based attention developed, resulting in some nice hypotheses, all displayed in this thesis. In hindsight, I think the approach of sticking to the relevant task and stimulus variables when discussing your own findings is a bit lazy and too cautious. One should at least consider pushing the interpretation further. As far as one can, actually.

Altogether, I obtained many insights, improved some previously neglected skills, and came out of this Ph.D. period a lot wiser than before. I noticed that some regard the above comments as critical. I don't think they are. A lot worse things can happen in a research project of four years duration, severe enough to make the Ph.D. student quit their job. I on the contrary always felt myself in a supportive environment, and I only observed some peculiarities in science with amusement. The few occasions where I felt frustrated were of short duration.

References

- Abbey, C. K., & Eckstein, M. P. (2007). Classification images for simple detection and discrimination tasks in correlated noise. *Journal of the Optical Society of America A*, 24(12), 110-124.
- Adams, R. B., Gordon, H. L., Baird, A. A., Ambady, N., & Kleck, R. E. (2003). Effects of gaze on amygdala sensitivity to anger and fear faces. *Science*, 300(5625), 1536.
- Adolphs, R., Gosselin, F., Buchanan, T. W., Tranel, D., Schyns, P., & Damasio, A. R. (2005). A mechanism for impaired fear recognition after amygdala damage. *Nature*, 433, 68-72.
- Aharon, I., Etcoff, N., Ariely, D., Chabris, C. F., O'Connor, E., & Breiter, H. C. (2001). Beautiful faces have variable reward value: fMRI and behavioral evidence. *Neuron*, 32(3), 537-551.
- Ahissar, M., & Hochstein, S. (2000). The spread of attention and learning in feature search: effects of target distribution and task difficulty. *Vision Research*, 40(10-12), 1349-1364.
- Aks, D. J., & Sprott, J. C. (1996). Quantifying Aesthetic Preference for Chaotic Patterns. *Empirical Studies of the Arts*, 14, 1-6.
- Alorda, C., Serrano-Pedraza, I., Campos-Bueno, J. J., Sierra-Vázquez, V., & Montoya, P. (2007). Low spatial frequency filtering modulates early brain processing of affective complex pictures. *Neuropsychologia*, 45(14), 3223-3233.
- Amadasun, M., & King, R. (1989). Textural features corresponding to textural properties. *Systems, Man and Cybernetics, IEEE Transactions on*, 19(5), 1264-1274.
- Anderson, A. K., & Phelps, E. A. (2001). Lesions of the human amygdala impair enhanced perception of emotionally salient events. *Nature*, 411(6835), 305-308.
- Antes, J. R., Chang, K. T., Lenzen, T., & Mullis, C. (1985). Eye movements in map reading. In R. Groner, G. W. McConkie & C. Menz (Eds.), *Eye movements and human information processing* (pp. 357-373). Amsterdam: North-Holland.
- Arcizet, F., Jouffrais, C., & Girard, P. (2008). Natural textures classification in area V4 of the macaque monkey. *Experimental Brain Research*, 189(1), 109-120.
- Ashikhmin, M. (2001). *Synthesizing natural textures*. Paper presented at the 2001 ACM Symposium on Interactive 3D Graphics, Research Triangle Park, North Carolina.
- Ashwin, C., Baron-Cohen, S., Wheelwright, S., O'Riordan, M., & Bullmore, E. T. (2007). Differential activation of the amygdala and the [] social brain during fearful face-processing in Asperger Syndrome. *Neuropsychologia*, 45(1), 2-14.
- Ball, V. K. (1965). The aesthetics of color: A review of fifty years of experimentation. *Journal of Aesthetics and Art Criticism*, 23(4), 441-452.
- Ballard, D. H., & Hayhoe, M. M. (2009). Modelling the role of task in the control of gaze. *Visual Cognition*, 17(6-7), 1185-1204.
- Baluch, F., & Itti, L. (2011). Mechanisms of top-down attention. *Trends in neurosciences*.
- Bancaud, J., Talairach, J., Morel, P., & Bresson, M. (1966). Le corne d'Ammon et le noyau amygdalien: effets cliniques et électriques de leur stimulation chez l'homme. *Revue Neurologique*, 115(3), 329-352.
- Bar, M., & Neta, M. (2007). Visual elements of subjective preference modulate amygdala activation. *Neuropsychologia*, 45(10), 2191-2200.
- Bargh, J. A. (1992). The ecology of automaticity: Toward establishing the conditions needed to produce automatic processing effects. *American Journal of Psychology*, 105(2), 181-199.
- Bartolomucci, A. (2007). Social stress, immune functions and disease in rodents. *Frontiers in neuroendocrinology*, 28(1), 28-49.
- Beason-Held, L. L., Purpura, K. P., Krasuski, J. S., Maisog, J. M., Daly, E. M., Mangot, D. J., et al. (1998). Cortical regions involved in visual texture perception: a fMRI study. *Brain Research. Cognitive Brain Research*, 7(2), 111-118.
- Beatty, J. (1982). Task-evoked pupillary responses, processing load, and the structure of processing resources. *Psychological Bulletin*, 91(2), 276-292.
- Beauregard, M., Levesque, J., & Bourgouin, P. (2001). Neural correlates of conscious self-regulation of emotion. *Journal of Neuroscience*, 21(18), 165.

- Ben-Eliyahu, S., Yirmiya, R., Liebeskind, J., Taylor, A., & Gale, R. (1991). Stress increases metastatic spread of a mammary tumor in rats: evidence for mediation by the immune system. *Brain, Behavior, and Immunity*, 5(2), 193-205.
- Ben-Shahar, O. (2006). Visual saliency and texture segregation without feature gradient. *Proceedings of the National Academy of Sciences*, 103(42), 15704.
- Bergen, J. R., & Adelson, E. H. (1988). Early vision and texture perception. *Nature*, 333(6171), 363-364.
- Bishop, S., Duncan, J., & Lawrence, A. (2004). State anxiety modulation of the amygdala response to unattended threat-related stimuli. *Journal of Neuroscience*, 24(46), 10364.
- Blanchette, I. (2006). Snakes, spiders, guns, and syringes: How specific are evolutionary constraints on the detection of threatening stimuli? *The Quarterly Journal of Experimental Psychology*, 59(8), 1484-1504.
- Bleich-Cohen, M., Mintz, M., Pianka, P., Andelman, F., Rotshtein, P., & Hendler, T. (2006). Differential stimuli and task effects in the amygdala and sensory areas. *NeuroReport*, 17(13), 1391.
- Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision*, 10(4), 433-436.
- Brand, M., Grabenhorst, F., Starcke, K., Vandekerckhove, M. M. P., & Markowitsch, H. J. (2007). Role of the amygdala in decisions under ambiguity and decisions under risk: evidence from patients with Urbach-Wiethe disease. *Neuropsychologia*, 45(6), 1305-1317.
- Breiter, H. C., Etcoff, N. L., Whalen, P. J., Kennedy, W. A., Rauch, S. L., Buckner, R. L., et al. (1996). Response and habituation of the human amygdala during visual processing of facial expression. *Neuron*, 17(5), 875-887.
- Brodatz, P. (1966). *Textures: A photographic album for artists and designers*. New York: Dover Publications.
- Brosch, T., & Sharma, D. (2005). The role of fear-relevant stimuli in visual search: A comparison of phylogenetic and ontogenetic stimuli. *Emotion*, 5(3), 360-364.
- Buckingham, G., Cant, J. S., & Goodale, M. A. (2009). Living in a material world: how visual cues to material properties affect the way that we lift objects and perceive their weight. *Journal of Neurophysiology*, 102(6), 3111-3118.
- Buswell, G. T. (1935). *How people look at pictures*. Chicago: University of Chicago Press.
- Calder, A. J. (1996). Facial emotion recognition after bilateral amygdala damage: Differentially severe impairment of fear. *Cognitive Neuropsychology*, 13(5), 699-745.
- Calvo-Merino, B., Jola, C., Glaser, D. E., & Haggard, P. (2008). Towards a sensorimotor aesthetics of performing art. *Consciousness and Cognition*, 17(3), 911-922.
- Calvo, M. G., & Marrero, H. (2008). Visual search of emotional faces: The role of affective content and featural distinctiveness. *Cognition and Emotion*, 23(4), 782-806.
- Calvo, M. G., & Nummenmaa, L. (2008a). Detection of emotional faces: Salient physical features guide effective visual search. *Journal of Experimental Psychology: General*, 137(3), 471-494.
- Calvo, M. G., & Nummenmaa, L. (2008b). Detection of emotional faces: Salient physical features guide effective visual search. *Journal of Experimental Psychology-General*, 137(3), 471-494.
- Canli, T., Sivers, H., Whitfield, S. L., Gotlib, I. H., & Gabrieli, J. D. E. (2002). Amygdala response to happy faces as a function of extraversion. *Science*, 296(5576), 2191.
- Canli, T., Zhao, Z., Desmond, J. E., Kang, E., Gross, J., & Gabrieli, J. D. E. (2001). An fMRI study of personality influences on brain reactivity to emotional stimuli. *Behavioral neuroscience*, 115(1), 33.
- Cant, J. S., Arnott, S. R., & Goodale, M. A. (2009). fMR-adaptation reveals separate processing regions for the perception of form and texture in the human ventral stream. *Experimental Brain Research*, 192(3), 391-405.
- Cant, J. S., & Goodale, M. A. (2007). Attention to form or surface properties modulates different regions of human occipitotemporal cortex. *Cerebral Cortex*, 17(3), 713-731.
- Carlson, J. M., Greenberg, T., & Mujica-Parodi, L. R. (2010). Blind rage? Heightened anger is associated with altered amygdala responses to masked and unmasked fearful faces. *Psychiatry Research: Neuroimaging*, 182(3), 281-283.
- Carlson, J. M., Reinke, K. S., & Habib, R. (2009). A left amygdala mediated network for rapid orienting to masked fearful faces. *Neuropsychologia*, 47(5), 1386-1389.
- Cavina-Pratesi, C., Kentridge, R., Heywood, C., & Milner, A. (2010a). Separate Channels for Processing Form, Texture, and Color: Evidence from fMRI Adaptation and Visual Object Agnosia. *Cerebral Cortex*, 20(10), 2319.

- Cavina-Pratesi, C., Kentridge, R., Heywood, C., & Milner, A. (2010b). Separate processing of texture and form in the ventral stream: Evidence from fMRI and visual agnosia. *Cerebral Cortex*, *20*(2), 433.
- Cela-Conde, C. J., Marty, G., Maestu, F., Ortiz, T., Munar, E., Fernandez, A., et al. (2004). Activation of the prefrontal cortex in the human visual aesthetic perception. *Proc Natl Acad Sci U S A*, *101*(16), 6321-6325.
- Chatterjee, A., Thomas, A., Smith, S. E., & Aguirre, G. K. (2009). The neural response to facial attractiveness. *Neuropsychology*, *23*(2), 135-143.
- Chatterjee, A., Thomas, A., Smith, S. E., & Aguirre, G. K. (2009). The neural response to facial attractiveness. *Neuropsychology*, *23*(2), 135.
- Chen, C. H., Lennox, B., Jacob, R., Calder, A., Lupson, V., Bisbrown-Chippendale, R., et al. (2006). Explicit and implicit facial affect recognition in manic and depressed states of bipolar disorder: a functional magnetic resonance imaging study. *Biological Psychiatry*, *59*(1), 31-39.
- Chen, Y., Norton, D., & McBain, R. (2008). Can persons with schizophrenia appreciate visual art? *Schizophrenia Research*, *105*(1-3), 245-251.
- Coelho, C. M., Cloete, S., & Wallis, G. (2010). The face-in-the-crowd effect: When angry faces are just cross (es). *Journal of Vision*, *10*(1), 1-14.
- Cornelissen, F. W., Bruin, K. J., & Kooijman, A. C. (2005). The influence of artificial scotomas on eye movements during visual search. *Optometry & Vision Science*, *82*(1), 27.
- Cornelissen, F. W., Peters, E. M., & Palmer, J. (2002). The EyeLink Toolbox: eye tracking with MATLAB and the Psychophysics Toolbox. *Behavior Research Methods Instruments and Computers*, *34*(4), 613-617.
- Costafreda, S. G., Brammer, M. J., David, A. S., & Fu, C. H. (2007). Predictors of amygdala activation during the processing of emotional stimuli: A meta-analysis of 385 PET and fMRI studies. *Brain Research Reviews*, 58-70.
- Cremers, H. R., Demenescu, L. R., Aleman, A., Renken, R., van Tol, M. J., van der Wee, N. J. A., et al. (2010). Neuroticism modulates amygdala--prefrontal connectivity in response to negative emotional facial expressions. *Neuroimage*, *49*(1), 963-970.
- Cunningham, W. A., Raye, C. L., & Johnson, M. K. (2004). Implicit and explicit evaluation: fMRI correlates of valence, emotional intensity, and control in the processing of attitudes. *Journal of Cognitive Neuroscience*, *16*(10), 1717-1729.
- Cunningham, W. A., Van Bavel, J. J., & Johnsen, I. R. (2008). Affective flexibility: evaluative processing goals shape amygdala activity. *Psychological Science*, *19*(2), 152-160.
- Dalton, K. M., Nacewicz, B. M., Johnstone, T., Schaefer, H. S., Gernsbacher, M. A., Goldsmith, H., et al. (2005). Gaze fixation and the neural circuitry of face processing in autism. *Nature neuroscience*, *8*(4), 519-526.
- Datta, R., Joshi, D., Li, J., & Wang, J. Z. (2006). Studying aesthetics in photographic images using a computational approach. *Lecture Notes in Computer Science*, *3953*, 288.
- Davis, M. (1992). The role of the amygdala in fear and anxiety. *Annual Review of Neuroscience*, *15*(1), 353-375.
- DeAngelus, M., & Pelz, J. B. (2009). Top-down control of eye movements: Yarbus revisited. *Visual Cognition*, *17*(6), 790-811.
- Delplanque, S., N'Diaye, K., Scherer, K., & Grandjean, D. (2007). Spatial frequencies or emotional effects? A systematic measure of spatial frequencies for IAPS pictures by a discrete wavelet analysis. *J Neurosci Methods*, *165*(1), 144-150.
- Deubel, H., & Schneider, W. X. (1996). Saccade target selection and object recognition: Evidence for a common attentional mechanism. *Vision Research*, *36*(12), 1827-1837.
- Di Dio, C., Macaluso, E., & Rizzolatti, G. (2007). The golden beauty: brain response to classical and renaissance sculptures. *PLoS ONE*, *2*(11), e1201.
- Dickie, E., & Armony, J. (2008). Amygdala responses to unattended fearful faces: interaction between sex and trait anxiety. *Psychiatry Research: Neuroimaging*, *162*(1), 51-57.
- Dolan, R. J., & Vuilleumier, P. (2003). Amygdala automaticity in emotional processing. *Annals of the New York Academy of Sciences*, *985*, 348-355.
- Donegan, N. H., Sanislow, C. A., Blumberg, H. P., Fullbright, R. K., Lacadie, C., Skudlarski, P., et al. (2003). Amygdala hyperreactivity in borderline personality disorder: implications for emotional dysregulation. *Biological Psychiatry*, *54*(11), 1284-1293.

- Dror, I. E., & Fraser-MacKenzie, P. A. F. (2008). Cognitive biases in human perception, judgment, and decision making: Bridging theory and the real world. In K. Rossmo (Ed.), *Criminal Investigative Failures* (pp. 53-67). London: CRC Press.
- Efros, A. A., & Leung, T. K. (1999). Texture Synthesis by Non-parametric Sampling. *IEEE International Conference on Computer Vision*, 2, 1033-1038.
- Eippert, F., Veit, R., Weiskopf, N., Erb, M., Birbaumer, N., & Anders, S. (2007). Regulation of emotional responses elicited by threat related stimuli. *Human Brain Mapping*, 28(5), 409-423.
- Ekman, G., Hosman, J., & Lindstroem, B. (1965). Roughness, Smoothness, and Preference: a Study of Quantitative Relations in Individual Subjects. *J Exp Psychol*, 70, 18-26.
- Etkin, A., Klemenhagen, K., Dudman, J., Rogan, M., Hen, R., Kandel, E., et al. (2004). Individual differences in trait anxiety predict the response of the basolateral amygdala to unconsciously processed fearful faces. *Neuron*, 44(6), 1043-1055.
- Fakra, E., Salgado-Pineda, P., Delaveau, P., Hariri, A. R., & Blin, O. (2008). Neural bases of different cognitive strategies for facial affect processing in schizophrenia. *Schizophrenia Research*, 100(1-3), 191-205.
- Fanselow, M. S., & LeDoux, J. E. (1999). Why we think plasticity underlying Pavlovian fear conditioning occurs in the basolateral amygdala. *Neuron*, 23(2), 229.
- Fichtenholtz, H. M., Dean, H. L., Dillon, D. G., Yamasaki, H., McCarthy, G., & LaBar, K. S. (2004). Emotion-attention network interactions during a visual oddball task. *Cognitive Brain Research*, 20(1), 67-80.
- Fitzgerald, D. A., Angstadt, M., Jelsone, L. M., Nathan, P. J., & Phan, K. L. (2006). Beyond threat: amygdala reactivity across multiple expressions of facial affect. *Neuroimage*, 30(4), 1441-1448.
- Fleming, R. W., & Bühlhoff, H. H. (2005). Low-level image cues in the perception of translucent materials. *ACM Transactions on Applied Perception (TAP)*, 2(3), 346-382.
- Fox, E., & Damjanovic, L. (2006). The eyes are sufficient to produce a threat superiority effect. *Emotion*, 6(3), 534.
- Fransella, F., & Bannister, D. (1977). *A Manual for Repertory Grid Technique*. London, UK: Academic Press Inc.
- Fu, C. H. Y., Williams, S. C. R., Brammer, M. J., Suckling, J., Kim, J., Cleare, A. J., et al. (2007). Neural responses to happy facial expressions in major depression following antidepressant treatment. *American Journal of Psychiatry*, 164(4), 599.
- Fusar-Poli, P., Placentino, A., Carletti, F., Landi, P., Allen, P., Surguladze, S., et al. (2009). Functional atlas of emotional faces processing: a voxel-based meta-analysis of 105 functional magnetic resonance imaging studies. *Journal of Psychiatry & Neuroscience*, 34(6), 418-432.
- Gallagher, M., & Schoenbaum, G. (1999). Functions of the amygdala and related forebrain areas in attention and cognition. *Annals of the New York Academy of Sciences*, 877, 397-411.
- Gamer, M., & Buchel, C. (2009). Amygdala activation predicts gaze toward fearful eyes. *Journal of Neuroscience*, 29(28), 9123.
- Ganzha, B. L. (1986). Olfactory rhythm in the electrical activity of the human amygdaloid nucleus. *Neurophysiology*, 18(1), 48-54.
- Goldin, P. R., McRae, K., Ramel, W., & Gross, J. J. (2008). The neural bases of emotion regulation: reappraisal and suppression of negative emotion. *Biological Psychiatry*, 63(6), 577-586.
- Gorno-Tempini, M. L., Pradelli, S., Serafini, M., Pagnoni, G., Baraldi, P., Porro, C., et al. (2001). Explicit and incidental facial expression processing: an fMRI study. *Neuroimage*, 14(2), 465-473.
- Graham, D. J., & Redies, C. Statistical regularities in art: Relations with visual coding and perception. *Vision research*.
- Graham, D. J., & Redies, C. (2010). Statistical regularities in art: Relations with visual coding and perception. *Vision Research*, 50(16), 1503-1509.
- Groner, M. T., Groner, R., & von Mühlhelen, A. (2008). The effect of spatial frequency content on parameters of eye movements. *Psychological Research*, 72(6), 601-608.
- Groner, R., & Menz, C. (1985). The effect of stimulus characteristics, task requirements and individual differences on scanning patterns. In R. Groner, G. W. McConkie & C. Menz (Eds.), *Eye movements and human information processing* (pp. 239). Amsterdam: North-Holland.
- Guadagnoli, E., & Velicer, W. F. (1988). Relation of sample size to the stability of component patterns. *Psychological Bulletin*, 103(2), 265-275.

- Gur, R. E., McGrath, C., Chan, R. M., Schroeder, L., Turner, T., Turetsky, B. I., et al. (2002). An fMRI study of facial emotion processing in patients with schizophrenia. *American Journal of Psychiatry*, 159(12), 1992.
- Gusnard, D. A., Akbudak, E., Shulman, G. L., & Raichle, M. E. (2001). Medial prefrontal cortex and self-referential mental activity: relation to a default mode of brain function. *Proceedings of the National Academy of Sciences of the United States of America*, 98(7), 4259.
- Gusnard, D. A., Akbudak, E., Shulman, G. L., & Raichle, M. E. (2001). Medial prefrontal cortex and self-referential mental activity: relation to a default mode of brain function. *Proceedings of the National Academy of Sciences*, 98(7), 4259.
- Haas, B. W., Omura, K., Constable, R. T., & Canli, T. (2007). Emotional conflict and neuroticism: Personality-dependent activation in the amygdala and subgenual anterior cingulate. *Behavioral neuroscience*, 121(2), 249.
- Habel, U., Windischberger, C., Derntl, B., Robinson, S., Kryspin-Exner, I., Gur, R. C., et al. (2007). Amygdala activation and facial expressions: explicit emotion discrimination versus implicit emotion processing. *Neuropsychologia*, 45(10), 2369-2377.
- Haralick, R. M., Shanmugam, K., & Dinstein, I. H. (1973). Textural Features for Image Classification. *Systems, Man and Cybernetics, IEEE Transactions on*, 3(6), 610-621.
- Harenski, C., & Hamann, S. (2006). Neural correlates of regulating negative emotions related to moral violations. *Neuroimage*, 30(1), 313-324.
- Hariri, A. R., Bookheimer, S. Y., & Mazziotta, J. C. (2000). Modulating emotional responses: effects of a neocortical network on the limbic system. *NeuroReport*, 11(1), 43.
- Hariri, A. R., Mattay, V. S., Tessitore, A., Fera, F., & Weinberger, D. R. (2003). Neocortical modulation of the amygdala response to fearful stimuli. *Biological Psychiatry*, 53(6), 494-501.
- Harlow, H. F., Harlow, M. K., Dodsworth, R. O., & Arling, G. (1966). Maternal behavior of rhesus monkeys deprived of mothering and peer associations in infancy. *Proceedings of the American Philosophical Society*, 110(1), 58-66.
- Hayhoe, M. M., Bensinger, D. G., & Ballard, D. H. (1998). Task constraints in visual working memory. *Vision Research*, 38(1), 125-138.
- Hayton, J. C., Allen, D. G., & Scarpello, V. (2004). Factor retention decisions in exploratory factor analysis: A tutorial on parallel analysis. *Organizational Research Methods*, 7(2), 191-205.
- Herpertz, S. C., Dietrich, T. M., Wenning, B., Krings, T., Erberich, S. G., Willmes, K., et al. (2001). Evidence of abnormal amygdala functioning in borderline personality disorder: a functional MRI study. *Biological Psychiatry*, 50(4), 292-298.
- Herwig, U., Baumgartner, T., Kaffenberger, T., Brühl, A., Kottlow, M., Schreiter-Gasser, U., et al. (2007). Modulation of anticipatory emotion and perception processing by cognitive control. *Neuroimage*, 37(2), 652-662.
- Hess, E. H., & Polt, J. M. (1960). Pupil size as related to interest value of visual stimuli. *Science*, 132(3423), 349-350.
- Ho, Y. X., Landy, M. S., & Maloney, L. T. (2006). How direction of illumination affects visually perceived surface roughness. *Journal of Vision*, 6(5), 634-648.
- Hofel, L., & Jacobsen, T. (2003). Temporal stability and consistency of aesthetic judgments of beauty of formal graphic patterns. *Percept Mot Skills*, 96(1), 30-32.
- Hoffman, J. E., & Subramaniam, B. (1995). The role of visual attention in saccadic eye movements. *Perception and Psychophysics*, 57(6), 787-795.
- Holden lund, C. (1988). Effects of relaxation with guided imagery on surgical stress and wound healing. *Research in Nursing & Health*, 11(4), 235-244.
- Holland, P. C., & Gallagher, M. (1999). Amygdala circuitry in attentional and representational processes. *Trends in Cognitive Sciences*, 3(2), 65-73.
- Hollingworth, A., & Franconeri, S. L. (2009). Object correspondence across brief occlusion is established on the basis of both spatiotemporal and surface feature cues. *Cognition*, 113(2), 150-166.
- Holmes, A., Winston, J. S., & Eimer, M. (2005). The role of spatial frequency information for ERP components sensitive to faces and emotional facial expression. *Brain Res Cogn Brain Res*, 25(2), 508-520.
- Hooge, I. T. C., & Erkelens, C. J. (1996). Control of fixation duration in a simple search task. *Perception and Psychophysics*, 58(7), 969-976.

- Hopf, J. M., Boelmans, K., Schoenfeld, M. A., Luck, S. J., & Heinze, H. J. (2004). Attention to features precedes attention to locations in visual search: Evidence from electromagnetic brain responses in humans. *Journal of Neuroscience*, *24*(8), 1822.
- Horstmann, G., Borgstedt, K., & Heumann, M. (2006). Flanker effects with faces may depend on perceptual as well as emotional differences. *Emotion*, *6*(1), 28-39.
- Hutcheson, F. (1973). An inquiry concerning beauty, order, harmony, design. The Hague: Martinus Nijhoff.
- Jacobs, R. H. A. H., Haak, K. V., Thumfart, S., Renken, R., Henson, B., & Cornelissen, F. W. (2010). Features and aesthetics. *submitted*.
- Jacobs, R. H. A. H., Haak, K. V., Thumfart, S., Renken, R., Henson, B., & Cornelissen, F. W. (2011). Aesthetics by numbers: Deriving perceived texture qualities from computed visual texture properties. *submitted*.
- Jacobs, R. H. A. H., Renken, R., Aleman, A., & Cornelissen, F. W. (2010). Searching for beauty in the mundane: Amygdalar guidance of feature-based attention during emotional decision-making. *submitted*.
- Jacobs, R. H. A. H., Renken, R., & Cornelissen, F. W. (2009). The amygdala selects information for emotional decision making. *Perception*, *38*S.
- Jacobs, R. H. A. H., Renken, R., Thumfart, S., & Cornelissen, F. W. (2010). Different judgments about visual textures invoke different eye movement patterns. *Journal of Eye Movement Research*, *3*(4), 1-13.
- Jacobsen, T., & Hofel, L. (2003). Descriptive and evaluative judgment processes: behavioral and electrophysiological indices of processing symmetry and aesthetics. *Cogn Affect Behav Neurosci*, *3*(4), 289-299.
- Jacobsen, T., Schubotz, R. I., Hofel, L., & Cramon, D. Y. (2006). Brain correlates of aesthetic judgment of beauty. *Neuroimage*, *29*(1), 276-285.
- Johnson, S. C., Baxter, L. C., Wilder, L. S., Pipe, J. G., Heiserman, J. E., & Prigatano, G. P. (2002). Neural correlates of self-reflection. *Brain*, *125*(8), 1808.
- Johnstone, T., van Reekum, C. M., Urry, H. L., Kalin, N. H., & Davidson, R. J. (2007). Failure to regulate: counterproductive recruitment of top-down prefrontal-subcortical circuitry in major depression. *Journal of Neuroscience*, *27*(33), 8877.
- Jolij, J., & Lamme, V. A. F. (2005). Repression of unconscious information by conscious processing: Evidence from affective blindsight induced by transcranial magnetic stimulation. *Proceedings of the National Academy of Sciences of the United States of America*, *102*(30), 10747.
- Jones, B. C., Little, A. C., Feinberg, D. R., Penton-Voak, I. S., Tiddeman, B. P., & Perrett, D. I. (2004). The relationship between shape symmetry and perceived skin condition in male facial attractiveness. *Evolution and Human Behavior*, *25*(1), 24-30.
- Julesz, B. (1981). A theory of preattentive texture discrimination based on first-order statistics of textons. *Biological Cybernetics*, *41*(2), 131-138.
- Juth, P., Lundqvist, D., Karlsson, A., & Ohman, A. (2005). Looking for foes and friends: Perceptual and emotional factors when finding a face in the crowd. *Emotion*, *5*(4), 379-395.
- Kaiser, H. F. (1958). The varimax criterion for analytic rotation in factor analysis. *Psychometrika*, *23*(3), 187-200.
- Kalisch, R., Wiech, K., Critchley, H., & Dolan, R. (2006). Levels of appraisal: a medial prefrontal role in high-level appraisal of emotional material. *Neuroimage*, *30*(4), 1458-1466.
- Kanan, C., Tong, M. H., Zhang, L., & Cottrell, G. W. (2009). SUN: Top-down saliency using natural statistics. *Visual Cognition*, *17*(6), 979-1003.
- Kaufman, J. D., & Dunlap, W. P. (2000). Determining the number of factors to retain: a Windows-based FORTRAN-IMSL program for parallel analysis. *Behav Res Methods Instrum Comput*, *32*(3), 389-395.
- Kawabata, H., & Zeki, S. (2004). Neural correlates of beauty. *Journal of Neurophysiology*, *91*(4), 1699-1705.
- Kawamoto, N., & Soen, T. (1993). Objective evaluation of color design. *Color Research and Application*, *18*, 260-266.
- Keightley, M. L., Winocur, G., Graham, S. J., Mayberg, H. S., Hevenor, S. J., & Grady, C. L. (2003). An fMRI study investigating cognitive modulation of brain regions associated with emotional processing of visual stimuli. *Neuropsychologia*, *41*(5), 585-596.

- Kelley, W. M., Macrae, C. N., Wyland, C. L., Caglar, S., Inati, S., & Heatherton, T. F. (2002). Finding the self? An event-related fMRI study. *Journal of cognitive neuroscience*, *14*(5), 785-794.
- Kelly, G. A. (1955). *The Psychology of Personal Constructs* (Vol. 1 & 2). New York, NY: Norton.
- Kennedy, D., & Adolphs, R. (2010). Impaired fixation to eyes following amygdala damage arises from abnormal bottom-up attention. *Neuropsychologia*.
- Kiehl, K. A., Laurens, K. R., Duty, T. L., Forster, B. B., & Liddle, P. F. (2001). An event-related fMRI study of visual and auditory oddball tasks. *Journal of Psychophysiology*, *15*(4), 221-240.
- Killgore, W. D., & Yurgelun-Todd, D. A. (2004). Activation of the amygdala and anterior cingulate during nonconscious processing of sad versus happy faces. *Neuroimage*, *21*(4), 1215-1223.
- Kim, H., Somerville, L. H., Johnstone, T., Polis, S., Alexander, A. L., Shin, L. M., et al. (2004). Contextual modulation of amygdala responsivity to surprised faces. *Journal of Cognitive Neuroscience*, *16*(10), 1745.
- Kim, M., Park, C., & Koo, K. (2005). Natural/man-made object classification based on Gabor characteristics. *Lecture notes in computer science*, *3568*, 550.
- Kim, S. E., Kim, J. W., Kim, J. J., Jeong, B. S., Choi, E., Jeong, Y. G., et al. (2007). The neural mechanism of imagining facial affective expression. *Brain Research*, *1145*, 128-137.
- Knight, D. C., Smith, C. N., Cheng, D. T., Stein, E. A., & Helmstetter, F. J. (2004). Amygdala and hippocampal activity during acquisition and extinction of human fear conditioning. *Cognitive, Affective, & Behavioral Neuroscience*, *4*(3), 317-325.
- Knill, D. C., Field, D., & Kersten, D. (1990). Human discrimination of fractal images. *Journal of the Optical Society of America A*, *7*(6), 1113-1123.
- Kowler, E., Anderson, E., Doshier, B., & Blaser, E. (1995). The role of attention in the programming of saccades. *Vision Research*, *35*(13), 1897-1916.
- Kriegeskorte, N., Lindquist, M. A., Nichols, T. E., Poldrack, R. A., & Vul, E. Everything you never wanted to know about circular analysis, but were afraid to ask. *Journal of Cerebral Blood Flow & Metabolism*, *30*(9), 1551-1557.
- Landy, M. S., & Bergen, J. R. (1991). Texture segregation and orientation gradient. *Vision Research*, *31*(4), 679-691.
- Lang, P. J., Bradley, M. M., & Cuthbert, B. N. (2005). *International affective picture system (IAPS): Affective ratings of pictures and instruction manual*: NIMH, Center for the Study of Emotion & Attention.
- Lange, K., Williams, L. M., Young, A. W., Bullmore, E. T., Brammer, M. J., Williams, S. C. R., et al. (2003). Task instructions modulate neural responses to fearful facial expressions. *Biological Psychiatry*, *53*(3), 226-232.
- Larson, C. L., Aronoff, J., Sarinopoulos, I. C., & Zhu, D. C. (2009). Recognizing threat: a simple geometric shape activates neural circuitry for threat detection. *Journal of Cognitive Neuroscience*, *21*(8), 1523-1535.
- Larson, C. L., Aronoff, J., & Stearns, J. J. (2007). The shape of threat: Simple geometric forms evoke rapid and sustained capture of attention. *Emotion*, *7*(3), 526-534.
- Laurens, K. R., Kiehl, K. A., & Liddle, P. F. (2005). A supramodal limbic paralimbic neocortical network supports goal directed stimulus processing. *Human Brain Mapping*, *24*(1), 35-49.
- Laws, K. I. (1980). Rapid texture identification. *Image processing for missile guidance*, 376-380.
- LeDoux, J. (1998). *The emotional brain: the mysterious underpinnings of emotional life*. New York: Simon & Schuster.
- LeDoux, J. E. (1992). Emotion and the amygdala. In J. P. Aggleton (Ed.), *The amygdala: Neurobiological aspects of emotion, memory, and mental dysfunction* (pp. 339-351). New York, NY: Wiley-Liss, Inc.
- LeDoux, J. E., Cicchetti, P., Xagoraris, A., & Romanski, L. M. (1990). The lateral amygdaloid nucleus: sensory interface of the amygdala in fear conditioning. *Journal of Neuroscience*, *10*(4), 1062-1069.
- Lesch, M. F., Chang, W. R., & Chang, C. C. (2008). Visually based perceptions of slipperiness: Underlying cues, consistency and relationship to coefficient of friction. *Ergonomics*, *51*(12), 1973-1983.
- Lévesque, J., Eugène, F., Joannette, Y., Paquette, V., Mensour, B., Beaudoin, G., et al. (2003). Neural circuitry underlying voluntary suppression of sadness. *Biological Psychiatry*, *53*(6), 502-510.

- Liberzon, I., Taylor, S. F., Fig, L. M., Decker, L. R., Koeppe, R. A., & Minoshima, S. (2000). Limbic activation and psychophysiological responses to aversive visual stimuli. Interaction with cognitive task. *Neuropsychopharmacology*, 23(5), 508-516.
- Liddell, B. J., Brown, K. J., Kemp, A. H., Barton, M. J., Das, P., Peduto, A., et al. (2005). A direct brainstem-amygdala-cortical 'alarm' system for subliminal signals of fear. *Neuroimage*, 24(1), 235-243.
- Lieberman, M. D., Eisenberger, N. I., Crockett, M. J., Tom, S. M., Pfeifer, J. H., & Way, B. M. (2007). Putting feelings into words: affect labeling disrupts amygdala activity in response to affective stimuli. *Psychological Science*, 18(5), 421-428.
- Lim, S. L., Padmala, S., & Pessoa, L. (2009). Segregating the significant from the mundane on a moment-to-moment basis via direct and indirect amygdala contributions. *Proceedings of the National Academy of Sciences*, 106(39), 16841.
- Lipp, O. V., Derakshan, N., Waters, A. M., & Logies, S. (2004). Snakes and Cats in the Flower Bed: Fast Detection Is Not Specific to Pictures of Fear-Relevant Animals. *Emotion*, 4(3), 233-250.
- Lipps, M., & Pelz, J. B. (2004). Yarbus revisited: task-dependent oculomotor behavior. *Journal of Vision*, 4(8), 115a.
- Mandler, G., & Shebo, B. J. (1983). Knowing and liking. *Motivation and Emotion*, 7(2), 125-144.
- Martindale, C., Moore, K., & Borkum, J. (1990). Aesthetic preference: Anomalous findings for Berlyne's psychobiological theory. *The American Journal of Psychology*, 53-80.
- Mather, G. (2006). *Foundations of perception*. Hove, UK: Psychology Press.
- McClure, E. B., Monk, C. S., Nelson, E. E., Parrish, J. M., Adler, A., Blair, R. J. R., et al. (2007). Abnormal attention modulation of fear circuit function in pediatric generalized anxiety disorder. *Archives of General Psychiatry*, 64(1), 97.
- Merabet, L., Thut, G., Murray, B., Andrews, J., Hsiao, S., & Pascual-Leone, A. (2004). Feeling by sight or seeing by touch? *Neuron*, 42(1), 173-179.
- Merabet, L. B., Swisher, J. D., McMains, S. A., Halko, M. A., Amedi, A., Pascual-Leone, A., et al. (2007). Combined activation and deactivation of visual cortex during tactile sensory processing. *Journal of Neurophysiology*, 97(2), 1633-1641.
- Merigan, W. H. (2000). Cortical area V4 is critical for certain texture discriminations, but this effect is not dependent on attention. *Visual neuroscience*, 17(06), 949-958.
- Modinos, G., Ormel, J., & Aleman, A. (2010). Altered activation and functional connectivity of neural systems supporting cognitive control of emotion in psychosis proneness. *Schizophrenia Research*, 118(1-3), 88-97.
- Mohanty, A., Egnér, T., Monti, J., & Mesulam, M. (2009). Search for a threatening target triggers limbic guidance of spatial attention. *Journal of Neuroscience*, 29(34), 10563-10572.
- Montagnini, A., & Castet, E. (2007). Spatiotemporal dynamics of visual attention during saccade preparation: Independence and coupling between attention and movement planning. *Journal of Vision*, 7(14).
- Moore, T., & Fallah, M. (2001). Control of eye movements and spatial attention. *Proceedings of the National Academy of Sciences*, 98(3), 1273-1276.
- Morgan, M. J. (2011). Features and the 'primal sketch'. *Vision Research*, 51(7), 738-753.
- Morris, J., Öhman, A., & Dolan, R. (1999). A subcortical pathway to the right amygdala mediating "unseen" fear. *Proceedings of the National Academy of Sciences*, 96(4), 1680-1685.
- Morris, J. S., Öhman, A., & Dolan, R. J. (1998). Conscious and unconscious emotional learning in the human amygdala. *Nature*, 393(6684), 467-470.
- Most, S. B., Chun, M. M., Johnson, M. R., & Kiehl, K. A. (2006). Attentional modulation of the amygdala varies with personality. *Neuroimage*, 31(2), 934-944.
- Motoyoshi, I., Nishizawa, T., & Uchikawa, K. (2007). Specular reflectance and the perception of metallic surfaces. *Journal of Vision*, 7(9), 451.
- Motoyoshi, I., Shin'ya Nishida, L. S., & Adelson, E. H. (2007). Image statistics and the perception of surface qualities. *Nature*, 447(7141), 206-209.
- Navalpakkam, V., & Itti, L. (2005). Modeling the influence of task on attention. *Vision Research*, 45(2), 205-231.
- Nichols, T. E., & Holmes, A. P. (2002). Nonparametric permutation tests for functional neuroimaging: a primer with examples. *Human Brain Mapping*, 15(1), 1-25.

- Ochsner, K. N., Bunge, S. A., Gross, J. J., & Gabrieli, J. D. E. (2002). Rethinking feelings: An fMRI study of the cognitive regulation of emotion. *Journal of Cognitive Neuroscience*, *14*(8), 1215-1229.
- Ochsner, K. N., Ray, R. D., Cooper, J. C., Robertson, E. R., Chopra, S., Gabrieli, J. D. E., et al. (2004). For better or for worse: neural systems supporting the cognitive down-and up-regulation of negative emotion. *Neuroimage*, *23*(2), 483-499.
- Öhman, A. (2005). The role of the amygdala in human fear: Automatic detection of threat. *Psychoneuroendocrinology*, *30*(10), 953-958.
- Öhman, A., Carlsson, K., Lundqvist, D., & Ingvar, M. (2007). On the unconscious subcortical origin of human fear. *Physiology & Behavior*, *92*(1-2), 180-185.
- Ohrmann, P., Rauch, A. V., Bauer, J., Kugel, H., Arolt, V., Heindel, W., et al. (2007). Threat sensitivity as assessed by automatic amygdala response to fearful faces predicts speed of visual search for facial expression. *Experimental Brain Research*, *183*(1), 51-59.
- Osgood, C. E., Suci, G. J., & Tannenbaum, P. H. (1957). *The Measurement of Meaning*. Urbana, Chicago: University of Illinois Press.
- Ousdal, O. T., Jensen, J., Server, A., Hariri, A. R., Nakstad, P. H., & Andreassen, O. A. (2008). The human amygdala is involved in general behavioral relevance detection: Evidence from an event-related functional magnetic resonance imaging Go-NoGo task. *Neuroscience*, *156*(3), 450-455.
- Over, E. A. B., Hooge, I. T. C., Vlaskamp, B. N. S., & Erkelens, C. J. (2007). Coarse-to-fine eye movement strategy in visual search. *Vision Research*, *47*(17), 2272-2280.
- Palmen, S., Durston, S., Nederveen, H., & Van Engeland, H. (2006). No evidence for preferential involvement of medial temporal lobe structures in high-functioning autism. *Psychological Medicine*, *36*(06), 827-834.
- Palmer, S. E., & Schloss, K. B. (2010). An ecological valence theory of human color preference. *Proceedings of the National Academy of Sciences*, *107*(19), 8877-8882.
- Parkhurst, D., Law, K., & Niebur, E. (2002). Modeling the role of salience in the allocation of overt visual attention. *Vision Research*, *42*(1), 107-123.
- Parkhurst, D., & Niebur, E. (2003). Texture contrast attracts overt visual attention in natural scenes. [SHORT COMMUNICATION]. *European Journal of Neuroscience*, *19*, 783-789.
- Partala, T., & Surakka, V. (2003). Pupil size variation as an indication of affective processing. *International Journal of Human-Computer Studies*, *59*(1-2), 185-198.
- Pasley, B. N., Mayes, L. C., & Schultz, R. T. (2004). Subcortical discrimination of unperceived objects during binocular rivalry. *Neuron*, *42*(1), 163-172.
- Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: Transforming numbers into movies. *Spatial vision*, *10*(4), 437-442.
- Pelz, J. B., Canosa, R., Lipps, M., Babcock, J., & Rao, P. (2003). Saccadic targeting in the real world. *Journal of Vision*, *3*(9), 310.
- Perry, B., & Szalavitz, M. (2007). *The Boy Who Was Raised as a Dog: And Other Stories from a Child Psychiatrist's Notebook--What Traumatized Children Can Teach Us About Loss, Love, and Healing*. New York, NY: Basic Books.
- Pessoa, L. (2005). To what extent are emotional visual stimuli processed without attention and awareness? *Current Opinion in Neurobiology*, *15*(2), 188-196.
- Pessoa, L., Japee, S., Sturman, D., & Ungerleider, L. G. (2006). Target visibility and visual awareness modulate amygdala responses to fearful faces. *Cerebral Cortex*, *16*(3), 366-375.
- Pessoa, L., Padmala, S., & Morland, T. (2005). Fate of unattended fearful faces in the amygdala is determined by both attentional resources and cognitive modulation. *Neuroimage*, *28*(1), 249-255.
- Peuskens, H., Claeys, K. G., Todd, J. T., Norman, J. F., Van Hecke, P., & Orban, G. A. (2004). Attention to 3-D shape, 3-D motion, and texture in 3-D structure from motion displays. *Journal of cognitive neuroscience*, *16*(4), 665-682.
- Phan, K. L., Fitzgerald, D. A., Nathan, P. J., Moore, G. J., Uhde, T. W., & Tancer, M. E. (2005). Neural substrates for voluntary suppression of negative affect: a functional magnetic resonance imaging study. *Biological Psychiatry*, *57*(3), 210-219.
- Phan, K. L., Taylor, S. F., Welsh, R. C., Ho, S. H., Britton, J. C., & Liberzon, I. (2004). Neural correlates of individual ratings of emotional salience: a trial-related fMRI study. *Neuroimage*, *21*(2), 768-780.
- Phelps, E. A., Ling, S., & Carrasco, M. (2006). Emotion facilitates perception and potentiates the perceptual benefits of attention. *Psychological Science*, *17*(4), 292-299.

- Pinkham, A. E., Griffin, M., Baron, R., Sasson, N. J., & Gur, R. C. (2010). The face in the crowd effect: Anger superiority when using real faces and multiple identities. *Emotion, 10*(1), 141-146.
- Plato. (2000). *The Republic*. Cambridge, UK: Cambridge University Press.
- Pont, S. C. (2006). Material-illumination ambiguities and the perception of solid objects. *Perception, 35*(10), 1331-1350.
- Posner, M. I., & Snyder, C. R. R. (1975). Attention and cognitive control. In R. L. Solso (Ed.), *Information Processing and Cognition: The Loyola Symposium* (pp. 55-85). Hillsdale, NJ: Erlbaum.
- Puce, A., Allison, T., Asgari, M., Gore, J. C., & McCarthy, G. (1996). Differential sensitivity of human visual cortex to faces, letterstrings, and textures: a functional magnetic resonance imaging study. *J Neurosci, 16*(16), 5205-5215.
- Ramel, W., Goldin, P. R., Eyler, L. T., Brown, G. G., Gotlib, I. H., & McQuaid, J. R. (2007). Amygdala reactivity and mood-congruent memory in individuals at risk for depressive relapse. *Biological Psychiatry, 61*(2), 231-239.
- Ravishankar Rao, A., & Lohse, G. L. (1996). Towards a texture naming system: Identifying relevant dimensions of texture. *Vision Research, 36*(11), 1649-1669.
- Ray, R. D., Ochsner, K. N., Cooper, J. C., Robertson, E. R., Gabrieli, J. D. E., & Gross, J. J. (2005). Individual differences in trait rumination and the neural systems supporting cognitive reappraisal. *Cognitive, Affective, & Behavioral Neuroscience, 5*(2), 156-168.
- Redies, C., Hänisch, J., Blickhan, M., & Denzler, J. (2007). Artists portray human faces with the Fourier statistics of complex natural scenes. *Network: Computation in Neural Systems, 18*(3), 235-248.
- Rolls, E. T. (1999). *The brain and emotion*. Oxford, UK: Oxford University Press.
- 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*(3), 308-317.
- Rothkopf, C. A., Ballard, D. H., & Hayhoe, M. M. (2007). Task and context determine where you look. *Journal of Vision, 7*(14), 12.
- Salthouse, T. A., & Ellis, C. L. (1980). Determinants of eye-fixation duration. *The American Journal of Psychology, 93*(2), 207-234.
- Sander, D., Grafman, J., & Zalla, T. (2003). The human amygdala: an evolved system for relevance detection. *Reviews in the Neurosciences, 14*(4), 303-316.
- Santos, A., Mier, D., Kirsch, P., & Meyer-Lindenberg, A. (2010). Evidence for a general face salience signal in human amygdala. *Neuroimage, 54*(4), 3111-3116.
- Sathian, K. (2005). Visual cortical activity during tactile perception in the sighted and the visually deprived. *Developmental Psychobiology, 46*(3), 279-286.
- Sathian, K., & Zangaladze, A. (2002). Feeling with the mind's eye: contribution of visual cortex to tactile perception. *Behavioural brain research, 135*(1-2), 127-132.
- Sathian, K., Zangaladze, A., Hoffman, J. M., & Grafton, S. T. (1997). Feeling with the mind's eye. *Neuroreport, 8*(18), 3877.
- Schaefer, S., Jackson, D., Davidson, R., Aguirre, G., Kimberg, D., & Thompson-Schill, S. (2002). Modulation of amygdala activity by the conscious regulation of negative emotion. *Journal of Cognitive Neuroscience, 14*(6), 913-921.
- Schira, G. (2003). Texture preference and global frequency magnitudes. *Environment and Planning B, Planning and Design, 30*, 297-318.
- Sehlmeyer, C., Dannlowski, U., Schöning, S., Kugel, H., Pyka, M., Pfleiderer, B., et al. (2011). Neural correlates of trait anxiety in fear extinction. *Psychological medicine, 41*(4), 789-798.
- Sergerie, K., Chochol, C., & Armony, J. L. (2008). The role of the amygdala in emotional processing: a quantitative meta-analysis of functional neuroimaging studies. *Neuroscience & Biobehavioral Reviews, 32*(4), 811-830.
- Sheline, Y. I., Barch, D. M., Donnelly, J. M., Ollinger, J. M., Snyder, A. Z., & Mintun, M. A. (2001). Increased amygdala response to masked emotional faces in depressed subjects resolves with antidepressant treatment: an fMRI study. *Biological Psychiatry, 50*(9), 651-658.
- Shepherd, M., Findlay, J. M., & Hockey, R. J. (1986). The relationship between eye movements and spatial attention. *Quarterly Journal of Experimental Psychology: Human Experimental Psychology, 38*(3-A), 475-491.
- Sheppard, L. C. (1994). Art and beauty as healing modalities. *Caring as healing: Renewal through hope, 102-110*.

- Shin, L. M., Wright, C. I., Cannistraro, P. A., Wedig, M. M., McMullin, K., Martis, B., et al. (2005). A functional magnetic resonance imaging study of amygdala and medial prefrontal cortex responses to overtly presented fearful faces in posttraumatic stress disorder. *Archives of general psychiatry*, *62*(3), 273-281.
- Silk, J. S., Siegle, G. J., Whalen, D. J., Ostapenko, L. J., Ladouceur, C. D., & Dahl, R. E. (2009). Pubertal changes in emotional information processing: Pupillary, behavioral, and subjective evidence during emotional word identification. *Development and Psychopathology*, *21*(01), 7-26.
- Sireteanu, R., Goertz, R., Bachert, I., & Wandert, T. (2005). Children with developmental dyslexia show a left visual. *Vision Research*, *45*(25-26), 3075-3082.
- Smith, M. L., Cottrell, G. W., Gosselin, F. A., & Schyns, P. G. (2005). Transmitting and decoding facial expressions. *Psychological Science*, *16*(3), 184.
- Soen, T., Shimada, T., & Akita, M. (1987). Objective evaluation of color design. *Color research and application*, *12*(4), 187-195.
- Somerville, L., Kim, H., Johnstone, T., Alexander, A., & Whalen, P. (2004). Human amygdala responses during presentation of happy and neutral faces: correlations with state anxiety. *Biological Psychiatry*, *55*(9), 897-903.
- Stamps, A. E. (2002). Entropy, visual diversity, and preference. *The Journal of general psychology*, *129*(3), 300-320.
- Stilla, R., & Sathian, K. (2007). Selective visuo-haptic processing of shape and texture. *Hum Brain Mapp.*
- Straube, T., Kolassa, I. T., Glauer, M., Mentzel, H. J., & Miltner, W. H. R. (2004). Effect of task conditions on brain responses to threatening faces in social phobics: an event-related functional magnetic resonance imaging study. *Biological Psychiatry*, *56*(12), 921-930.
- Straube, T., Mentzel, H. J., & Miltner, W. H. R. (2006). Neural mechanisms of automatic and direct processing of phobogenic stimuli in specific phobia. *Biological Psychiatry*, *59*(2), 162-170.
- Takahashi, S. (1995). Aesthetic properties of pictorial perception. *Psychological Review*, *102*(4), 671-683.
- Tamura, H., Mori, S., & Yamawaki, T. (1978). Textural features corresponding to visual perception. *IEEE Transactions on Systems, Man and Cybernetics*, *8*(6), 460-473.
- Taylor, S. F., Phan, K. L., Decker, L. R., & Liberzon, I. (2003). Subjective rating of emotionally salient stimuli modulates neural activity. *Neuroimage*, *18*(3), 650-659.
- Thomas, K. M., Drevets, W. C., Dahl, R. E., Ryan, N. D., Birmaher, B., Eccard, C. H., et al. (2001). Amygdala response to fearful faces in anxious and depressed children. *Archives of general psychiatry*, *58*(11), 1057-1064.
- Thumfart, S., Jacobs, R., Haak, K., Cornelissen, F., Scharinger, J., & Eitzinger, C. (2008). Feature based prediction of perceived and aesthetic properties of visual textures. *Proceedings Materials & Sensations*, 55-58.
- Todorov, A., & Engell, A. D. (2008). The role of the amygdala in implicit evaluation of emotionally neutral faces. *Social Cognitive and Affective Neuroscience*, *3*(4), 303.
- Torralba, A., Oliva, A., Castelhana, M. S., & Henderson, J. M. (2006). Contextual guidance of eye movements and attention in real-world scenes: the role of global features in object search. *Psychological Review*, *113*(4), 766-786.
- Tsuchiya, N., Moradi, F., Felsen, C., Yamazaki, M., & Adolphs, R. (2009). Intact rapid detection of fearful faces in the absence of the amygdala. *Nature neuroscience*, *12*(10), 1224-1225.
- Tuceryan, M., & Jain, A. (1998). Texture analysis. In C. Chen, L. Pau & P. Wang (Eds.), *The Handbook of Pattern Recognition and Computer Vision* (2nd ed., pp. 207-248). New Jersey: World Scientific Publishing.
- Underwood, G., Foulsham, T., & Humphrey, K. (2009). Saliency and scan patterns in the inspection of real-world scenes: Eye movements during encoding and recognition. *Visual Cognition*, *17*(6), 812-834.
- Unema, P. J. A., Pannasch, S., Joos, M., & Velichkovsky, B. M. (2005). Time course of information processing during scene perception: The relationship between saccade amplitude and fixation duration. *Visual Cognition*, *12*(3), 473-494.
- Urry, H., van Reekum, C., Johnstone, T., Kalin, N., Thurow, M., Schaefer, H., et al. (2006). Amygdala and ventromedial prefrontal cortex are inversely coupled during regulation of negative affect and predict the diurnal pattern of cortisol secretion among older adults. *Journal of Neuroscience*, *26*(16), 4415-4425.

- Ursin, H., & Kaada, B. R. (1960). Functional localization within the amygdaloid complex in the cat. *Electroencephalography and clinical Neurophysiology*, *12*(1), 1-20.
- Valdez, P., & Mehrabian, A. (1994). Effects of color on emotions. *J Exp Psychol Gen*, *123*(4), 394-409.
- Van Der Gaag, C., Minderaa, R. B., & Keysers, C. (2007). The BOLD signal in the amygdala does not differentiate between dynamic facial expressions. *Social Cognitive and Affective Neuroscience*, *2*(2), 93-103.
- Van der Laan, L. N., De Ridder, D. T. D., Viergever, M. A., & Smeets, P. A. M. (2010). The first taste is always with the eyes: A meta-analysis on the neural correlates of processing visual food cues. *Neuroimage*, *55*(1), 296-303.
- Van Reekum, C. M., Johnstone, T., Urry, H. L., Thurow, M. E., Schaefer, H. S., Alexander, A. L., et al. (2007). Gaze fixations predict brain activation during the voluntary regulation of picture-induced negative affect. *Neuroimage*, *36*(3), 1041-1055.
- Vartanian, O., & Goel, V. (2004). Neuroanatomical correlates of aesthetic preference for paintings. *Neuroreport*, *15*(5), 893-897.
- Velichkovsky, B. M., Dornhoefer, S. M., Pannasch, S., & Unema, P., J. A. (2000). *Visual fixations and level of attentional processing*. Paper presented at the Proceedings of the 2000 symposium on Eye tracking research & applications.
- Vessel, E. A., & Rubin, N. (2010). Beauty and the beholder: Highly individual taste for abstract, but not real-world images. *Journal of Vision*, *10*(2), 1-14.
- Victor, J. D., Chubb, C., & Conte, M. M. (2005). Interaction of luminance and higher-order statistics in texture discrimination. *Vision Research*, *45*(3), 311-328.
- Victor, J. D., & Conte, M. M. (1996). The role of high-order phase correlations in texture processing. *Vision Research*, *36*(11), 1615-1631.
- Vincent, B. T., Troscianko, T., & Gilchrist, I. D. (2007). Investigating a space-variant weighted salience account of visual selection. *Vision Research*, *47*(13), 1809-1820.
- Vuilleumier, P., Armony, J. L., Driver, J., & Dolan, R. J. (2001). Effects of attention and emotion on face processing in the human brain: an event-related fMRI study. *Neuron*, *30*(3), 829-841.
- Vuilleumier, P., Armony, J. L., Driver, J., & Dolan, R. J. (2003). Distinct spatial frequency sensitivities for processing faces and emotional expressions. *Nat Neurosci*, *6*(6), 624-631.
- Wadlinger, H. A., & Isaacowitz, D. M. (2006). Positive mood broadens visual attention to positive stimuli. *Motivation and Emotion*, *30*(1), 87-99.
- Wager, T. D., Davidson, M. L., Hughes, B. L., Lindquist, M. A., & Ochsner, K. N. (2008). Prefrontal-subcortical pathways mediating successful emotion regulation. *Neuron*, *59*(6), 1037-1050.
- Wang, L., LaBar, K. S., & McCarthy, G. (2006). Mood Alters Amygdala Activation to Sad Distractors During an Attentional Task. *Biological Psychiatry*, *60*(10), 1139-1146.
- Watanabe, T., & Cavanagh, P. (1993). Transparent surfaces defined by implicit X junctions. *Vision Research*, *33*(16), 2339-2346.
- Whalen, P. J., Kagan, J., Cook, R. G., Davis, F. C., Kim, H., Polis, S., et al. (2004). Human amygdala responsivity to masked fearful eye whites. [Brevia]. *Science*, *306*, 2061.
- Whalen, P. J., Kagan, J., Cook, R. G., Davis, F. C., Kim, H., Polis, S., et al. (2004). Human amygdala responsivity to masked fearful eye whites (Vol. 306, pp. 2061-2061): American Association for the Advancement of Science.
- Whalen, P. J., & Phelps, E. A. (2009). *The Human Amygdala*. New York, NY: The Guilford Press.
- Whalen, P. J., Rauch, S. L., Etkoff, N. L., McInerney, S. C., Lee, M. B., & Jenike, M. A. (1998). Masked presentations of emotional facial expressions modulate amygdala activity without explicit knowledge. *Journal of Neuroscience*, *18*(1), 411.
- Wilensky, A. E., Schafe, G. E., Kristensen, M. P., & LeDoux, J. E. (2006). Rethinking the fear circuit: the central nucleus of the amygdala is required for the acquisition, consolidation, and expression of Pavlovian fear conditioning. *The Journal of neuroscience*, *26*(48), 12387.
- Williams, D., & Julesz, B. (1992). Perceptual asymmetry in texture perception. *Proceedings of the National Academy of Sciences of the United States of America*, *89*(14), 6531.
- Williams, L. M., Phillips, M. L., Brammer, M. J., Skerrett, D., Lagopoulos, J., Rennie, C., et al. (2001). Arousal dissociates amygdala and hippocampal fear responses: evidence from simultaneous fMRI and skin conductance recording. *Neuroimage*, *14*(5), 1070-1079.

- Williams, M. A., Morris, A. P., McGlone, F., Abbott, D. F., & Mattingley, J. B. (2004). Amygdala responses to fearful and happy facial expressions under conditions of binocular suppression. *J Neurosci*, *24*(12), 2898-2904.
- Winston, J., O'Doherty, J., & Dolan, R. (2003). Common and distinct neural responses during direct and incidental processing of multiple facial emotions. *Neuroimage*, *20*(1), 84-97.
- Winston, J., Strange, B., O'Doherty, J., & Dolan, R. (2005). Automatic and Intentional Brain Responses Evaluation of Trustworthiness of Faces. *Social neuroscience: key readings*, 199.
- Wooding, D. (2002). *Fixation maps: quantifying eye-movement traces*. Paper presented at the Proceedings of the 2002 symposium on Eye tracking research & applications, New Orleans, Louisiana.
- Wright, C. I., Martis, B., McMullin, K., Shin, L. M., & Rauch, S. L. (2003). Amygdala and insular responses to emotionally valenced human faces in small animal specific phobia. *Biological Psychiatry*, *54*(10), 1067-1076.
- Wright, P., Albarracín, D., Brown, R. D., Li, H., He, G., & Liu, Y. (2008). Dissociated responses in the amygdala and orbitofrontal cortex to bottom-up and top-down components of emotional evaluation. *Neuroimage*, *39*(2), 894-902.
- Wright, P., & Liu, Y. (2006). Neutral faces activate the amygdala during identity matching. *Neuroimage*, *29*(2), 628-636.
- Yaniv, D., Desmedt, A., Jaffard, R., & Richter-Levin, G. (2004). The amygdala and appraisal processes: stimulus and response complexity as an organizing factor. *Brain Research Reviews*, *44*(2-3), 179-186.
- Yarbus, A. L. (1973). *Eye movements and vision* (B. Haigh & L. A. Riggs, Trans.). New York: Plenum press.
- Yeshurun, Y., Montagna, B., & Carrasco, M. (2008). On the flexibility of sustained attention and its effects on a texture segmentation task. *Vision Research*, *48*(1), 80-95.
- Zeki, S. (1999). *Inner vision: An exploration of art and the brain*. Oxford: Oxford University Press.
- Zhang, M., Weisser, V. D., Stilla, R., Prather, S. C., & Sathian, K. (2004). Multisensory cortical processing of object shape and its relation to mental imagery. *Cognitive, Affective, & Behavioral Neuroscience*, *4*(2), 251-259.
- Zhang, Y., Feick, L., & Price, L. J. (2006). The Impact of Self-Constraint on Aesthetic Preference for Angular Versus Rounded Shapes. *Personality and Social Psychology Bulletin*, *32*(6), 794.
- Zysset, S., Huber, O., Ferstl, E., & von Cramon, D. Y. (2002). The anterior frontomedian cortex and evaluative judgment: an fMRI study. *Neuroimage*, *15*(4), 983-991.