Individual differences in visual perception and memory

Colizoli, O.

Citation for published version (APA):
Chapter 7. Summary and Discussion

There is substantial variation in perception and memory in humans. The focus of this thesis was on visual perception and memory. I explored part of the range of variation in visual perception and memory, the neural basis of the variation and whether training can alter visual perception and memory. I will first give a summary of the overall results obtained and general conclusions of each section. I will briefly describe the ongoing ‘individual differences’ research project in our group and how it relates to the research presented in the thesis. Thereafter, I discuss the current state of affairs concerning training perceptual associations (i.e. synesthesia) in more detail. I argue that perception/memory training paradigms should not only be adopted, but are necessary for the advancement of the cognitive neuroscience of individual differences.

Summary

In Part 1 of the thesis, the phenomenon of synesthesia was used as a window into the relationship between the range of perception on the one hand, and variation in brain function and structure on the other hand. In Chapter 2, a review of the brain areas involved in synesthesia was presented. Across multiple neuroimaging studies (mainly using magnetic-resonance imaging), we found evidence for three distinct neural networks related to synesthesia: the sensory processes, the attentional (or binding) processes, and the cognitive control mechanisms. In addition, we proposed that the trait of synesthesia is inherited, while the environment determines the type of synesthesia. Chapter 3 presented a case study on synesthete SC, who experiences taste, smell and physical sensations induced by hearing or reading words. SC’s brain showed activation related to her synesthesia in regions that process taste and smell (sensory processes) in addition to brain regions involved in binding sensory features under attention (superior parietal lobe). Although it was not clear whether cognitive control mechanisms were involved in the experimental paradigm (SC passively viewed or listened to all stimuli), these results were in line with our hypotheses about synesthesia-related neural networks across sub-types of synesthesia. Activation found in certain neural networks seems to be specific to the sub-type of synesthesia (the sensory processes), while activation found in other networks seem to be related across sub-types (the binding processes) to the trait of having synesthesia.

Part II of the thesis, inspired by grapheme-color synesthesia, explored to what extent letter-color associations could be trained by reading in color. In addition, we investigated whether effects of training were evident in experience-dependent brain plasticity (both functional and structural) of the visual system. In Chapter 4, we showed that automatic letter-color associations could be learned by reading in color. This training method is different in the sense that the learned associations are a byproduct of the reading process, because they do not need to be consciously rehearsed. A correlation between the Stroop effect and the self-report rating of experiencing letters in color hinted at underlying factors that may determine individual differences in the learning effect, such as visual mental imagery ability. In contrast to the automatic (or semantic) effects measured with the modified Stroop task, we did not find strong evidence for low-level perceptual effects of color, as tested with a visual crowding task. In
Chapter 5, we replicated the main behavioral results from the original reading in color study. We furthermore tested for functional and structural plasticity of the visual system in addition to possible genetic factors related to grapheme-color synesthesia. We found effects of congruency and training in brain activation, which differed between (non-synesthetic) relatives of synesthetes and matched controls (both groups trained an equal amount) in brain areas known to be related to grapheme-color synesthesia (such as area V4). Differences in brain function and structure were present in the absence of differences in any behavioral measure. There is empirical evidence showing that synesthesia has a genetic component (Asher et al., 2009; Tomson et al., 2011). The neural differences between relatives of synesthetes and matched controls imply that underlying genetic mechanisms related to synesthesia are present in non-synesthetic relatives of synesthetes. The absence of behavioral differences between relatives and matched controls in the Stroop effect may be taken to indicate that the presence of possible ‘synesthetic genes’ was not enough to facilitate learning letter-color associations in this case. However, future research with ideally more extensive training is needed in order to justify this conclusion.

Part III investigated whether individual differences in face recognition ability could be predicted from brain structure. In this section, the normal range of face recognition ability was investigated, in contrast to the extreme or unusual variation in perception and memory, as is the case with synesthesia and prosopagnosia. Grey-matter and white-matter structure in the face-recognition network (Gobbini & Haxby, 2007) were tested for predictive ability using multiple regression analysis. We found that white-matter structure (measured with fractional anisotropy) significantly predicted about 15% of the variance in face recognition ability, while grey-matter structure (measured with voxel-based morphometry) did not predict face recognition ability. Increased structural connectivity in the face-network regions was related to better face recognition performance, the best predictor of face recognition ability being the fusiform face area. Furthermore, the regions differed in their relative contribution to familiar and unfamiliar face area. Overall, the results highlight some of the possibilities, but also limitations, in predicting individual differences in memory ability from brain structure.

My overall conclusion from the research presented in this thesis is that individual differences in both visual perception and memory ability are reflected in brain function and structure in related networks to a certain degree. To what extent individual differences in perception and memory can be reliably predicted from brain function and structure at the individual level remains an open question for future research. The current literature lacks a coherent investigation into if and how individual differences in visual working memory ability for many different categories of visual stimuli are reflected in variation in brain function and structure. Since visual information is processed in a largely hierarchical fashion (Zeki, 1993), it follows naturally to look at the variation within these visual hierarchies to see if there are category-specific or process-specific neural correlates of the within-category memory abilities. Following this line of reasoning, we have conducted a large-scale study on individual differences in category-specific brain networks. Due to the fact that the research is ongoing at the present moment, in addition to the large-scale nature of the project, I was not able to include this study in the thesis. As the study is however within the scope of the thesis, I will summarize it below.
Ongoing research: Individual differences in category-specific brain networks

Ongoing research in our group is testing the hypothesis that category-specific visual memory ability is reliably reflected in category-specific brain networks in the visual system. In the MRI study, our aim is to relate specific visual memory abilities to underlying neural correlates in order to be able to say that an individual's memory ability directly relates to the network properties of his or her brain. If our research is successful, we will be able to say that certain people are better or worse at remembering certain categories of visual information because their brains are more or less suited for it.

In order to test this hypotheses, we created a battery of internet-based visual working memory (2-back) tests with 32 different categories of visual images, in addition to a Corsi-block tapping task, and the subjective (Marks, 1973; Cui et al., 2007) and objective visual mental imagery questionnaires. The first objective of this study is to uncover the factor structure of visual memory: are certain categories of visual images related to one another more so than others? Or is there one underlying factor that determines visual memory ability across all categories of visual images? The second objective is to determine whether performance on distinct categories of visual memory tasks relates to neural measures in areas that process the category-specific type of visual information. Specifically, we would like to test our prediction that performance on the different categories of the memory tasks correlate with (a) grey-matter density or white-matter connectivity in category-specific regions and (b) the mean BOLD activation in category-specific regions. In addition, we would like to test the prediction that (c) BOLD activation in category-specific regions correlates with grey-matter density and white-matter connectivity within these regions. This study is not only relevant for understanding the relationship between visual memory ability and neural networks, but it is also relevant for understanding how different measures of brain function and structure are related to each other.

During the MRI session, structural T1 MRI images were acquired at the beginning and end of the session in order to quantify the density of grey matter in each voxel and for registration purposes. Diffusion tensor images were acquired in order to assess white-matter connectivity measured with fractional anisotropy per voxel. For functional analyses (fMRI), brain regions that respond to specific categories of visual images (faces, houses, objects, words, colors and textures) were localized by having participants passively view images from the five categories in half of the experimental runs. In the other half of the runs, using the same stimuli, subjects were instructed to perform a series of 2-back working memory tasks on these categories. By having both a passive viewing and memory condition, we are able to compare category-specific localization of regions with and without a memory task. The pilot study (data not presented in this thesis) confirmed that we have developed a successful paradigm in which to test our hypothesis that working memory ability for different categories of visual images correlates with brain networks in areas associated with processing those stimuli. The analysis of both the internet-based visual memory battery data as well as the functional and structural MRI data is currently a work in progress, and therefore, could not be included in the thesis.
Discussion

Correlation is not causation
A well-known and influential study by Maguire et al. (2000) showed a relationship between quantifiable measures of brain anatomy and the navigation experience of London taxi-cab drivers on the individual level. The authors investigated the structural properties of the hippocampal cortex (a structure known for its role in spatial context and memory) of London taxi-cab drivers and found that the grey matter volume of the posterior hippocampal cortices of taxi-cab drivers was significantly increased compared to the control group (with anterior hippocampal cortex showing the reverse trend). A spectacular finding in this study was that the grey matter volumes of the individual hippocampal cortices were related to the years spent as a taxi driver, showing a direct relationship (i.e. correlation) between the size of navigation-related areas and experience as a navigator.

Although correlation analyses can be very informative and predictive at the individual level, as illustrated above, it is important to move towards determining causal relationships between perception, memory, brain networks and genes in order to fully understand the nature gene-brain-environment interactions (Draganski & May, 2008). By actively manipulating variables, causal mechanisms can be uncovered using training paradigms that test individuals before and after they have been trained, in order to follow possible changes that may be induced in behavior, brain function and structure, as well as phenomenology. For example, learning new color names was shown to cause increases in grey matter volume in the visual cortex in regions known to mediate color vision (Kwok, et al., 2011). However, the authors did not report any correlations between the visual learning effect and the amount of increase in grey matter in visual regions. Without such a correlation, no reliable prediction of sensitivity to learning at the individual level can be made. The main results of training types of studies have profound implications into learning and neuroplasticity (Draganski & May, 2008), furthermore, they also serve as examples of the type of information that can be gained through an approach that combines group-based (or averaging-based) analyses with correlations of individual differences. Using a combination of an individual differences approach with a training paradigm, causal inference (and prediction) at the individual level can be made.

What follows is an argument in favor of adopting training paradigms in order to show the potential this approach has for the cognitive neuroscience of individual differences in visual perception and memory. The current state of affairs concerning training synesthesia is used as an example for how training perception and memory overall can be fruitful for the research field. Only by manipulating variables, can we probe the ‘chicken and egg’ scenario: are perceptual experiences the result of certain patterns in brain structure or are the differences in brain structure the result of having certain perceptual experiences?

Why ‘training synesthesia’ is beneficial for cognitive neuroscience
In the cognitive neuroscience of perception and memory, consciousness is inherently involved in many aspects of our research questions. Studying the neural mechanisms involved in synesthesia provides a window into the realm of qualia, the phenomenological experience that
is subjective by definition. Furthermore, synesthesia can highlight the relationship between subjective experience, genes and environment (Brang & Ramachandran, 2011). Besides being able to answer fundamental research questions concerning how the brain is organized and operates, the presence of synesthesia is associated with benefits in memory in the domains related to the sub-type of synesthesia (Luria, 1968; Smilek et al., 2002; Mills et al., 2006; Tammet, 2007; Yaro & Ward, 2007; Rothen & Meier, 2010a; Cohen Kadosh et al., 2012; Rothen et al., 2012; Terhune et al., 2013). Training synesthesia may even be an avenue for techniques designed to enhance memory and learning strategies (Foer, 2011). An important point to make is that developmental synesthesia also entails ‘training’ in the sense that many types of synesthesia are at least partially dependent on culture-specific environmental constraints or semiotic inducers, such as letters. We are not born with a letter ‘A’ in our brains, let alone a red ‘A’.

Researchers have tried to train or induce synesthesia in the past (for a summary of studies see Deroy & Spence, 2013). There have been 11 known synesthesia training studies since 1935 (in 78 years), which is about 1.5 times per decade in less than one century. Most of these studies used different techniques from one another. There is a current debate in the field over the purpose and validity of synesthesia training experiments (Deroy & Spence, 2013). Deroy and Spence (2013) argued that since no synesthetic training paradigm has worked yet (meaning that none of the participants reported perceptual experiences of color in the absence of real color after training), we might as well give up now. We take a different position: the ‘glass is half full’ instead of the ‘glass is half empty’ viewpoint. Even if synesthesia training paradigms can never produce ‘real’ synesthetes, they are still relevant for understanding what makes the difference between synesthetes and non-synesthetes. For example, whether the distinction between groups is continuous or categorical. This is especially relevant for cognitive neuroscientists studying brain mechanisms related to consciousness, perception and memory. If synesthesia can be trained, we will have gained an understanding about what kind of individual is more likely to become a synesthete and why. If synesthesia cannot be trained, we still gain an understanding about what the necessary and sufficient conditions must be in order to develop it (e.g. certain genes).

In several studies using different training methods with non-synesthetes, differences in behavior, most of all the Stroop effect, have been found (Meier & Rothen, 2009; Rothen et al., 2011; Colizoli et al., 2012; Kusnir & Thut, 2011; Rothen et al., 2013) and the size of this learned effect has been found to be correlated with other measures (Colizoli et al., 2012; Kusnir & Thut, 2011). Some effects, such as a conditioned response (Meier & Rothen, 2009; Rothen et al., 2013) or a crowding effect (Colizoli et al., 2012) have not been found. Other effects, for example, binocular rivalry of competing synesthetic colors (Paffen et al., 2011) or bistable and apparent motion (Kim et al., 2003) have yet to be tested in trained non-synesthetes. Whether the presence of such effects in trainees (and how many effects or how strong the effects are) should be considered diagnostic of synesthesia is debatable and should be the topic of open discussion in the field.
Another factor to consider is the duration of previously tested synesthesia training studies. The longest training period tested in a group of individuals so far has been 7 weeks (Deroy & Spence, 2013). A study by Simner et al. (2009) however shows that it may take years before the consistent and strong associations are stabilized. Why not try training associations over several years then? As far as we know, only one study so far investigated learned grapheme-color associations over a prolonged period (many years). The associations were not learned in a typical language-related manner: Elias et al. (2003) compared a grapheme-color synesthete to a trained control who sewed using a number-color mapping for eight years. A pitfall to such an approach is that the individual was perhaps selected to be compared to the synesthete exactly because of the fact that he did not have perceptual color concurrents after so many years consistently mapping numbers to colors. This is comparable to the now dispelled ‘all synesthetes must be geniuses’ argument, based on a few cases of synestheses with exceptional memories (Luria, 1968; Smilek et al., 2002; Mills et al., 2006; Tammet, 2007), the rationale behind which was actually the result of selection bias (Yaro & Ward, 2007; Rothen & Meier, 2009; Rothen et al., 2012). While there are specific memory advantages related to synesthesia, having synesthesia does not entail having an overall extraordinary memory or intellect (Rothen & Meier, 2009), although some individuals with extraordinary memories also have synesthesia (Luria, 1968). Similarly, although some individuals may train ‘synesthetic’ associations over many years, they may never become synesthetes. This does not logically entail that it is impossible for anyone who tries to become a synesthete after extensive training.

Some open questions on the development of synesthesia that training paradigms can help to answer are the following: Is there a critical period necessary for developing synesthesia? If so, when and what is the duration of this critical period? How ‘moldable’ are the inducer-concurrent mappings during the critical period? Are there individual differences in the critical period? There have been to date no developmental neuroimaging studies on synesthesia. No training studies have tried to train synesthetic associations in children in ‘critical periods’ of development, when children’s brain are extremely plastic (e.g. Schlaug et al., 2009). At the same time, studies have shown that specific colors can stem directly from childhood toys (Hancock, 2005; Witthoft & Winawer, 2013). In order to characterize the interaction between genes and environment in perceptual development, understanding the developmental pattern in synesthesia is a crucial step in unlocking this knowledge. Training paradigms can help probe interactions involved in development, for example, by employing a ‘reading in color’ training paradigm in elementary schools while children are learning to read and write.

The future of the cognitive neuroscience of individual differences in perception and memory

Improvements in technology open up doorways to training both perception and memory in at least two essential ways: training methods can be more easily implemented and new training methods can be devised. Computer programs can now be made, for example, in order to color letters, numbers, words and symbols in a customizable fashion. Example code for such a program in Visual Basic is given in Colizoli, Murre and Rouw (2013). Multisensory interfaces, such as the vOICe (Auvray et al., 2007) or Eye Music (Levy-Tzedek et al., 2012) are now being developed for blind individuals and may soon be available for regular consumers for affordable prices. The blind can learn to ‘see’ color through sound, even when not using the device
(Proulx, 2010). Training methods combined with neuroimaging techniques can shed light on functional and structural brain plasticity and neural-network organization. For example, functional reorganization in the brains of blind people after training on these devices has been demonstrated (Amedi et al., 2007; Striem-Amit et al., 2012a; 2012b). Lastly, internet-based training makes long-term lab-independent training experiments possible.

The rise of technology opens doorways into previously untested training methods. For example, training methods used in conjunction with transcranial direct current stimulation or transcranial magnetic stimulation can be tested in order to see if direct manipulation of neural circuitry can enhance or interfere with perceptual learning. Computers make it possible to develop associative training paradigms that have never been tested, such as with planning (time-space), reading music (music notation-color/form), and DJing, producing and mixing sound (sound-color/form). Related to face recognition ability, training programs may be effective in overcoming some of the perceptual deficits in face recognition that are characteristic of prosopagnosia (Schmalz et al., 2008) as well as improving the face recognition abilities of non-prosopagnosics interested in doing so (Malpass et al., 1973; Goldstein & Chance, 1985). Stimulating neuronal reorganization or strengthening face-recognition networks (e.g. within and between the core and extended face-recognition networks) may be the result of face-recognition training paradigms.

Two main considerations have come to light over the course of my research concerning an individual differences approach to training visual perception and memory. First, implicit training is more feasible over the long term than explicit training. In Howells’ (1944) study on the experimental development of tone-color synesthesia, he concluded the following concerning the boring and repetitive nature of the task: ‘Actually the impression of the writer was that unwittingly the experiment had achieved about as much success in developing neurosis as in creating synesthesia.’ Our reading in color method has the ability to incorporate the perceptual training as a byproduct of the main task at hand (i.e. reading comprehension). In general, the focus of long-term training paradigms should be on integrating the training with life-related tasks so that the trained effect becomes a byproduct of another action that people will do anyway. Second, training programs should be customizable. In addition to the range of naturally occurring perceptual experiences, there are also differences between pre-existing preferences for certain associations both between (e.g. I prefer a red ‘a’ but someone else prefers a blue ‘a’) and within individuals (e.g. I prefer a red ‘a’ but not a red ‘e’). These types of preferences have an effect on the learned associations in training paradigms. Therefore, individual differences in preferences in addition to experience should be taken into account by allowing software for training programs to be customizable.

It is my opinion that there is great practical potential to training visual perception and memory. Apart from the scientific significance, there may also be potential clinical applications. For example, a ‘synesthetic training’ approach has inspired methods for sensory substitution in the blind using substitution devices (Auvray et al., 2007; Levy-Tzedek et al., 2012). I would propose testing new methods for rehabilitation of sensory deficits, for example with prosopagnosia mentioned above, in addition to conceptual deficits, for example for dyslexia and dyscalculia.
Using dyslexia as an example, I propose that specialized letter-color applications may be able to serve as treatment for certain cognitive dysfunctions by training and strengthening the healthy or functioning networks (e.g. color processing networks) that bypass the malfunctioning brain networks (e.g. the visual word form area). This has been shown to be possible in reading through sound in the blind: different neural networks can achieve the same end result, for example, comprehension while reading through different sensory modalities (Strieman-Amit, 2012a).

An individual differences approach to cognitive neuroscience combined with training paradigms targeting perception and memory is the future. Such training and treatment programs not only inform science of the factors that make certain individuals sensitive or prone to acquire certain traits, but may also help to increase the quality of life of individuals, especially those with perceptual deficits. In addition, training and treatment programs can be customized and therefore optimized at the individual level. Predictive ability at the individual level is necessary for a full understanding of a single individual's brain. The future of the cognitive neuroscience of individual differences in (visual) perception and memory certainly is a bright one.