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KADI TULVER

An investigation of individual differences in the effects of priors on visual perception

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An investigation of individual differences in the effects of priors on visual perception

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**These authors contributed equally to this work.*

The author of the present dissertation contributed to these publications as follows:

- In **Study I**, wrote the manuscript as the main author.
- In **Study II**, participated in refining the experimental design, collecting the data and writing the manuscript.
- In **Study III**, developed the design, conducted the experiments, carried out the data analysis and wrote the manuscript as the main author.
- In **Study IV**, participated in developing the paradigm and collecting the data; carried out the data analyses and co-wrote the manuscript sharing the status of the first author.

1. INTRODUCTION

Vision is considered the dominant sense in humans. Most of our learning, understanding of the world, decisions and actions are built upon information acquired via vision. We rely primarily on our visual senses to interpret and predict the behaviours of others, to spot threat or danger in our environment, to orient in three-dimensional space and to derive meaning from contextual cues. It should therefore be of no surprise that an enormous body of work has been devoted to understanding how visual perception works. Perceptual processing entails much more than simple awareness of the sensory attributes of visual stimuli (i.e. sensation) – it also requires selecting the relevant information and suppressing the irrelevant, integrating the features into a cohesive whole and interpreting its significance. Somehow, we are able to transform meaningless signal inputs into a globally meaningful scene and do so seemingly effortlessly.

Despite extensive research, there is still a lot we do not understand about the underlying structure of visual perception and the many complex cognitive mechanisms involved in creating a seamless phenomenological experience of our surroundings. Across a literature of disparate findings, there has been a growing need for a unitary framework to encompass and organize the current state of our knowledge as well as add new perspectives. One promising theory that is inspiring novel approaches to this field of research is the predictive processing framework (e.g., Friston, 2005; Hohwy, 2013; Rao & Ballard, 1999). Placed at the centre-stage of this theory is an impressive body of computational and empirical research which has delved into the theoretical and neurobiological implications of the effects of top-down processing on perception. It is widely accepted that humans are not merely passive vessels in acquiring information, but rather active participants in creating their own individual perceptual experience. In addition to the features of objective sensory information, our past experiences, knowledge, expectations and context all play a role in determining the qualitative and quantitative nature of the subjective percept. Relying on a generative model of previously gathered information, the perceptual system predicts the most likely perceptual experience and makes corrections to the hypothesis if the actual sensory signals violate these expectations. Optimal perceptual processing therefore depends on a balanced integration of top-down and bottom-up signals. The idea of the brain as a hypothesis-testing system was proposed already in the 19th century by Hermann von Helmholtz (1867) and was further developed during the mid-20th century cognitive revolution (e.g., Gregory, 1980; Neisser, 1967). However, compared to the earlier state of this general theoretical stance, current research has developed a better understanding of the brain systems mediating the top-down elaboration of sensory data as well as worked out apt computational models of the cognitive-perceptual information processing systems. It is therefore easy to understand why this approach has become prevalent across several domains of scientific research.

Importantly, the predictive processing framework offers new ways to approach individual differences research in vision. Individual variance in perception can arise from a range of different sources. Two people can arrive at a different perceptual experience of the same objective scene due to optical aberrations (Porter, Guirao, Cox, & Williams, 2001) or structural differences in early visual cortices (Schwarzkopf, Song, & Rees, 2011). A new perspective on top-down influences on perception also allows us to consider that individual differences can result from dissimilar past experiences and beliefs, or alternatively because of a trait-like cognitive bias in the relative weighting of prior expectations versus sensory information. This opens up a whole array of topical research questions which have the potential to clarify the structure of vision, as it is still not well understood how interindividual differences in determining the subjective perceptual experience are acquired and organized in the mind and brain. A better understanding of how predispositions related to predictive mechanisms are expressed in individual perceptual behaviour can also prove useful for developing diagnostic and screening tests when linked to atypicalities in perceptual processing symptomatic of mental disorders. With this in mind, the current dissertation hopes to contribute to the ongoing efforts towards elucidating the cognitive organization of visual perception. Let it be noted that the focal point of this work is within the subjective (self-reported clarity of percepts) and behavioural (discrimination of stimuli) dimension with less emphasis on the neural dimension of perceptual processing (Ward, 2019).

1.1. Aims of the dissertation

The general aim of the current dissertation was to study the expression and structure of interindividual differences in top-down effects on visual perception. Cognitive higher-level factors, such as beliefs and expectations, have been shown to affect perceptual processing across several information processing stages, as demonstrated by performance on various perceptual paradigms (for reviews, see de Lange, Heilbron, & Kok, 2018; Gilbert & Li, 2013; O'Callaghan, Kveraga, Shine, Adams, & Bar, 2017). To this end, I ask several related research questions: a) Can individual differences in the effects of priors be partially explained by a general overarching latent factor of prior effects on perception or are such effects better described by more narrow and specific categories?; b) To what extent does non-veridical perception, as induced by expectations, display variability between individuals and between tasks?; c) Can individual differences in the effects of priors be linked to certain trait dimensions, specifically those measured along the spectrum of schizotypy and autism?

In this dissertation I will argue that systematic research into stable individual differences in perception (in this instance, individual differences in top-down effects) can offer new and relevant insight into the mechanisms and principles of perceptual processing in general. A large portion of our knowledge regarding perceptual processing has been acquired through data averaged over groups of people and generalized across populations, often downplaying or even ignoring the stable effects of interindividual differences on visual processes. Nevertheless, mapping out persistent individual variability in perceptual functions is necessary for developing general models of perception. I will also emphasize the relevance of applying multiple perceptual paradigms to help interpret empirical results and clarify the theoretical constructs of the otherwise very broad psychological phenomena related to individual differences research in the domain of visual perception.

Pertaining to that general goal, the following four publications each contribute to a specific aspect of knowledge addressed in depth throughout this dissertation.

- **Study I** provides a theoretical background to the topic with a review of recent work published on the structure of individual differences in vision. The study aims to put into perspective the weight and complexity of this field of research, as well as highlighting some of the pitfalls researchers have come across when applying latent variable analysis methods to behavioural data.
- **Study II** lays the groundwork of the current dissertation by illustrating the presence of individual differences in basic conscious visual perception in relation to nonspecific global network activity which spreads from higher-level brain areas to the lower levels. Interindividual variance was reflected in behavioural measures as well as measures of brain correlates.
- **Study III** offers a novel approach to the study of prior effects on perception. We compiled a battery of established perceptual paradigms where top-down effects on perception had been previously demonstrated. By applying latent variable analysis we sought to answer the question whether the effects of priors could be viewed as a cohesive construct or whether that is an overgeneralized approach. Links with autistic traits and schizotypy were also analyzed.
- In **Study IV**, we developed and compared several analogous tasks where experimentally conditioned expectations of stimulus pairs resulted in participants reporting subjective experience of the missing stimulus. We were able to show that this effect is common and can be reliably elicited in a paradigm where attention is diverted from the critical stimulus. Interestingly, the level of expression of this effect differed between individuals as well as between different tasks. We also asked whether individual differences in susceptibility to such misperception were linked to autistic traits.

2. VISION: THE BASIC STRUCTURE AND INDIVIDUAL DIFFERENCES

There is already a great deal we know about how early visual processing is structured in the brain. Collectively, the neural cells situated in different hierarchical levels of the brain compute and represent the contents of the visual stimulation (Chalupa & Werner, 2004; Robson, 1980). The primary visual cortex (V1) contains specialized cells tuned to specific features of the world around us which enable the basic detection of edges, orientations, wavelengths and light intensity. Combined information from the simple cells in the primary visual cortex is sent via multiple pathways to other higher regions of the extra-striate cortex which respond not only to very simple receptive field stimulation, but also to many different kinds of input: a range of orientations, a range of spatial frequencies, input signalling motion (e.g., in V5), colour and surface attributes (e.g., in V4). The higher up in the hierarchical architecture of perceptual processing, the more integral and abstract the visual representations become, as input from the lower level more narrowly tuned neurons is integrated into specific and intricate categorical level information about objects and scenes.

As outlined above, we have a fairly comprehensive grasp on the sensory processing stages of vision. However, which mechanisms are involved in higher-level perceptual organization and how the visual system manages to form a meaningful percept from two-dimensional image features has still not been exhaustively elucidated. In order to recognize an object, top-down input of past memories and category representations must be called upon. One central problem of the perceptual system is in overcoming the uncertainty inherent to sensory information when inferring three-dimensional objects and scenes from two-dimensional inputs. Any two-dimensional spread of data, as it is projected to the retina, has more than one possible source and thereby allows for multiple interpretations. Moreover, the system has to be efficient in disregarding noise signals from gleaning the gist of the image. Based on current brain-imaging data and the prevalent conceptualization of a hypothesis-testing brain, visual perception can essentially be viewed as a system of *probabilistic inference* steered by top-down, memory dependent contextual modulation (e.g., Albright, 2012; Olshausen, 2004, 2014). In other words, the product of bottom-up processing becomes modulated and biased by perceptual and conceptual knowledge acquired by (associative) learning and former experience. This implies that the brain is tuned to extract statistical regularities from the environment and can apply those regularities to guide lower-level processing via feedback connections, thereby inferring a more probable percept and facilitating perception. The precise neural characteristics of the proposed hierarchical architecture of complex feedback and feedforward signalling are still under investigation, but the general principle is overall supported by empirical evidence (e.g., Lee & Mumford, 2003). For instance, it has been shown that activity in V1 is suppressed if the stimulus is predictable compared to novel input (for a review, see Auksztulewicz & Friston, 2015), hence reducing redundant neural activity. In the context of the current dissertation, however, I mainly focus on the cognitive structure of top-down effects on perception and the relevance of individual differences for their investigation.

2.1. Individual differences in perception

Traditional vision science has focused primarily on studying the general rules and robust phenomena of visual processing in humans without concerning itself too much with individual variability (Boff, Kaufman, & Thomas, 1986; de-Wit & Wagemans, 2015). Most of our current understanding regarding basic perceptual mechanisms is based on experiments inspired by the school of psychophysics which is dedicated to studying the mechanisms of how physical stimuli are perceived (and interpreted) in the brain. This can be researched by systematically varying the physical properties of various stimuli and measuring the effects on the subjective experience of the "averaged", typical observer. Such studies are traditionally performed using a large number of repetitions but a small number of participants, as it relies on the assumption that the general principles of visual perceptual processing are common across most people with little interindividual variance. Any individual differences in such research are usually treated as a source of noise, which is averaged out across groups in favour of detecting underlying rules and tendencies common to all human vision (Kanai & Rees, 2011). Nevertheless, stable individual differences continue to emerge at different stages and modalities of visual processing and should be viewed as a valuable research tool for understanding perception (de Wit & Wagemans, 2015; Mollon, Bosten, Peterzell, & Webster, 2017).

The notion that not everyone perceives the world in the same manner is not a new one. In 1975 Jules Davidoff (Davidoff, 1975) penned an extensive review about the various short-term and long-term differences in internal percepts that may occur between two observers looking at the same external input. Individual differences in perceptual processing are multiple and varied, ranging from differences in colour vision (Webster, 2015) and contrast sensitivity (Peterzell & Teller, 1996) to contradictory interpretations of ambiguous figures. It stands to reason that such differences are likely systematic and ultimately rooted in important differences of neural, structural and cognitive nature (Mollon et al., 2017). For instance, behavioural results in visual abilities have been successfully linked to structural differences in cortical volume (Kanai & Rees, 2011) and neurotransmitter concentration (Van Loon et al., 2013). As a result, the hidden potential in investigating the sources of variance in group data is being discovered by researchers more and more.

The purpose of studying individual differences in visual perception is related to several research driven goals. Firstly, studying stable individual differences in vision and how they are grouped together helps to identify common sources of variance and thereby improve our understanding of visual mechanisms.

Secondly, consistent research into individual variance – especially by applying multiple comparable paradigms on one sample – is a way to establish construct validity of theoretical concepts in the field, by assessing whether ostensibly similar tasks truly measure the same constructs. Lastly, it is possible to link individual differences in perception to other personality measures and clinical disorders with perceptual symptomatology, offering potential practical implications. Once we understand the separate sources behind clusters of symptoms in a complex disorder, this knowledge can be used to improve the specificity of diagnostic criteria, with hope to eventually aid in the early detection and treatment of disorders. In the following sections, I will describe four studies that have aimed to contribute to each of these goals.

2.2. The latent factorial structure of vision

The first step in understanding the structure of individual differences is to investigate patterns and common mechanisms underlying sources of individual variance. One such approach entails measuring the behavioural results of a large subject sample on multiple visual tasks and applying an exploratory factor analysis to the results in order to establish the factorial structure underlying the data. For example, Thurstone (1944) administered 40 perceptual tests of a wide scope on 170 participants and concluded that the data was best summarized by 11 perceptual factors, capturing several basic visual abilities. Alternatively, one might have a prior hypothesis regarding the structure of individual differences in a specific dimension of vision and only choose tasks which are purported to tap into a common mechanism. For instance, Webster and MacLeod (1988) only measured individual differences in colour matching tasks and explored the factor structure behind this specific dimension of perception.

Recent years have witnessed a renewed interest in defining the factorial structure of individual differences in vision. Studies have attempted to group vision into factors not only by the more basic early visual processing abilities, but also based on higher cognitive structure and function. In other words, individuals can differ not only in areas such as visual acuity or colour perception, but also in how they group visual elements together or in the way they are inclined to interpret the source of incoming sensory stimuli. For instance, it has been suggested that some subgroups of people are more likely to preferentially process local shapes as opposed to global shapes (Happé & Frith, 2006), whereas some people are more susceptible to perceptual illusions than others (Schwarzkopf et al., 2011).

Study I

In Study I, I reviewed work published in the recent decade which has attempted to map out the factorial structure of vision. One recurring question which has not yet been conclusively answered is whether there exists a general 'v' factor of vision, similar to the *g* factor which has been proposed in many intelligence studies (for a comprehensive treatment on the *g* factor, see Jensen, 1998). This notion of a 'v' factor is based on the hypothesis that there may be some common mechanism (e.g., neural or structural) which affects all lower level perceptual abilities, such that some people are simply better at visual acuity and discrimination tasks than others. Hence, when measuring subjects on a range of basic visual tasks one would expect a common factor to emerge which loads on most measures. Another hypothesis, although not mutually exclusive of the first one, would suggest that visual perception is better described as multiple more narrow and specific visual abilities related to different perceptual functions and processing stages. Evidence from work reviewed in Study I seems to favour the latter. Although some support for a general factor of perceptual performance was reported in a study by Bosten and colleagues (2017), it was only able to explain around 20% of the total variance in their experiment with 25 measures, which may not suffice to infer the existence of a general factor (Lubinski, 2000). Other publications reviewed in Study I that tested for a general factor of visual perception did not find evidence to support this hypothesis (Cappe et al., 2014; Ward, Rothen, Chang & Kanai, 2017). Instead, most studies found that performance on numerous low-level perceptual tasks was better explained by several specific factors, such as factors of magno- and parvocellular activity (Ward et al., 2017), perceptual capacity and working memory factors (Eayrs & Lavie, 2018), or the eight specific visual factors proposed by Bosten and colleagues (2017).

In addition to low-level visual performance factors, it has been suggested that perceptual performance may be grouped by some higher order cognitive commonalities. For example, one dimension in perceptual processing proposed to share a source mechanism is the global versus local cognitive style. It has been suggested that most people exhibit an automatic bias in favour of global structure, whereas individual differences in this processing style have been related to expertise (Stoesz, Jakobson, Kilgour, & Lewycky, 2007) and even psychopathology (Moritz & Wend, 2006; Scherf, Luna, Kimchi, Minshew, & Behrmann, 2008), implying long-term dispositional individual differences in this dimension. Nevertheless, the work reviewed in Study I (Chamberlain et al., 2017; Milne & Szczerbinski, 2009) found low intercorrelations and no common factor between different tasks purported to measure differences in global-local processing.

Furthermore, some studies have proposed that people may exhibit trait-like variance in their susceptibility to experiencing perceptual illusions (e.g., Thurstone, 1944). Although individual differences have been reported in this domain and have even been linked to structural differences (Schwarzkopf et al., 2011), there have been some inconsistent findings concerning whether or not susceptibility to illusions could be regarded as a stable trait or cohesive factor in perception. In a more recent study Grzeczkowski and colleagues (Grzeczkowski, Clarke, Francis, Mast, & Herzog, 2017) measured the magnitude of illusions on six separate illusions but found no evidence of a common factor for illusion strength, even when only comparing groups of similarly categorized spatial illusions. They did, however, report correlations between different versions of the same illusions (e.g., versions of the Ponzo illusion and Ebbinghaus illusion), indicating that there is no general tendency for susceptibility to various kinds of illusions, but there may exist specific factors for narrower categories of illusions. Also, previous studies may have used tasks which were too similar, giving an inflated impression of a general factor of illusions.

The review of work presented in Study I revealed that despite many well-designed studies having been published in the field there is still no clear and cohesive understanding of how individual differences are structured in vision, and several questions still remain unanswered. Although applying the factor analytic approach can be very helpful for elucidating underlying sources of functional dimensions and clarifying theoretical constructs, it bears stressing that to improve comparability between different studies published in the same field the motivations for choices of statistical analyses as well as interpretations of factors should be explicitly stated in all publications.

One relevant factor which may have been overlooked in some of these studies and which may deserve more consideration when designing experiments with perceptual tasks is the role of top-down effects and experience on different levels of perceptual processing. Predictive processing theories have grown in popularity and are currently accepted as the basic principle that best encapsulates how adaptively successful vision works, which has resulted in an enormous body of work of varying levels of specificity. It is therefore of topical relevance to investigate the specific and non-specific factors that determine the involvement of top-down predictive processing in creating the subjective perceptual experience.

3. TOP-DOWN EFFECTS ON PERCEPTION

At every waking moment our senses are bombarded with complex and varied input. In order for our brains to be able to process this information rapidly and with optimal use of resources, it is beneficial to initially only extract fast projections of low spatial frequency information from the environment, thereby forming a general gist of the scene and a likely hypothesis of its potential source (Bar, 2004). A good perceptual hypothesis helps to organize the sensory input and make sense of the data without thoroughly processing each marginal feature. Moreover, delving into too much specific and varied detail may derail perception from its main task – to quickly discover and prioritize the most relevant and salient information from our surroundings which may be vital to survival. It has been shown that observers first fixate on the most informative aspects of a scene (Henderson & Hollingworth, 1999), indicating that the perceptual system is motivated to extract relevant contextual information from the earliest processing stages.

Currently, the predictive processing approach to perception and cognition has become a dominant force in scientific inquiry on how sensory data and cognitive mechanisms interact. It has been well established that perceptual processing is enhanced (i.e., the object is recognized faster and more accurately) if a stimulus is encountered repeatedly, therefore becoming more predictable – a process known as repetition priming (e.g., Tulving & Schacter, 1999). Additionally, if a specific context or category is introduced prior to stimulus presentation, this will influence how the stimulus is perceived. For example, the same object can be perceived as a hairdryer or a drill, depending on whether it is presented in the context of a bathroom or a garage (Bar, 2004). Such findings clearly challenge the traditional view that vision is by and large defined by what is signalled with the inflow of sensory information. Instead, earlier experience and predictions formed in higher cortical levels have been shown to affect perception much more and in a much more dramatic way than has been recognized before.

3.1. Predictive coding account of perception

As a rule, most would agree that the purpose of vision is to accurately reflect the current state of the environment. It is of vital importance that we be able to identify potential threats or relevant social cues in a timely and veridical fashion. Overall, as light reflects off surfaces and objects and enters the eye to be translated from light energy to neural energy, a realistic representation of the environment is formed. Nevertheless, ample empirical evidence demonstrates that our perception is far from infallible and is, in fact, quite susceptible to various optical illusions and misperceptions. This is often induced by stimuli which play on habitual patterns acquired from our experience with the world. A good example of this is the light from above prior, as illustrated in Figure 1. The colour gradation on a two-dimensional image of a shape can indicate shadow placement, which in a real-world environment is induced by light falling on the object. Since we live in a world where the light is generally emitted from a source located overhead, shadows appearing at the bottom of the image will make the object appear convex, whereas darker gradation at the top will make the shape appear concave. Similarly, the image on the left of Figure 1 depicts the phenomenon of illusory contours. Despite knowing that there is no objective contour to indicate the presence of a white disc on the image – in other words, there objectively is no disc at all – it is nearly impossible to not perceive a disk overlaid on top of black lines and circles (reviews: Bachmann, 1978; Murray & Herrmann, 2013), as it seems more unlikely to encounter four circle fragments and two pairs of lines "accidentally" aligned in a collinear arrangement.

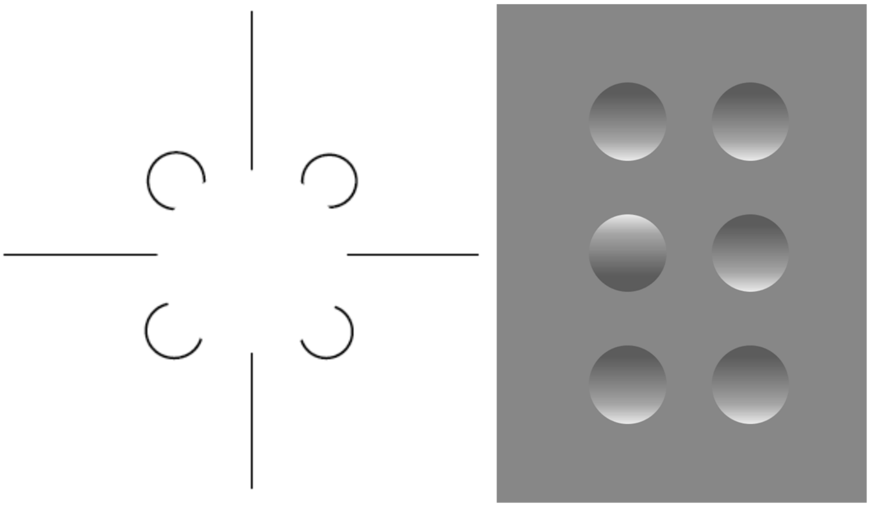

Figure 1. Examples of the effects of priors on subjective perceptual experience. The image on the left is an example of the "illusory contours" illusion, wherein objectively only black lines are drawn, but subjectively a clear impression of a circle occluding the pattern of lines emerges. In some cases, viewers even report experiencing the surface of the illusory circle as being lighter than the background, hence inducing a vivid percept of an object delineated by illusory contours where in fact there is none. The image on the right depicts an example of the "light from above" prior. The middle circle in the left column is perceived as convex whereas the other circles appear concave. As our experience from the environment dictates that sources of light generally shine on the objects they illuminate from above, the shadow appearing at the bottom of the shape (as opposed to appearing at the top of the shape) will create an impression of a convex object.

By no means a novel idea (e.g., von Helmholtz, 1867; Gregory, 1980), it has now been accepted as fact that perception is not formed only by the incoming sensory input, but as a combination of both bottom-up sensory processes as well as top-down expectations and predictions. Object recognition is a prime example of the role of top-down processing in perception – every day people are tasked with recognizing three dimensional objects in the environment based on two dimensional images that fall on our retina which look unique from every angle and may be explained in several ways. Moreover, objects in the environment are often not presented in full view. Yet, somehow we are able to recognize a cat with ease, even when it is occluded by a fence and could be interpreted as separate parts of a cat by a less refined visual system (Hohwy, 2013). Our brains can make such inferences rapidly and automatically by relying on stored memories of past experiences with objects which in this case would insist that encountering a whole cat behind a fence is simply a much more probable sight.

Accumulated earlier experience is what probabilistically predicts and therefore modulates the results of ongoing actual perception. The probabilistic inferences that the neural machinery performs are captured by Bayes' rule which is a theorem of probability theory. According to Bayesian accounts of predictive coding (Clark, 2015; Hohwy, 2013; Lee & Mumford, 2003; Rao & Ballard, 1999), our brains operate as hypothesis-testing machines, as they are constantly comparing incoming sensory information (likelihood) to an internal prediction of its source (prior). The predictions are formed based on a pre-existing model of the world which is built upon previous knowledge and expectations about the probability of encountering each visual scene. Predictive top-down signals carried by feedback connections are compared to incoming sensory information from bottom-up feedforward connections in a hierarchically organized fashion. Any residuals that cannot be explained away by the descending predictive hypothesis are transmitted to higher level areas as error signals which lead to the updating of the prediction (and, if necessary, the generative model) with the goal to minimize prediction error and improve the generative model. Prediction errors are also weighted by precisions which determine their relative influence on the subjective percept. Efficient perception is therefore the result of an optimally balanced exchange between top-down and bottom-up signals. The perceptual system arrives at a uniform percept due to a balanced weighting of sensory input and prior predictions. If the conditions surrounding the sensory information seem reliable (e.g., looking at an unoccluded object in daylight) then sensory input leads the investigation. However, when the sensory information is deemed too noisy or uncertain (e.g., an ambiguous shape in the dark) then prior beliefs are awarded more weight which can occasionally lead to illusions and misperceptions.

This principle of prediction error minimization has implications even beyond perceptual processing. According to Friston's free energy principle (Friston, 2005; 2010) all living systems are motivated to actively minimize prediction error (or more generally, free energy) and thereby reduce the entropy of their sensory and physiological states (see also Badcock, Friston, Ramstead, Ploeger, & Hohwy, 2019). This can be achieved through modifying predictions or adjusting actions to fit the predictions by actively seeking out and revisiting a limited set of characteristic phenotypic states. Although in itself a much broader computational and philosophical concept that can be applied to all biological organisms, the free energy principle is also the foundation for predictive coding theories, as it explains action and perception as the means to minimize prediction error. Hence, predictive coding can provide a cohesive framework not only for perception, but for explaining a wide scope of psychological processes such as cognitions, emotions and actions (Clark, 2016; Hohwy, 2013).

In the following sections, I will introduce Studies II, III and IV which delve into the different types of top-down effects on perception, with implications for the predictive coding theory and the issue of individual differences.

Study II

In Study II, we were interested in investigating whether global top-down effects modulate objective performance on a low-level perceptual task. The aim of the experiment was to study transcranial magnetic stimulation (TMS) masking effects on perception when TMS is applied to higher cortical areas in the frontal cortex. Previously it has been consistently shown that a visual stimulus can be rendered invisible when disruptive TMS pulses are targeted to the early visual cortex after stimulus onset (Bachmann & Francis, 2014), but also approximately 60–80 ms before the stimulus has been presented (Jacobs, Goebel, & Sack, 2012). We asked the question whether we would be able to elicit stimulus masking by applying pre-stimulus TMS pulses to the frontal cortex, i.e. far from posterior visual cortices and high up in the hierarchy of processing levels. If an unspecific burst of top-down neural impulses from the frontal cortex can affect subsequent visual discrimination, then it is possible that the top-down effects may be mediated not only by feedback from the frontal areas *after* visual stimulus specific information has arrived at higher cognitive control levels, but also by some unspecific top-down flow of presynaptic afference. To test the temporal dynamics of the putative top-down effects we used a range of TMS-to-target delays, including the critical time frame of 60 ms before stimulus onset. Secondly, as the effects of TMS masking have been shown to vary considerably over subjects (Corthout, Uttl, Walsh, Hallett, & Cowey, 1999; Jacobs et al., 2012), we wanted to know whether individual differences in the expected behavioural effects were reflected in ERP component amplitudes or their latencies.

To answer these questions, we designed an experiment where subjects conducted a simple low-level discrimination task with a small grey Landolt-type stimulus presented at fixation. The task was to identify on which side of the square a gap was located, as well as to give an estimation of the perceived clarity of the stimulus on the Perceptual Awareness Scale (Overgaard, Rote, Mouridsen, & Ramsøy, 2006). To be able to analyze individual differences in top-down modulated perception which are not the result of basic differences in visual acuity, we first determined individual contrast levels for the Landolts in a pre-experiment. Each individual's contrast threshold was selected via fitted curve based on six contrast levels to match the level where they had responded correctly on 50% of the trials. In addition to the behavioural task we applied TMS stimulation to the right frontal cortex of the participants and measured EEG from posterior electrodes. TMS was targeted at electrode F2 of the 10–20 placement system. The TMS pulses (at 55% of maximal output) were applied either 140 ms or 60 ms before the stimulus appeared or 20 ms after stimulus presentation.

Results showed that, indeed, objective discrimination performance in the perceptual task dropped in the critical -60 ms SOA condition with TMS compared to the SHAM stimulation condition. This confirms that TMS pulses can affect performance on a perceptual task even when stimulation is directed to the frontal cortex *prior* to stimulus onset. As anticipated, Study II also revealed extensive individual variability in behavioural performance, both in the objective performance on the discrimination task, as well as the subjective clarity ratings. To elucidate the source of this variance, we analyzed EEG data collected from 27 electrodes posterior to Cz. We found that the peak latency of a late TMS-evoked ERP component P270 was related to the TMS effect on behaviour – the earlier the P270 peak was observed, the bigger the observed decrease in performance at -60 ms SOA.

This is a novel finding, because it introduces a new type of masking which does not entail masking by another visual stimulus nor is it directly affecting visual-processing areas. The effect is therefore nonspecific, as it does not originate from areas which encode specific visual features of the target nor as a direct result of the specific content processing activity engaged by the frontal cortex. The fact that in the condition which led to maximum masking effects TMS pulses were applied before a modal visual stimulus had been presented stresses the putative non-specificity of the effect. Furthermore, with an additional pilot dataset (behavioural results reported in supplementary materials, available in the online version of the article) we also managed to show that this effect was not locally limited to the stimulated F2 area, but the behavioural results were equivalent when pulses were targeted to the F4 electrode (purportedly targeting the dorsolateral prefrontal cortex (e.g., Karton, Rinne, & Bachmann, 2014), providing further support that the effect can be interpreted as disruption to some globally ongoing pre-stimulus activation, rather than a local disruption directed at frontal visual areas (e.g., the frontal eye fields, FEF). This result points to the necessity for future research to experimentally control and disentangle specific and nonspecific top-down effects on visual perception, especially in light of the assumed content-dependence of predictive coding theory.

The results of Study II support the notion that the way external inputs are processed is not determined only by the nature and features of the input, but also depends on the prior state of the brain (Jacobs, de Graaf, & Sack, 2014). Differences in this baseline activation can potentially explain why subjects respond differently to the same stimulus. For instance, Hesselmann and colleagues (Hesselmann, Kell, Eger, & Kleinschmidt, 2008) managed to demonstrate that the subjective percept of an ambiguous figure (the well-known face/vase figure) was dependent on the individual's pre-stimulus activity in the fusiform face area (FFA). Specifically, activity in the FFA was higher when subjects subsequently reported perceiving a face instead of a vase. In Study II, we showed that not only does this hold true for specific brain-regions, but the state of a nonspecific global network in the prefrontal cortex can also be linked to subsequent stimulus processing. Seemingly, there exists a baseline set of expectations providing general context and nonspecific activation in preparation for perceptual input (Bar, 2009; Clark, 2015).

In this study we were able to induce a decrease in object discrimination as a result of TMS pulses directed to the frontal cortex 60 ms prior to stimulus presentation, hence demonstrating global higher-level effects on objective perceptual performance. Whether the obtained masking effect is caused by top-down suppression of visual target signals or top-down facilitation of some sources of neural noise remains to be studied in further research. Also, we showed that there were substantial individual differences in this effect, reflected both in behavioural results as well as in EEG signals. In summary, the results from Study II illustrate the importance of descending neural pathways in modulating perception. Furthermore, higher-level factors need to be accounted for when studying individual differences in perception.

3.2. General and specific effects of priors

The study presented in the previous section provided some empirical support for the role of top-down global networks in modulating low-level perception. However, this result implicated some non-specific global modulation effect which is difficult to relate to any concrete predictive processes. In the following sections, I set out to investigate whether subjective perceptual experience can be grouped into a general factor as measured by behavioural perceptual tasks, or whether individual differences in perception are better explained by specific factors of prior effects. This question was also motivated by the issue of construct validity, as highlighted in Study I. The drawback of an all-encompassing framework such as predictive coding is in an overly generalized approach towards some of its pillar concepts, leading to inconsistent findings. It may in fact be that various tasks which are purported to measure the same theoretical construct actually capture several independent sources of variance – similarly to the global-local dimension (Milne & Szczerbinski, 2009) or the theorized factor of susceptibility to illusions (Grzeczkowski et al., 2017). Hence, we set out to investigate the sources of specific and non-specific individual variance in the effects of priors on perception.

Study III

To tackle the question of whether the effects of priors might share an underlying latent factor, we designed Study III where we compiled a battery of four behavioural tasks in which top-down effects on perception could be elicited. The four paradigms included a Mooney face recognition task, a blur detection task, an illusory contours task and a representational momentum task, as further detailed below:

1) In the Mooney face recognition task people were shown upright, inverted and scrambled Mooney targets (Mooney, 1957) which had been created from a freely available database of faces. Original photographs of the faces were shown in between blocks of Mooneys, so that the photo from which a stimulus was created was presented after the block where the Mooney first appeared and before the block where it appeared a second time, thus allowing for a comparison between conditions. The subjects' task was to respond whether the Mooney target corresponded to a face or not. The Mooney task has been frequently used to illustrate the effect of prior knowledge on perception, as otherwise meaningless Mooney targets become disambiguated and are easily recognized as faces after the original image has been introduced. We also extracted individual measures to evaluate the benefit on recognition from being presented an upright compared to an inverted Mooney face, as well as a rate for false positive responses.
2) In the blur detection task (Lupyan, 2017) subjects were required to adjust the blur level in one letter string to match the blur level of another letter string presented simultaneously. The individual letters in the two stimulus strings were identical, except that in one of the stimuli they were arranged to create a meaningful word. The task illustrates an effect wherein subjects adjust the blur level of the target to be sharper if matching it to a meaningful word compared to scrambled letters, indicating that intelligible words appear subjectively sharper, i.e., in order to experience an equal level of sharpness the meaningless string of letters has to be adjusted to a more fine-grained level of spatial frequency. The effect is thought to result from the enhanced perceptual processing of predictable (familiar) types of stimuli, such as words.
3) In the illusory contours task subjects were shown a Varin shape (Varin, 1971) wherein the illusory percept of a square is induced by symmetrically placed "occluded" circles. Participants were asked to rate the subjective clarity of the illusory square on a four-point perceptual awareness scale (PAS). The inducing circles were presented at varying contrast levels, which allowed us to extract threshold measures of subjective visibility. The task was meant to probe a possible trait-like tendency of individuals to rely on the expectation of a more probable shape (square on top of circles) as opposed to the less likely yet objectively veridical scenario of symmetrically placed partial circles.

4) Lastly, the representational momentum task was hypothesized to capture the relative reliance on predictions as expressed by the magnitude of forward displacement. The representational momentum task illustrates an effect where subjects misperceive the vanishing point of a moving stimulus when it disappears without warning. Arguably, to make up for the delay in processing a moving stimulus, the visual system predicts the upcoming location of the stimulus based on information gathered from its previous trajectory, leaving the impression of smooth movement. Hence, the percept of the moving stimulus is always somewhat lagging in relation to its objective location, causing the forward displacement or perceived inertia of the target. This is supported by findings which have shown that the size of displacement in the representational momentum task depends on the speed of the target (Freyd & Finke, 1985), as well as the predictability of its movement (Kerzel, 2002).

For the purpose of this experimental study we chose paradigms where participants had been shown to consistently report a subjective perceptual experience which differed from the objective qualities of the task stimulus, arguably as a result of top-down effects. The stimuli used in these tasks were purposefully distinct, the tasks thereby involving the processing of facial configurations, words, illusory contours and even movement. Our goal was to use paradigms which only had one particular component in common – the stimuli presented were noisy or ambiguous enough so that prior beliefs would be given more weight in the subjects' subjective perceptual experience. We hypothesized that if there exists a general factor of "reliance on priors" then people who exhibit a tendency to rely on prior beliefs relatively more in one task would also be more inclined to weight priors with more precision in the other tasks. In other words, if subjects were ranked from most to least likely to report a veridical experience of the presented stimulus in each task then these lists of rank order would be inter-correlated. Following that reasoning, we would expect positive correlations between the task measures and an emerging general factor of relative reliance on priors.

Our results revealed that one common factor for the relative reliance on priors could not be surmised from these four behavioural tasks. The factor analysis did not favour a one factor solution, but rather two factors were able to best describe our dataset, possibly reflecting the different hierarchical levels of the priors recalled in the different tasks. The first factor loaded strongest on the Mooney task "false positive" score (i.e., seeing faces where there was a non-face stimulus) and the "benefit of meaning" blur detection task score. The second factor loaded on the illusory contours task score "subjective vividness" as well as the Mooney task "benefit of orientation" score. When taking a closer look at the possible explanations for this division of tasks, we can hypothesize that the first factor captured relatively higher-level priors than the second factor (see also the discussion in section 3.3). It would appear that the specific characteristics or "types" of priors are of relevance in determining the relative weighting of prior information when confronted with ambiguous or noisy perceptual input, which are dependent on the specific tasks used.

As a limitation to this study, it should be noted that although we interpreted the results from Study III so as to indicate that there was no common factor of the effects of priors, it may be that the tasks chosen were simply too different. This means that whether a common factor for different tasks can be found may depend on the set of tasks chosen. Additionally, despite having one process of interest in common, this may not have been the only source of individual variance we were measuring. Although we were following in the footsteps of previous work in a similar vein, it remains a possibility that other studies have also erred against this principle. It may also be that the factor analytic approach is not the best method to apply on varied behavioural data when measured on modest sample sizes.

Study IV

Study III explored tasks where priors had influenced the subjective perception and interpretation of actually present stimuli. In Study IV, we created a situation where the subjective percept was of a stimulus which had not been presented at all. The series of tasks compiled for these experiments, including one which was used in an earlier work by Aru and Bachmann (2017; see also Bachmann & Aru, 2016), resemble the phenomenon introduced by Ellson (1941) and illustrated more recently by Powers, Mathys and Corlett (2017) wherein the repeated presentation of a visual and auditory stimulus simultaneously will lead to the "hallucination" of the auditory stimulus when on some trials only the light is presented. In other words, by conditioning the expectation of the two stimuli always being presented together a misperception of the stimulus that is absent from the screen can be evoked. We managed to show that this phenomenon also occurs when two *visual* stimuli are simultaneously presented by using a dual-task setup where one stimulus was more relevant to task performance than the other.

In Study IV, we conducted two experiments (E1 and E2) with analogous versions of the same general task wherein attention is diverted towards a main task while the secondary task stimulus is occasionally removed from the screen. Participants were repeatedly shown two types of simultaneously presented stimuli (for example a face and a square around the face, as in E1) while they maintained central gaze fixation. After the briefly visible stimulus screen had disappeared from view, they were either asked a categorical question about the face or to rate the clarity of the square on a PAS-like scale. In the majority of trials, the question was about the face, making it the main and therefore the expected stimulus, and only in about 10% of trials were participants asked to rate the secondary stimulus. In a few critical trials (six in E1 and four in E2) the secondary stimulus was absent from the screen while participants were still asked to provide clarity ratings. To compare, an experimental situation where an attended task-relevant stimulus is suddenly absent from the screen would elicit a prediction error (and the subject would likely notice its disappearance). However, in a situation where attention is divided between two spatially separate stimuli, such that one of those stimuli is more relevant to the task goals than the other, the secondary stimulus is deemed less relevant and processed in less detail. The degraded sensory information of the auxiliary stimulus will then in turn allow for more weighting of the expectation to see both stimuli in unison, even though in some trials one of the stimuli is actually absent.

In addition to the original task introduced in earlier experiments (Aru & Bachmann, 2017; Mack, Erol, Clarke, & Bert, 2016) we developed two new tasks for the purpose of this study with a slightly different experimental design, varying some aspects of the tasks such as stimulus content (faces and simple square shapes instead of letters and circles as in the earliest version) and the position of the critical stimulus (presented at fixation or in the periphery). We also added more critical trials compared to the original work to ascertain whether this effect is indeed as common as we suspected. To allow for better comparison, two tasks in E2 were applied to the same sample – since the degree of illusory perception being experienced relied on subjects not being made aware of the true purpose of the experiment, we refrained from conducting all three tasks on the same sample (also the long runtime would have been very taxing).

The results of the study showed that, indeed, in all three tasks most people reported having perceived the missing stimulus on at least one of the critical trials, although individuals varied greatly in the amount of illusory perception reported. The correlation between illusory perception scores in the two tasks measured on the same sample did not reach significance. However, the two tasks did differ in some respects, including task difficulty and types of stimuli used, which may account for the low correlation. We also found that illusory perception is qualitatively different from real perception, as the ratings given to real squares were higher compared to illusory squares. This indicates that the phenomenon we measured might be comparable to studies which have managed to superimpose mental imagery to real stimuli (Brockmole, Wang, & Irwin, 2002). In this case, the expectation to see the square could have evoked a mental representation of the square from memory which was superimposed on the visual scene. However, because the scene at the locus of the expected stimulus was empty and the subjective vividness of true perception is arguably higher than that of imagery, the clarity ratings for the "hallucinated" stimuli had to be relatively lower. In other words, the illusory percept was convincing enough to induce several reports of clear perception, but the overall subjective quality of the illusory percept was poorer. Also, the reaction times to critical trials were slower, indicating that there was a moment of hesitation before replying.

One could argue that in this study we might have measured judgement or decision bias rather than differences in true percepts, especially considering that clarity ratings between critical trials and regular trials were correlated. It is true that we could not disentangle actual perceptual experience from judgement, as we measured illusory perception via self-reported awareness ratings. Nevertheless, there are arguments in favour of having captured a real subjective experience of an illusory object. Firstly, from a procedural standpoint it should be noted that we debriefed participants after participating in the experiments presented in Study IV and found that many subjects responded with sincere surprise, having been convinced that the auxiliary stimulus was present throughout all trials. Secondly, it is not very likely that participants would use more than one level of clarity ratings for "hallucinated" stimuli when responding according to pure response bias without a concomitant phenomenal experience of the expected stimulus. Thirdly, from the perspective of the questions posed in the framework of this dissertation I would argue that although a valid qualm, it can be viewed as a secondary issue to the main research question. We were specifically interested in the effects of expectations on the subjective perceptual experience which may inherently include a degree of judgement. However, to further verify this hypothesis we aim to include EEG measures in future work to investigate whether there are differences in brain correlates between critical trials where illusory perception was experienced and those where no misperception occurred.

3.3. Different types of priors

In the previous section, I summarized the results from Study III and Study IV. We found that no one general factor of reliance on priors emerges when people perform several tasks where the subjective perceptual experience of a stimulus differs from its objective qualities. We also found that even two very similar tasks where expectation creates the misperception of a missing stimulus were only poorly correlated. This indicates that there may in fact be many different types of priors which are dependent of the specific task at hand.

Types of priors can be classified in several different ways. For example, Seriès and Seitz (2013) proposed a broad conceptual distinction of contextual and structural priors. This is a simple division which is intuitively easy to grasp. Contextual priors are limited to the specific situational expectations, such as task instructions and priming by previously presented contextual cues, and are thereby more malleable by short-term influences. On the other hand, structural priors are acquired through long-term learning and are less susceptible to external influences from instructions and general knowledge. Structural priors are also rather broad which means that they can be generalized to different contexts. For example, consider the illusory-contoured object and light-from-above prior depicted in Figure 1: even though we *know* that most of the contours are illusory, we cannot shake the illusion in our *perception*. The structure of the depicted features and their arrangement enforces the automatic illusion of a more probable geometrical shape occluding some parts of the symmetrically placed line arrangements. Likewise, the light-from-above prior is a low-level structural expectation which we have acquired due to living in an environment where the light is usually emitted from above. The same illusion would automatically be evoked with other shapes which have respectively shaded areas in the top or bottom parts of the objects. Nevertheless, even structural priors such as the light from above prior can be contextually updated as a result of relearning, although this effect has been shown to be temporary (Adams, Kerrigan, & Graf, 2010; Kerrigan & Adams, 2013).

Using the example of the Mooney task from Study III, for instance, the three measures we extracted from the task all fall somewhat differently on the structural-contextual axis (also, see Figure 2 for an illustration of where each task used in Studies III and IV might be placed along this dimension). The benefit of seeing an upright face compared to an inverted face on accurately recognizing a Mooney target as a face can be interpreted as the most structural prior of the three measures. A preference for recognizing upright faces compared to inverted faces is a well-documented effect (e.g., Farah, Tanaka, & Drain, 1995; Valentine, 1988; Yovel & Kanwisher, 2005) which is thought to develop in children (to a comparable level as the face inversion effect in adults) between 5 and 10 years of age (Pascalis, Demont, de Haan, & Campbell, 2001; Sangrigoli & de Schonen, 2004). It is likely that the emergence of this preference develops due to years of accumulated experience with predominantly upright faces. The false positive score in the Mooney task, however, implicates a somewhat more contextual prior of having the expectation to look for and see faces within the context of the task. Even more contextual still (although, note that this measure was removed from the final analysis in Study III) is the benefit in recognition after viewing the original face photograph which helps to disambiguate a previously incoherent Mooney target. Clearly, this effect is induced by a very short-term temporary prior and is unlikely to be generalized to other Mooney shapes seen during the rest of the experiment.

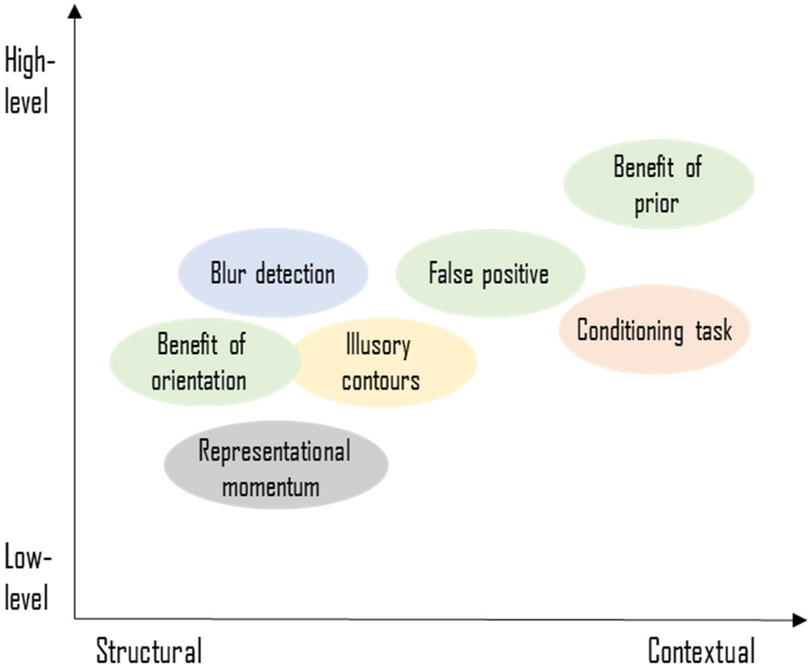

Figure 2. An illustrative conceptualization of the tasks used in Study III and Study IV, as approximated based on the types of priors evoked. Depicted is their placement on the structural-contextual dimension (x-axis) as well as along the relative hierarchical processing levels (y-axis). The conditioning task (in pink) indicates the mutually analogous tasks used in Study IV; the tasks in green ovals represent the different measures extracted from the Mooney task.

Seriès and Seitz (2013) did not implicate a specific hypothesis regarding the neuronal basis for structural and contextual priors, nor is it clear whether they share the same overall mechanism in the brain or are dichotomous entities. Instead, this distinction could be better thought of as a functional dimension, distinguishing priors by how they were acquired (innate/long-term versus short-term priors) and whether they are general or contextually specific. An alternative and somewhat complementary dimension for operationalizing the effects of priors on perception, which is more rooted in the neural architecture of perceptual processing, concerns the relative positioning of the evoked prior within the cortical hierarchy. A low-level prior induced by basic perceptual features functions at a hierarchically lower level than priors which are related to more complex associated features or semantic content. It can be argued that individual differences in the effects of higher-level priors which affect priors at higher processing levels (such as task instructions, individual beliefs) are less effective in modulating low-level priors which may depend more on differences in sensory processing (Figure 3). In other words, low-level priors (e.g., the light-from-above prior) are more likely to be shared by most individuals (Hohwy, 2013) and be less malleable to induced shifts in knowledge. Support for this notion can be found in literature on brain anatomy, which posits that individual variability is significantly greater in the association cortex compared to more low-level unimodal cortical regions (e.g., Laumann et al., 2015; Mueller et al., 2013). In short, individual differences probably exist in all dimensions of priors, but may be induced by different triggers. Hence, tasks which employ higher level priors are likely to not correlate well with tasks which rely on low-level priors and may exhibit orthogonal correlations with other phenomena (see also the discussion on schizotypy in section 4.2).

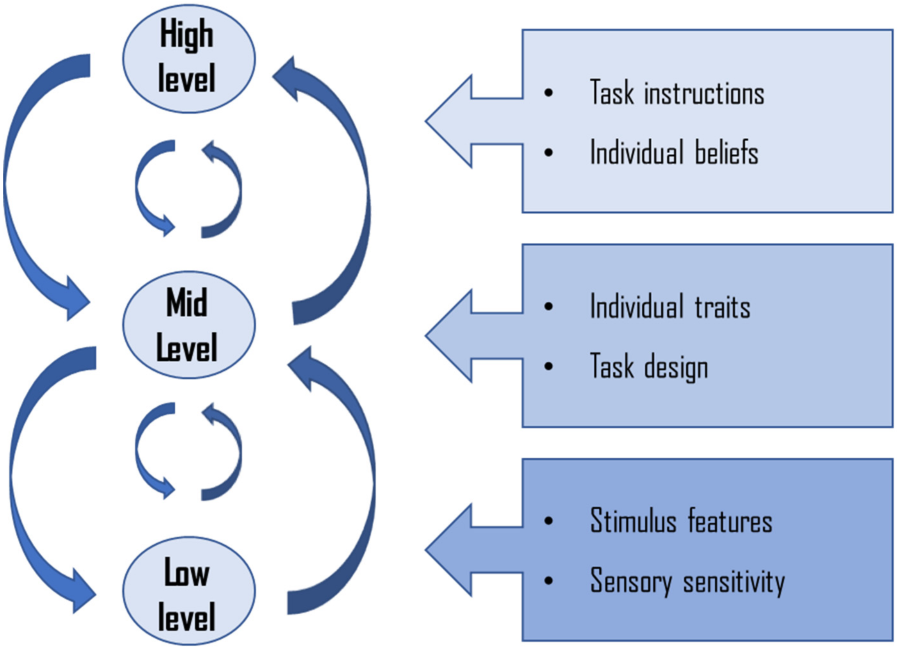

Figure 3. A general abstract framework for conceptualizing the various factors that affect priors at different levels of the perceptual processing hierarchy. Individual differences may occur at all processing levels, but arguably to a different degree, as higher-level priors are more susceptible to individual differences (lighter shade of blue) than lower level priors (darker shade). The boxes on the right exemplify some factors which can influence priors at different levels, suggesting that higher level priors are more malleable to contextual manipulations.

As described in section 3.2, both the Mooney “benefit of orientation” score and the illusory contours “subjective vividness” score captured in the first factor of Study III can be interpreted to represent effects of mid-level priors involved in perceptual organization, as they reflect preferential processing of familiar shapes (upright face compared to an inverted face; square on top of circles as opposed to symmetrical circles with slices cut out of them). Long-term experience with squares as common geometrical shapes induces the perceptual experience of a square occluding four stacked circles as opposed to a less likely occurrence of circles with symmetrical slices cut out of them. Similarly, long-term experience with faces creates the preferential processing of upright versus inverted faces. Both can also be seen as structural expectations acquired through life-long experience and are thereby unlikely to be dependent on situational context. The second factor loaded on the Mooney task “false positive” score and the “benefit of meaning” blur detection task score which can be placed relatively higher on this dimension, as they call upon the use of more category-specific priors. Participants were tuned to expect words and faces due to the task design which activated a narrower category of expectations than in the first factor. However, some effects of structurally imprinted syntax rules of learned language acting in an automatic mode may be also hypothesized. It should be noted that none of the measures from Study III captured truly high-level attributes, such that would be induced by introducing shifts to the explicit knowledge and beliefs of the participants. The representational momentum “displacement” score, in turn, could be seen as the odd one out, as it arguably evoked the most low-level prior compared to the other tasks and loaded most weakly (and negatively) on the factors. It also included a moving stimulus whereas the other tasks applied static targets.

4. SUBOPTIMAL PERCEPTUAL PROCESSING

Another question that this dissertation aimed to address is whether these individual differences in the effects of priors that we were able to demonstrate within the neurotypical population can also be linked to other individual trait measures, specifically those related to the autism spectrum and schizotypy.

In the previous chapters I have discussed some of the predictive mechanisms that have been implicated in determining how the sensory input and prior beliefs are integrated to form a subjective percept. The goal of this system is ultimately to minimize prediction errors and to identify the model that most veridically captures reality. An optimal perceptual system can estimate the reliability of the incoming sensory information in order to judge whether to continue sampling the environment at an even deeper level of scrutiny or to trust the predictive hypothesis. The occasional errors or misperceptions illustrated by optical illusions are merely the trade-off cost for having an automatic and efficient processing brain and are normally easy to correct by actively participating in the environment (e.g. moving an ambiguous object to a more illuminated area or touching its surface to ascertain its identity). This delicate balancing act of top-down and bottom-up signalling implies that if any systematic flaw were to occur in such a complex mechanism, it could lead to very real disadvantages in navigating daily life.

The predictive coding framework has, among other things, been used to explain the cognitive mechanisms involved in certain mental disorders, most commonly the processes involved in the symptomatology related to autism and schizophrenia. Although two distinct neuropsychiatric disorders, autism and schizophrenia share certain phenotypic similarities and occasional comorbidity (Chisholm, Lin, Abu-Akel, & Wood, 2015). For example, both exhibit mentalizing and social functioning deficits (Ciaramidaro et al., 2014) as well as atypical characteristics in sensation and perception. Historically, autism and schizophrenia were even hypothesized to be the same disorder (De Crescenzo et al., 2019), or alternatively two diametric opposites of the same spectrum (Crespi & Badcock, 2008; Crespi, Stead, & Elliot, 2010). According to predictive processing models, although the two are viewed autonomously, both autism and schizophrenia display perceptual symptoms which can be understood in terms of an imbalance between top-down signals and bottom-up sensory information.

4.1. Autism

Autism spectrum disorder (henceforth ASD) is a neurodevelopmental disorder characterized by social communication deficits and repetitive restrictive behaviours and interests (DSM-5, American Psychiatric Association, 2013). Individuals with ASD often exhibit a strict adherence to rigid routines and may experience distress in response to small changes. ASD has also been linked to enhanced perceptual functioning in several perceptual tasks, including superior performance in visual search and discrimination tasks and an overall detail-focused processing style (Frith & Happe, 1994; Joseph, Keehn, Connolly, Wolfe, & Horowitz, 2009; Mottron, Dawson, Soulieres, Hubert, & Burack, 2006), as well as a decrease in global processing (Happé & Frith, 2006). This pattern of increased attention to detail along with a failure to contextualize sensory information into global regularities translates well into predictive processing terms as an expression of the suboptimal balance of prior and likelihood weighting where the balance is shifted away from prior knowledge (or towards sensory information). It has been suggested that individuals with ASD experience the world in an overly realistic way due to the increased imprecision of predictions or alternatively from increased sensory precision (Friston, Lawson, & Frith, 2013; Lawson, Rees, & Friston, 2014; Pellicano & Burr, 2012; Van de Cruys et al., 2014). More specifically, they may have trouble generalizing information into generative models based upon which predictions are formed. For instance, this could explain why autistic individuals find social contexts challenging, as they may have trouble inferring general rules of social interaction from the specific characteristics presented by every unique person, thereby treating each encounter as a novel experience. Additionally, due to increased weighting of prediction errors, new and uncertain conditions evoke relentless prediction error signals, causing distress to the individual. In recent years more nuanced hypotheses on the predictive processing account of autism have been proposed, including for example the role of volatile environments as a trigger to the aforementioned perceptual atypicalities. However, there is still no clear consensus about whether autistic traits inevitably lead to deviant effects of priors on perception (e.g., Utzerath, Schmits, Kok, Buitelaar, & de Lange, 2019), leaving the question open for additional research.

As there is much heterogeneity along the autism spectrum, it has been proposed that autistic-like traits can also be found in the neurotypical population (e.g., Ruzich et al., 2015). The continuum hypothesis of psychopathology suggests that some of the symptomatology underlying clinical disorders may be expressed as extreme deviations in characteristics which also vary in the neurotypical population (Van Os, Linscott, Myin-Germeys, Delespaul, & Krabbendam, 2009; Verdoux & Van Os, 2002). In order to test whether autistic traits measured in a neurotypical population would exhibit this general tendency of attenuated priors in our selected perceptual tasks we included the Autism-Spectrum Quotient (AQ) questionnaire in Studies III and IV. The AQ is a self-administered questionnaire with 50 items which was developed by Baron-Cohen and colleagues (2001) to measure the continuum of autistic traits both in the clinical and non-clinical samples. The AQ has been shown to be an effective tool in distinguishing those with ASD from people without such a diagnosis (Wakabayashi, Baron-Cohen, & Weelwright, 2006), but its measurements also follow a normal distribution of variance in the neurotypical population (Ruzich et al., 2015). Following the reasoning of the continuum hypothesis, we moved forward with the assumption that the AQ can serve as a measure of relative positioning along the autistic spectrum in the neurotypical population. We reasoned that if the hypothesis of attenuated priors in autism (Pellicano & Burr, 2012) held true, then people who scored higher on the Autism Quotient scale (i.e., displayed more autistic traits) would experience (and report) more veridical percepts of stimuli which have typically shown strong modulation by priors; i.e., they would exhibit relatively less reliance on priors in the perceptual tasks compared to people who scored lower on the questionnaire.

In Experiment 1 of Study IV (E1), we found a significant negative correlation between the AQ score and the illusory perception score. In other words, people who reported more autistic traits on the questionnaire experienced *less* illusory perception. This supports the general hypothesis that autistic traits are related to a more realistic perception of the physical world. Importantly, we did not find a correlation between the AQ score and visibility ratings in trials where the auxiliary stimulus was present, therefore we cannot explain this link merely with the autistic trait signalling greater attention to detail and better perception in general. However, in the other two tasks the correlations between the frequency of illusory perception and AQ scores were not significant. While we cannot say with certainty why this pattern of results emerged, it implies that previously suggested links between the autistic trait and performance on a perceptual task depend greatly on the specific features and demands of each task. In this case, participants reported more illusory perception in E1 compared to the tasks in E2. The task in E1 had six critical trials where no auxiliary stimulus appeared compared to the tasks in E2 which only had four critical trials. This may have allowed for more individual variety to be revealed, possibly explaining why the correlation with AQ scores was only significant in this task. It has also been suggested that most perceptual atypicalities in autism are revealed only in volatile or unstable environments (Cassidy, 2018). Although we did not specifically manipulate or control for volatility in our tasks, it could be argued that the use of occasionally invalid arrow cues in E1 may have rendered the experimental design relatively more volatile compared to the tasks in E2 where the stimulus screen setups were more predictable.

In Study III, we did not find any links between the AQ score and the five extracted measures of relative reliance on priors. Again, we may cite the lack of volatility in the experimental paradigms as one possible reason why we were unable to find evidence in support for the weak priors hypothesis. Certainly, this is one aspect which should be better controlled for in future experiments. However, there are other experimental factors which may have affected this result as well. Numerous studies have reported differences in the perceptual performance of people with autism in various kinds of tasks (Behrmann, Thomas, & Humphreys, 2006), yet not all of these links have been replicated when using slightly different paradigms or conditions. For instance, while it is widely reported that autistic people experience a local processing bias instead of global precedence as most neurotypical people do (for a review see Happé & Frith, 2006), others have shown that there are no group differences between the autistic and control group in global-local tasks (e.g., Rinehart, Bradshaw, Moss, Brereton, & Tonge, 2000). Therefore, the effect may depend on the specific paradigm and conditions used.

Another possible explanation for the lack of correlations in our studies is that the continuum hypothesis simply may not be accurate for the autism spectrum. There have been conflicting findings regarding whether tendencies found in a clinical sample carry over to the neurotypical population, or if they can be replicated to a comparable degree (Karvelis, Seitz, Lawrie, & Seriès, 2018; Van de Cruys et al., 2017; Williams, 2018). Differences between a clinical sample and a non-clinical sample may be more pronounced which results in distinctive patterns of perceptual processing between the two groups. Alternatively, the AQ may not be the best measure for ranking neurotypical individuals on the autistic spectrum. While the AQ has been widely used to quantify autistic traits both in the clinical and non-clinical populations, it relies only on self-ratings of behaviour and subjective experience and hence may not be applicable as a proxy for ASD proper (Gregory & Plaisted-Grant, 2016).

In summary, autism, much like most clinical constructs is a very complex phenomenon of phenotypically diverse and interacting features. There may be more intricate predictive models that are a better fit for explaining the complexity of different clusters of symptoms. It has recently become a point of public discourse that the construct of autism may well be too broad to capture precisely enough the full scope of the multifaceted symptomatology present in individuals who have received this diagnosis. Not all autistic individuals are characterized by the same symptoms, therefore individual profiles need to be considered when trying to make inferences regarding the underlying cognitive mechanisms in autism. As it can be problematic to rely only on questionnaire measures to score individuals on a diagnostic spectrum, consulting with clinicians at different stages of empirical research should also be considered a requirement. Currently, the exact nature of perceptual differences in autism still remains unclear.

4.2. Schizophrenia

The schizophrenia spectrum is another group of disorders that has been attempted to be explained in predictive processing terminology, partly due to its extensive sensory and perceptual symptoms. Schizotypal personality disorder (SPD), although categorized as a personality disorder, is included in the schizophrenia spectrum. It can be distinguished from schizophrenia by subthreshold symptoms that are associated with persistent personality features (DSM-5, American Psychiatric Association, 2013) and may sometimes precede the onset of schizophrenia. The main features of SPD include pervasive social and interpersonal deficits, cognitive or perceptual distortions and eccentricities of behaviour, including magical thinking, paranoid ideation and unusual perceptual experiences.

As opposed to the weak priors hypothesis of autism, the hallucinations characteristic to the schizophrenia spectrum and psychotic disorders can be explained as resulting from overly strong priors (Powers et al., 2017; Schmack et al., 2013; Teufel et al., 2015). Hallucinations are perhaps the most extreme form of illusory perception, as they are percepts which have not been activated by any corresponding external stimulus (Tracy & Shergill, 2013) and can therefore be assumed to consist only of internal input. The fact that the content of hallucinations often reflects personal beliefs as well as cultural background (e.g., Kent & Wahass, 1996) supports the idea that hallucinations emerge within the context of individual and subjective prior experience.

Importantly, links with suboptimal perceptual processing have also been detected in non-clinical samples in covariance with psychosis proneness, as approximated by higher scores on schizotypy measures (Partos, Cropper, & Rawlings, 2016; Teufel et al., 2015; for a review see also Nelson, Seal, Pantelis, & Phillips, 2013). To measure individual differences in schizotypal personality in the non-clinical population we included the Schizotypal Personality Questionnaire-Brief (SPQ-B, Raine & Benishay, 1995) in Study III. The questionnaire was developed as a self-report measure to assess features of SPD (as defined by DSM-III-R) in the general population, both for research and early screening purposes. From the perspective of our research question, we were especially interested in possible correlations between task performance and the Cognitive-Perceptual Deficits sub-factor of the SPQ questionnaire.

In our study we found that the SPQ-B subfactor score was significantly and negatively correlated with the representational momentum “displacement” score and the Mooney “benefit of orientation” score, indicating that participants with higher scores for schizotypal traits relied relatively less on prior knowledge in these tasks. Although some studies have suggested the opposite – that schizotypal traits are related to stronger priors (Teufel et al., 2015, Powers et al., 2017), studies published in recent years tend to support the opposite hypothesis (Stuke, Weilnhammer, Sterzer, & Schmack, 2019; however, see Corlett, Horga, Fletcher, Alderson-Day, Schmack, and Powers, 2018, on the remaining controversies concerning this hypothesis). Sterzer and colleagues have greatly contributed to providing a framework which would be able to explain some of the opposing accounts on the very complex and multifaceted symptoms related to schizophrenia (Sterzer et al., 2018; Heinz et al., 2018), including the possibly separate cognitive mechanisms that contribute to the development of hallucinations and delusions. As such, they have also highlighted differences in the hierarchical levels of processing – namely, that low-level processing in schizotypal individuals has been associated with decreased priors, whereas higher level processing has been linked to increased use of priors (see also Schmack et al., 2013). This is usually explained to mean that inherently weak or imprecise priors at lower levels are compensated for by a reliance on overly precise high-level priors. Our results are in general consistent with this hypothesis, since both the representational momentum task as well as the inversion effect in face processing represent relatively low-level priors.

In conclusion, the role of priors and prediction errors in autism and schizophrenia is still unclear. From the studies presented here it is evident that the previously proposed hypotheses for explaining the perceptual atypicalities found in autism and schizophrenia are overly simplistic. More nuanced theoretical hypotheses have been put forward in recent years and will hopefully bring more clarity to this relevant issue. It has been proposed that different types of priors are linked to symptoms of schizophrenia in different ways. The same may be true for autism – for instance, some studies have shown that there are no group differences between ASD patients and controls in the effects of low-level priors (e.g., Croydon, Karaminis, Neil, Burr, & Pellicano, 2017). This suggests that aberrant precision in autism may only emerge in the higher associative stages of predictive processing related to making inferences about more complex contextual sensory context (such as social interactions). There are still inconsistent findings regarding whether tendencies found in a clinical sample carry over to the non-clinical population (Karvelis, Seitz, Lawrie, & Seriès, 2018; Van de Cruys et al., 2017; Williams, 2018), but there is potential in continuing research also with non-clinical samples to systematically study the mechanisms underlying varying degrees of atypical perceptual processing. It would however be more prudent to link such differences to narrower clusters of symptoms instead of making inferences on a broad spectrum of disorders to help develop more sensitive instruments in assessing symptom-based markers of individual vulnerability to suboptimal perceptual processing.

5. SUMMARY AND CONCLUSIONS

The predictive coding theory offers an appealing framework not only for studying how the brain is organized, but also how the mind works in general and in all its individual varieties. In this dissertation I provided some theoretical background as well as an overview of gaps in our current knowledge regarding the structure of individual differences in visual perception. I also highlighted the role of predictive processes as an important factor in shaping the individual perceptual experience. While studying robust group effects has provided us with invaluable knowledge regarding general principles of perceptual mechanisms, it is the individual (mind's) eye that holds a vault of treasures yet to be discovered.

In the empirical part of this dissertation, I introduced four published studies with the aim to contribute to ongoing work in the field. In **Study I**, I provided a review of recent research which has attempted to clarify general and specific factors in vision, also stressing some common pitfalls related to the factorial analytic approach. In **Study II**, we demonstrated a novel masking effect in a basic visual discrimination task which emerged when applying non-specific TMS pulses to the frontal cortex at a critical timeframe before stimulus onset, illustrating the role of descending neural pathways in early visual processing. In **Study III**, we compiled a battery of perceptual tasks where prior effects of subjective perception had been demonstrated, to explore whether there is a general factor for relative reliance on priors. We found that individual variance in those tasks was better described by two factors which reflected the different hierarchical levels of the priors evoked. In **Study IV**, we showed that illusory perception of an absent stimulus can be reliably evoked in a dual-task setup by repeatedly strengthening the expectation to see two stimuli presented simultaneously. The results suggest that illusory perception is quite common under certain conditions, but also displays rather large differences between individuals as well as between analogous tasks. Lastly, we used questionnaire measures of the autistic and schizotypal traits in **Study III** and **Study IV** to investigate whether the predictive processing account of suboptimal prior precision in autism and schizophrenia would find support within the neurotypical population. Overall, we concluded that the proposed hypotheses are likely too simplistic to capture the complexities of perceptual atypicalities in these spectrums.

Due to the small sample sizes across these experiments (which were motivated by practical constraints), the findings presented in this dissertation ought to be replicated and expanded upon. Ideally, future research should aim to be more interdisciplinary and collect data from larger samples using multiple comparable tasks. Brain measures should also be included to further explore links with structural and neural differences, as well as the mechanisms behind nonspecific versus specific activation which has been shown to influence subjective perception.

The main takeaways from this dissertation are as follows:

1) Studying individual differences is useful for understanding how the mind is organized. In this dissertation I have argued that studying systematic individual variability helps to elucidate the cognitive mechanisms involved in perceptual processing, as well as providing an important research tool for construct validity.
2) Specifically, measuring performance in multiple paradigms that share a common mechanism helps to test the conceptual applicability of a construct. Studies using different paradigms to make inferences about the same phenomenon has led to a literature of conflicting findings, as even small task differences may affect results. On the one hand, this is reflected in an existing replication crisis, but may also hint at a problem of construct validity in the field. While a theoretical framework is necessary and useful for posing hypotheses and designing experiments, an overly broad or generalized conceptualization of constructs will, however, muddle rather than clarify the state of our understanding.
3) The aforementioned rationale was illustrated by several studies into the effects of priors on perception. Based on findings highlighted in this dissertation, I argued that there is no one universal underlying factor for the relative reliance on priors, rather there are multiple types of priors which are also modulated by the specifics of each task.
4) Using a multi-paradigm design allows for the application of latent variable analysis which is a favoured approach when trying to detect common factors or shared mechanisms of interest. Nevertheless, it is important to maintain experimental and statistical rigour and be transparent in reporting results to such analyses to improve the possibility of comparing results which is essential to get a full picture of the structure of vision.
5) Understanding the sources of long-term individual differences in perceptual processing is relevant not only for understanding optimal perception, but also the mechanisms underlying suboptimal perceptual processing. This offers potential for practical implications in the clinical field for the purpose of clarifying the clusters of symptoms that could share a common mechanism. Some of the previous hypotheses suggested for explaining disorders such as autism and schizophrenia have been too broad, and a more nuanced approach is necessary.

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SUMMARY IN ESTONIAN

Uurimus individuaalsetest erinevustest ennustuste mõjus nägemistajule

Viimaste aastekümnete jooksul on üheks mõjukaimaks lähenemiseks kogniivse neuroteaduse valdkonnas kujunenud ennustava kodeerimise teooria, mis kätkeb endas elegantset ja intuitiivselt kergesti hoomatavat raamistikku ajutegevuse ja inimkäitumise paremaks mõistmiseks. Erinevalt klassikalisest nägemistaju käsitlusest, mille kohaselt on tajusisu kujundatud eelkõige välismaailmast tuleva tunnetust toitva infotulva poolt (n-ö alt-üles signaalid), postuleerib ennustav kodeerimine, et erinevates töötlusetappides on kriitiline roll ka aju enda genereeritud hüpoteesidel ehk ennustustel sisendi võimaliku päritolu ja iseloomu kohta (n-ö ülalt-alla aktiivsus). Nimelt toimub aju hierarhilises närvivõrgustikus paralleelselt kahes suunas liikumine, kui ülalt-alla suunduvaid hüpoteese esindavaid aktiivsusmustreid eri töötlustasemetel sissetulevate signaalidega võrreldakse. Selliseid ennustusi suudab aju tekitada olemasoleva mudeli põhjal, mis hõlmab aastate jooksul akumuleerunud kogemuslikke teadmisi ümbritseva keskkonna tunnuste tõenäosuslikest seaduspärasustest. Ennustuse eesmärk on pakkuda välja ammendav seletus tunnetuslikele signaalidele; kui aga ennustus eksib, vallandub veasignaal, mis omakorda saadetakse ajukoore hierarhia kõrgematele tasemetele, et uuendada ennustust ning vajadusel ka olemasolevat mudelit. Üldjuhul on keskkond, milles me eksisteerime, stabiilne ja toimib ootuspäraste reeglite ja printsiipide alusel. Näiteks võime üsna enesekindlalt lähtuda eeldusest, et päike valgustab objekte suunaga ülevalt allapoole. Taoline eeldus võib aga mõnikord põhjustada tajupetteid (näiteks nagu kujutatud joonisel 1). Kuna aju tõlgendab kahemõõtmelise kujutise puhul tumedamaid piirkondi varjudena ning lähtub eeldusest, et ülalt suunduva valgusjoa tõttu langeksid varjud objekti allosasse, võib varjude paigutumine vertikaalsel teljel jätta muude omaduste poolest samast objektist mulje kui vastavalt reljeefsest „muhkjast“ või „lohkjast“ objekti pinnast. Erinevad optilised illusioonid ongi kõige värvikamaks näiteks sellest, et kiire ja efektiivse taju eesmärgil võib tajusüsteem meid teinekord petta, kuna lähtub ka kahedimensionaalsete kujutiste tõlgendamisel reeglitest, mis püstitatud kolmedimensionaalses keskkonnas õpitud seaduspärasuste alusel.

Käesolev väitekiri keskendub individuaalsete erinevuste uurimisele eespool kirjeldatud raamistikust lähtudes. Kuna ennustav kodeerimine sätestab, et tajukogemus koosneb alati nii objektiivse sensoorse info kui ka subjektiivse ennustuse kombinatsioonist, on püsivad individuaalsed erinevused subjektiivses tajukogemuses selgitatavad ebakõlaga nende kahe komponendi vahelises tasakaalus. Näiteks on selle käsitluse abil püütud seletada mõningaid vaimseid häireid, mida iseloomustab ebatüüpiline tajukogemus. Sellisteks häireteks on muuhulgas autism ja skisofreenia. Ühe hüpoteesi järgi võiks autismi selgitada kui sensoorse signaali tähtsustamise poole kaldu olevat süsteemi – selliselt, et välismaailmast omandatud informatsiooni on raskem üldistada ühtseks mudeliks, mille põhjal teha olukorda sobituvaid ennustusi. Seetõttu on autistlikud inimesed tihtipeale sotsiaalses keskkonnas ülekoormatud ja stressis, kuna ei suuda rakendada inimeste sotsiaalsete vihjete tõlgendamiseks üldiseid seaduspärasusi ning tajuvad kõiki detaile kui uudset informatsiooni, mis kurnab tajusüsteemi ja vallandab häirivaid veasignaale. Skisofreeniat seevastu on püütud tõlgendada kui liigset toetumist ennustussignaalidele, mis seletaks hallutsinatsioonide ja sundmõtete tugevalt subjektiivset komponenti.

Väitekirja üheks eesmärgiks oli anda ülevaade värsketest edusammudest individuaalsete erinevuste ja nende struktuuri uurimises nägemistaju valdkonnas, kuna seni pole veel ühtse selge arusaamani jõutud. Sellega tegeles **Uuring I**, mis andis ülevaate viimase kümne aasta jooksul tehtud nägemistajuga seonduvatest faktorstruktuuri uuringutest. Muuhulgas on püütud leida nägemistaju soorituses mõõdetavat analoogi intelligentsusuuringutes levinud üldisele „g faktorile“ ehk teisisõnu nn „v faktorit“, mida saaks seletada kui üldist ühisosa, mis on seotud kõikide madala taseme nägemisülesannete sooritustega. Seega, kui üks inimene on osav mõnes tajulises eristusülesandes, on tal tõenäoliselt kõrgem tulemus ka teistes tajusooritusülesannetes. Ülevaatelisest meta-taseme uuringust ilmnes, et sellist faktorit nägemistajus tõenäoliselt ei esine ning nägemistaju funktsioonid on pigem paremini kategoriseeritavad kitsamate visuaalsete oskustena, mis piirnevad sarnast tüüpi ülesannetega. Samuti kajastas ülevaateuuring eksperimente, mis olid keskendunud kõrgema taseme faktorite tuvastamisele nägemistajus, näiteks seoses individuaalsete erinevustega globaalse-lokaalse töötluse automaatses eelistuses või üldises tendentsis olla vastuvõtlikum illusioonide tekkimisele. Tulemustest võis järeldada, et rakendades ühel valimil mitut erinevat katseparadigmat (mida on varasemalt kasutatud vastava dimensiooni mõõtmiseks), ei suudetud ühist faktori leida. See viitab probleemile konstruktivaliidsusega, millest tingituna võivad näiliselt sama mehhanismi illustreerivad katseparadigmad mõõta tegelikult erinevaid asju.

Sellest probleemistikust lähtuvalt püstitasime küsimuse, kas individuaalsed erinevused ülalt-alla mehhanismide mõjus nägemistajule võiksid samuti tuleneda mingist ühisest allolevast allikast, näiteks üldisest tendentsist toetuda tajuotsuste tegemisel suhteliselt rohkemal või vähemal määral ennustushüpoteesile. Esmalt viisime läbi **Uuringu II**, mis püüdis vaadelda ülalt-alla signaalide mõju lihtsa tajuülesande sooritusele. Planeerisime eksperimendi, kus katseisiku ülesandeks oli lahendada lihtsat tajuülesannet, samal ajal kui suunasime parempoolsesse frontaalsesse ajukoore sagarasse transkraniaalse magnetstimulatsiooniga (TMS) magnetimpulsse, mis olid ajastatud kolmel erineval ajahetkel stiimuli ilmumise suhtes. Tulemused näitasid, et katseisikute sooritus halvenes märkimisväärselt katsetingimuses, kus TMS impulss suunati ajukoorde 60 ms enne stiimuli ilmumist. Ka varasemalt on näidatud, et *nägemispiirkonda* (nt esmastes nägemiskeskustes kuklasagaras) TMS-iga stimuleerides võib juba enne stiimuli esitamist kutsuda esile soorituse halvenemise. Küll aga on tegemist uudse leiuga, kuna stimuleerisime *eesmist ajukoort*, mis on otsestest nägemistaju töötluspiirkondadest kaugemal. Seega näib, et ka üldine mittespetsiifiline neuraalse aktiivsuse foon mõjutab tõenäoliselt ülalt-alla juhteteid pidi madala taseme nägemistaju protsesse. Samuti leidsime, et TMS-iga esile kutsutud maskeerimisefektis oli märkimisväärseid individuaalseid erinevusi, mis kajastusid ka elektroentsefalograafiga (EEG) mõõdetud elektrilises aktiivsuses.

Lisaks tahtsime teada, kas ülalt-alla ennustuste mõju individuaalsetele erinevustele võiks ka käitumuslikes tulemustes grupeeruda ühe ühise faktorina või pigem mitme spetsiifilistele mehhanismidele omase faktorina. Selleks valisime **Uuringu III** jaoks välja neli tajuülesannet, mille puhul oli varasemates uurimustes näidatud, et üldiselt raporteerivad inimesed sellist subjektiivset tajukogemust, mis erineb mõne omaduse poolest objektiivsest kujutisest, mida ekraanil näidatakse. Näiteks näevad inimesed geomeetrilise kujundi illusoorseid kontuure, mis tegelikult moodustuvad ainult sümmeetriliselt paigutatud joonte koosmõjul, kuigi tajutud geomeetrilist kujutist reaalselt ei olegi (vt joonis 1) või tajutakse kahe uduse tähekombinatsiooni puhul teravamana seda, mis moodustab tähendusliku sõna, võrreldes kombinatsiooniga, millel tähenduslik sisu puudub. Selliste ülesannete puhul arvatakse, et kuna tunnetuslik sisend on nendes situatsioonides mõnevõrra ebamäärane või mitmeti tõlgendatav, toetutakse tajukujutise loomisel rohkem ennustusele, mis kasutab selleks varasemaid kogemusi ja pakub välja hüpoteesi kõige tõenäolisema tajukujutise kohta. Väljavalitud nelja tajuparadigma andmeid analüüsides leidsime, et üks ühine faktor ei suuda ära seletada individuaalseid erinevusi, mis ilmnesid ennustuste mõjus tajule. Pigem seletas antud katse tulemusi paremini kahefaktoriline mudel, mis näis peegeldavat tajusüsteemi hierarhilist struktuuri: omavahel olid rohkem seotud ülesanded, mis rakendasid madalama taseme ennustusi ning teisalt need ülesanded, mis kutsusid esile mõnevõrra kõrgema taseme ennustusi. On siiski võimalik, et omavahel sarnasemate ülesannete puhul oleks mingi üldisem faktor välja joonistunud.

Seega planeerisime **Uuringu IV**, kus kavandasime kolm analoogset tajuülesannet, mis põhinesid samal nähtusel – kui esitada ekraanil lühikese kestvusega kaks stiimulit, mis ilmuvad ja kaovad alati samaaegselt, on võimalik „tingida“ tugev ootus, et tegemist on usaldusväärse seaduspärasusega, mistõttu kui üks stiimulitest jääb mõnel katsekorral esitamata, siis inimesed raporteerivad endiselt subjektiivset tajukogemust kujutisest, mida tegelikult ekraanil ei olnud. Sellist olukorda võib tõlgendada seega kui ootuse mõju illusoorse taju tekitamisel. Siiski kasutasime taolisi katsekordi katse jooksul pigem vähe (umbes 2% tervest katsest), kuna vastasel juhul võiks katseisik märgata reeglis muutust ning ennustust uuendada. Antud katsega suutsime näidata, et sellistel tingimustel „hallutsineerimine“ on pigem tavaline ning seda esines enamikul katseisikutest vähemalt ühel korral katse jooksul. Küll aga ilmnesid märkimisväärsed erinevused nii indiviidide kui ka erinevate ülesannete vahel, mis viitab sellele, et antud nähtuse täpseid toimimistingimusi tuleks veel põhjalikumalt uurida.

Viimaks, et uurida individuaalsete erinevuste võimalikke seoseid autistlike ning skisotüüpsete joontega, lisasime **Uuringusse III ja IV** küsimustikud, mõõtmaks nende seadumuslike joonte esinemist tavapopulatsioonis. Tahtsime teada, kas hüpoteesid, mis on püstitatud kliinise populatsiooni põhjal seoses patoloogia tingimustes häirunud tajuga, oleksid tajuerisustega seotud ka tavapopulatsioonis. Tulemused osutasid, et vaatamata ühes osas katsetest leitud seosele need hüpoteesid meie valimi ja ülesannete puhul tervikuna paika ei pidanud. See võis olla tingitud asjaolust, et tavapopulatsioonis ei väljendu need seosed nii selgelt. Samuti võis üldkehtiva seadupärasuse mitteleidmine tuleneda ülesannete erisustest. Patoloogiakalduvuse suhtes tundlik võib olla vaid kitsalt spetsiifiline ülesanne. Samuti on tõenäoline, et sedavõrd lihtsad hüpoteesid, mis tõlgendavad häireid kui ebakõla sensoorse info ja ennustuse tasakaalus, on liialt lihtsustatud ning komplekssete sümptomite mõistmiseks peaks rakendama märksa nüansirohkemaid seletusi.

Kokkuvõtvalt panustas käesolev väitekiri olemasolevate teadmiste täiendamisse mitmes olulises aspektis. Esiteks näitasin erinevat tüüpi tajuülesannete toel, et ennustused mõjutavad nii subjektiivset tajukogemust (Uuring III, IV) kui ka objektiivset tajusooritust (Uuring II, III). Samuti sai kinnitust, et subjektiivset tajukogemust stiimulist, mida tegelikult ei nähtud, on võimalik ennustusi "tingides" esile kutsuda mitmes omavahel analoogses ülesandes (Uuring IV), näitlikustades seeläbi, et tegemist on normipärase tajutöötluse omadusega. Olulise uuendusena vastas Uuring III küsimusele, kas individuaalseid erinevusi ennustuste mõjus saaks vaadelda kui ühisest allikast tulenevaid. Tulemustest ilmnes, et ühte ühist faktorit antud uuringus kasutatud ülesannete puhul andmetest järeldada ei saa – pigem peegeldasid tajumõõdikute omavahelised seosed erinevaid töötlushierarhia tasemeid.

Lisaks empiirilisele panusele argumenteerisin väitekirja teoreetilises osas individuaalsete erinevuste uurimise olulisuse üle, mis on väärtuslikuks tööriistaks nägemistaju universaalsete mehhanismide ja strukturaalse ülesehituse kaardistamiseks. Lisaks optimaalse tajustruktuuri lahtimõtestamisele aitab individuaalsete erinevuste uurimine paremini mõista mõningaid vaimseid häireid iseloomustava suboptimaalse tajutöötluse alusmehhanisme ning leida, millised katseparadigmad on perspektiivikamad vaimse seisundi haavatavuse seiretestide väljatöötamiseks. Sealjuures tasub eksperimendi kavandamisel kaasata mitu sama protsessi mõõtvat ülesannet, et tagada konstruktivaliidsus ja tuua esile võimalikud ülesandespetsiiflised erisused ja sarnasused.

PUBLICATIONS

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DISSERTATIONES PSYCHOLOGICAE UNIVERSITATIS TARTUENSIS

1. **Jüri Kruusvall.** Environmental and social influence on human activity. Tartu, 1994, 135 p.
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