The Role of Affective Experience in Visual Perception:

Insights from Predictive Processing

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Nils Pascal Kraus

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Erstgutachter: Prof. Dr. Guido Hesselmann

Zweitgutachter: Prof. Dr. Michael Niedeggen

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Acronyms

AFC - alternative forced choice

BOLD – Blood oxygen level dependent

CP – Cognitive penetrability

EEG – Electroencephalography

ERP – Event-related potential

IFC – Inferior frontal cortex

IU – Intolerance of uncertainty

MEG - Magnetoencephalography

PE – Prediction error

PEM - Prediction error minimization

PP – Predictive processing

PW – Precision weighting

RDK – Random dot kinematogram

RT – Reaction time

STAI - State-Trait Anxiety Inventory

UI – Uniformity Illusion

1. Summary

In traditional psychological theories, the link between emotional experience and perception has mostly been considered as unidirectional. Specifically, emotions are assumed to arise from the contents of perception. The contents of perception, on the other hand, have been conceived to be independent of any perceiver-based mental variables such as affect or mood. The implied temporal processing order of this approach makes intuitive sense, as perceiving something can be considered as a necessary prerequisite for it to evoke an emotional response. Thus, our emotional appraisal of something (e.g., fear of it) will not affect our perceptual experience of it. However, more contemporary models of mental processing allow for a bidirectional approach to understanding the interactions of affect and perception.

In this dissertation, I describe a general framework of mental action called predictive processing (PP) and the specific applications of this framework to visual perception as well as to affect and mood. Based on these theoretical considerations, I will then derive a hypothesized formal relationship of the two constructs which allows for perception, and more specifically, perceptual precision weighting, to be influenced by affective variables. I continue with describing and summarizing the three dissertation studies, which have all looked at different aspects of positive and negative affect (state, trait, induced) and their relation to visual phenomena. I will end by discussing the implications of the observed effects on the debate over potential influences of affective variables on visual perception.

All conducted experiments aimed at relating affective variables with parameters of visual precision weighting (PW), i.e., how much weight is ascribed to prior information and current sensory inputs, respectively. In study 1, we have shown that individuals with higher trait anxiety tend to rely stronger on a predictive cue rather than on actual sensory evidence when they were asked to judge the direction of a motion stimulus. Study 2 suggests that induced negative affect leads to less susceptibility to perceptual filling-in in the uniformity illusion (UI), indicating attenuated reliance on priors when affective state valence is negative. In study 3, we showed that affective states influenced perceptual stability in binocular rivalry. Specifically, positive baseline affect was linked to longer phase durations, suggesting a stronger influence of priors, while induced negative affect was related to a reduced stimulus

specific bias, suggesting a reduced influence of priors. Importantly, all studies were conducted with affectively neutral stimuli and in samples of healthy participants. The findings are thus unlikely to stem from attentional mood congruency biases or altered stimulus processing in patient groups.

In summary, these results suggest an influential role of affect in visual perception. The findings highlight specifically the role of affective state valence, showing that more negative valence was associated with less reliance on priors. The specific influence of affective traits on the other hand was found less consistently across the different studies. While we found trait anxiety to be associated with a tendency to disregard new sensory evidence and to make stronger use of priors in a motion direction detection task, this link was not found during binocular rivalry. These findings are difficult to explain invoking traditional conceptions of independent affective and perceptual processing, whereas they are largely in line with a predictive processing approach to emotion-perception interactions. In this account, changing prediction error rates are accompanied by short-term variations in affective state and function to incentivize initiation of changes in current PW parameters. However, we found only limited evidence for conceptualizing affective traits as long-term tendencies to incorporate new sensory evidence into one's current perception. This holds important implications for different conceptions of affective states and traits, their involvement in perceptual processing, as well as for closely related topics such as the general debate about the cognitive penetrability of perception.

2. Introduction: Affective Realism in Visual Perception

Traditionally, affect and perception have been considered as mostly independent mental processes. Established theories of visual perception typically aimed to explain how single optical features are integrated into higher level objects and visual scenes, independent of their potential to subsequently evoke emotions (Gordon, 2004). Theories of emotion, however, often presuppose completed perceptual stimulus processing, so that the contents of perception can be appraised with respect to their emotional relevance. Note, that while it is widely accepted that emotions influence a wide variety of bodily and mental processes like physiological arousal or allocation of attention, the mere contents of perception themselves have traditionally been considered as functionally independent from emotional processing. This view is in accordance with the notion of a modular mind (Fodor, 1983), in which sensory information is processed in a feedforward manner throughout functionally encapsulated modules. Although there is no consensus among even strong proponents of modularity over which mental faculties are restricted by functional encapsulation, visual perception is frequently used as a classical example of domain specific information processing that is proposed not to be susceptible to influences of extra-perceptual factors such as beliefs or emotions (i.e., that is cognitively impenetrable; Firestone & Scholl, 2016; Pylyshyn, 1999).

Recently, this view has been challenged by the notion of affective realism (Anderson et al., 2012; Barrett & Bar, 2009). This concept rests on the assumption that affect in particular, as compared to other perceiver-based variables, would yield a significant influence on perception. Several empirical studies have been brought forward to argue in favor of this view. Siegel et al. (2018) demonstrated that a scowl face, masked by continuous flash suppression, led participants to rate a simultaneously presented neutral face more negatively. Importantly, the authors did not interpret this to be an effect of affective information acting upon other top-down variables such as deliberative judgements. In this view, stimuli that were actually perceived to be affectively neutral would merely be rated to appear more negatively by the participants. Instead, the authors proposed that affective information is constantly integrated into a continuous stream of sensory inputs, thereby contributing to an overall context in light of which the brain is construing its current perception of the world. Interestingly, these effects were only observable if the visible neutral face was presented simultaneously to the suppressed scowl face, but not when the neutral face was preceded by the affective one (150 ms stimulus onset asynchrony; Wormwood et al., 2019). This has been interpreted by the authors as evidence against established explanations of similar effects such as priming or misattribution. For a detailed review of the role of emotions in masking and priming experiments, see Rohr & Wentura (2021).

If correct, an affective realism interpretation of findings like these would bear important implications not only for the role of affect in visual perception, but for our understanding of the temporal and structural dynamics of mental processes in general. Specifically, it would provide evidence for the notion of cognitive penetrability (CP) of perception. The CP debate is held over the question of whether any perceiver-based mental variable, be it personality traits or emotions, that is typically not considered as perceptual in nature, can influence the contents of perception. Despite the basic openness of this notion towards all conceivable constructs that could in principle infuse perception, affective variables have received particular attention within the debate.

In their widely recognized target article, Firestone & Scholl (2016) named affective variables[1] as a major candidate faculty that has been proposed to alter what and how we see. The authors discussed several studies claiming to provide empirical examples of CP of vision through affect. These included, among others, studies showing that participants who were asked to recall positive as opposed to negative self-related memories later judged a flashlight to be brighter (Banerjee et al., 2012) or that higher physiological arousal was associated with elevated levels of height estimation (Storbeck & Stefanucci, 2014). Critics of these studies have labelled these effects as post-perceptual, thus claiming that affect would not influence the processing of low-level perceptual features of a stimulus, e.g., its brightness. Instead, what is suggested is that affective variables would modulate deliberative judgements of these same features at a later stage of stimulus processing such as memory recall (Raftopoulos, 2017, 2019). Experimentally, this criticism can be addressed by showing that affect differentially influences

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[1] To the best of the authors knowledge, there is no commonly shared definition or use of the different terms concerning emotional experience (e.g., affect, emotion, mood, etc.). For the sake of clarity, the umbrella term of affective variables is used for now and will be further differentiated and defined in section 2.3..

perception but not deliberative judgements as well as by using real-time proxy measures of perception (e.g., trough electroencephalography (EEG)). However, in its essence, this critique is difficult to counter through empirical studies of perception, since neither behavioral nor neuroimaging data is unanimously considered as a valid proxy measure for subjective moment-to-moment perceptual experience (for a discussion, see Tagliabue et al., 2019).

Some authors have suggested that in addition to methodological concerns over the measurement of perceptual experience, the debate over CP has further been complicated by traditionally established distinctions of research disciplines such as research on visual perception and emotions (Clore & Proffitt, 2016; Ochsner et al., 2009). Drawing from these distinctions could facilitate category mistakes, leading to an arbitrary separation of otherwise closely interconnected mental processes. In order to avoid such category mistakes, it appears useful to rely on theories of general mental functioning that include specific accounts for both constructs in question (i.e., affect and visual perception). For this purpose, this thesis specifically focusses on the predictive processing (PP) framework and its implications for the notion of CP in vision through affective variables.

2.1 Predictive Processing

Predictive processing is a formalized scheme describing information flow in the brain. Originally, this scheme was applied to message-passing in the visual cortex (Rao & Ballard, 1999), rendering its application especially suitable as a theory of perception (see section 2.2.). According to PP, the brain forms a generative model of the self and its environment in order to actively predict upcoming changes in sensory streams through anticipatory computation. For this purpose, the flow of information within the brain serves the imperative of constantly maximizing model evidence (i.e., minimizing false assumptions of the generative model, Friston, 2010). This is achieved by the implementation of a Bayesian updating scheme in which in a first-order stream, new information is matched with prior predictions, resulting in a prediction error (PE). Information about the PE then ascends to and informs higher levels of processing that typically encode more abstract and generalized mental contents that are composed of the lower-level contents. Simultaneously, expectations that are encoded at higher levels of processing can influence the flow of information at lower levels through modulatory backward connections, thereby implementing top-down influences (for a schematic prototypical coding scheme, see Fig. 1). In the form of a second-order stream, the precision (i.e., inverse variance) of the PE and the precision of prior expectations are encoded. Weighting these two parameters is necessary in order to update prior expectations on the basis of new evidence (i.e., precision weighting; PW). The selective optimization of precision estimates of both, priors and PE in PP, is conceived as attention (Ainley et al., 2016). Attention modulation is assumed to be achieved by selectively elevating the synaptic gain of PE neurons that are currently receiving inputs from prediction neurons (Hohwy, 2012). Since the precision of PE is inherently coupled to sensory states, attention further entails the optimization of certainty estimates over the inferred causes of those sensory states (Feldman & Friston, 2010). While both phenomena (PW and attention) describe functionally distinct computations, elevated sensory precision (as could result from heightened attention) will make reliance on sensory evidence during PW more likely.

As mentioned, this general scheme can be applied to conceptualize a multitude of neurocognitive phenomena such as imagination (Clark, 2012), attention (Feldman & Friston, 2010), or learning (Friston et al., 2016). Since information processing is bound by the imperative of long-term reduction of experienced PE (prediction error minimization; PEM), two mechanisms have been determined to be most effective in achieving this. Firstly, PE can be minimized by adjusting and optimizing prior expectations about the environment on the basis of sensory data (i.e., perceptual inference; Friston, 2012). This encompasses the continuous learning of environmental contingencies through an iterative cycle of generating predictions, observing, matching observed and predicted events, and refining subsequent predictions based on the results of matching. Secondly, PEM can be achieved by acting on one's environment (i.e., active inference; Friston et al., 2016). Seth and Tsakiris (2018) further differentiated between two kinds of active inference: instrumental and epistemic. Through instrumental actions, one can actively change sensory inputs to make them match with prior expectations, thereby minimizing PE (e.g., painting a pink wall white, thereby making it more in line with one's predictions of how a wall is supposed to look like). Epistemic actions on the other hand serve an exploratory purpose, where sampling of new information is enabled by behaviors like turning your head or making a saccade. Note, that these mechanisms are hard to distinguish and largely interdependent in any given situation, especially in explorative behaviors. As the principle of PEM and its implementation within visual processing bears important implications for the topic of this thesis, the following section will explore the PP account of visual perception in more depth.

2.2 Predictive Processing in Visual Perception

A theory aiming to explain subjective perceptual experience of the environment needs to address what is typically called the inference problem, i.e., how the brain is able to construe the causes of sensory inputs. PP addresses this issue by casting perception as probabilistic Bayesian inference (Friston, 2012). This follows from applying the message-passing scheme described in the previous section to a perceptual neuronal network. Note, that there are multiple possible coding schemes (e.g., Bastos et al., 2012; Friston, 2005; Rao & Ballard, 1999) that meet the basic requirements that have been formulated to comply with the assumptions of a system trying to maximize its model evidence (Adams et al., 2014). However, all of these possible implementations share common features: I) Hierarchical message passing II) Lateral processing of predictions (P) and PE in different neuronal populations III) Bidirectional information flow in which predictive information descends to inform lower levels and PE ascends to higher levels to update predictions IV) Accounting for the respective certainty estimates of P and PE in order to determine the posterior (for a prototypical implementation see Fig. 1). Perception is thus conceived as a form of hypothesis testing, in which new information is constantly updating the brain's best guess of what is causing the current sensory inputs. For illustration purposes, one can draw a comparison to computing a t-test: two distributions are subtracted from each other, taking into account the standard error of each distribution. The resulting t-statistic would be equivalent to the precision weighted PE. This conception not only brings with it explanatory frameworks for a multitude of perceptual phenomena such as repetition suppression (Auksztulewicz & Friston, 2016), sensory attenuation (Kiepe et al., 2021), optical illusions (Watanabe et al., 2018), hallucinations (Sterzer et al., 2018), or bistable perception (Weilnhammer et al., 2017). It also has important implications for the debate over CP of perception (Lupyan, 2015).

It states directly that visual perception will always be informed and influenced by prior expectations and beliefs, especially if the precision of prior beliefs is high and the precision of sensory evidence is low (De Lange et al., 2018). Further, this will happen at every level of visual processing, from single line orientation to processing of motion or faces. Importantly, opponents of CP consider *beliefs* explicitly as a top-down factor, which is by definition implemented functionally independent of perceptual processing (Firestone & Scholl, 2016). A belief could thus well alter the appraisal of any given stimulus after its perception, but not its qualitative appearance (e.g., its subjectively perceived visual features). PP, however, conceptualizes beliefs as a-priori assumptions about the most probable environmental states within a generative model. Those assumptions are encoded, and therefore will influence activity at every level of the visual hierarchy. Further, predictive information arising from those assumptions can be passed along laterally as well as descend to lower levels (Friston, 2005), thus, content and precision of higher-level beliefs will influence PW at lower levels and allow for CP (Lupyan, 2015).

Following these premises, there would be no clear distinction between cognition and perception since activity at lower levels can be influenced by predictive information of higher

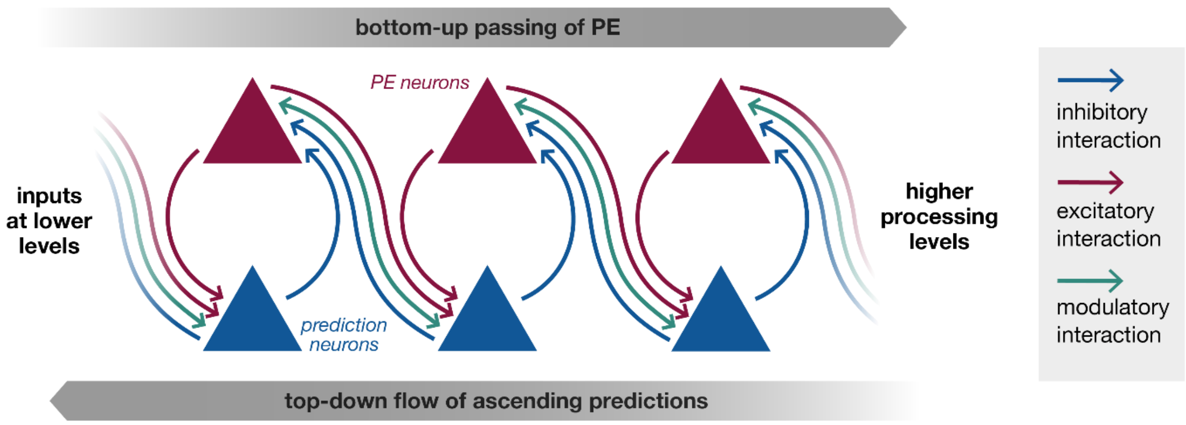

Figure 1: A generalized PP scheme of neuronal message passing. For the case of perception, input from sensory organs is matched with prior predictions (blue units) at the first level of processing. Resulting PEs (red units) are conveyed to higher processing levels and thus update posterior estimates of what is causing sensory inputs. Predictions on the other hand are either ascending to lower levels or being processed laterally. Precision estimates are exchanged bilaterally across different levels through modulatory connections. Note that PE, and thus affective value, although it is represented at every level of processing is globally minimized trough iteratively adapting priors to sensory inputs. Adapted from Edwards et al., 2012.

levels through the differential weighting of predictions and sensory evidence. This renders PW as the central route to cognitive penetrability in PP (Cermeño-Aínsa, 2021; Hohwy, 2017). PW is informed by current rates and precision of PE, which have also been linked to affective experience in PP. This makes affective variables promising candidates in the search for observer based, extraperceptual variables that could potentially influence subjective perceptual experience.

2.3 Predictive Processing and Affective Experience

Since there is significant variance in how affective variables are defined even within the established literature on this topic, for the sake of clarity, I will first briefly describe what I would consider as commonly used definitions of the affective nomenclature. I will then further elaborate on PP accounts of affective experience and point out the differences in the two approaches.

A central distinction that is often made in the literature on this topic is between affective states (affect and emotions) and trait variables. Affect (also called affective state or core affect) usually describes a rather unspecific, transient, subjective and short-lived quality of experience characterized by the dimensions of arousal (low/high activation) and valence (pleasure/displeasure; Duncan & Barrett, 2007). By way of contrast, emotions are often considered as affect encompassing, but more complex, situation-specific reactions that bring specific cognitive appraisal structures with them (e.g., feeling angry implies being in a highly arousing, negatively valenced state that an individual attributes to be caused by a rule violation; Barrett, 2017a). Affective traits, on the other hand, describe stable tendencies of individuals to experience specific emotional reactions across different situations (e.g., anxiety).

There have been several attempts to place constructs related to one's affective experience in the PP framework. Reviewing the existing literature on PP models of affective states, Fernandez Velasco & Loev (2021) outlined two major approaches: Interoceptive Inference Theories (IITs) and Error Dynamics Theories (EDTs). Interoceptive Inference Theories (e.g., Barrett, 2017b; Seth, 2013; Seth & Friston, 2016) focus on the relationship between the detection of somatic changes and Bayesian inference over their assumed causes. An important concept in this context is allostasis. It comprises the constant detection of deviations from a set of biologically determined parameters (i.e., biological priors) that ensure survival, such as body temperature or blood glucose levels. During exteroception (i.e., perception of the external world), the brain is assumed to constantly monitor deviations in its environment from expected inputs and derive the cause of these inputs from that. IITs propose to extend this mechanism to the constant monitoring of changes in somatosensory signaling. An emotion is henceforth perceived as causing the detected somatic changes, solving the inference problem for otherwise involuntary (i.e., non-deliberative) changes of interoceptive signals. Importantly, emotional inference can also be based on information from the external world, as data from all sensory modalities is assumed to be incorporated by the integration of lateral information flow between sensory processing units (Friston, 2005). Standing right next to a cliff would therefore serve as an important hint that it is most likely fear which is causing one's elevated heart rate. Importantly, while external information can serve as clues during emotional inference, IITs highlight the importance of somatosensory information, as it is specifically those signals that need to be explained. IITs have therefore been compared to the James-Lange theory of emotion, which conceives emotion as resulting from the detection and interpretation of physiological arousal (Lang, 1994), but with a "predictive twist" (Clark, 2015, p.233). The role of prediction in IITs gains relevance when considering the difference between the sensation of bodily signals versus the subjective qualities of an emotion.

As IITs originate from PP theories of interoception, they attempt to further explain the different subjective qualities that result from exteroceptive versus interoceptive inference (Fernandez Velasco & Loev, 2021). Seth and Friston (2016) emphasized that in contrast to mere perception of bodily signals (i.e., interoception), emotions only derive from inferences that cause predictions over future changes in allostatic variables, i.e., that are relevant for survival. To illustrate this point, the perception of a smoke or fire in an office building initiates a prediction that higher oxygen levels in the bloodstream will be necessary for a successful response (fleeing or extinguishing the fire), resulting in an elevated heartbeat. Seth and Tsakiris (2018) further emphasize this point by applying their differentiation between epistemic and instrumental active inference to interoceptive inference (see section 2.1). In their view, mere detection of one's bodily signals would be considered epistemic, while instrumental interoceptive inference refers to an active change of somatic parameters to bring them in alignment with prior predictions.

Error Dynamic Theories (e.g., Joffily & Coricelli, 2013; Van de Cruys, 2017) conceive emotional experience to be a direct corollary of weighted PE rates over time. As the amount of experienced PE is reflective of the ability to accurately predict and explain current sensory streams, it is a crucial variable for the brain while working under the constraint of surprise minimization. From this, the concept of valence can be derived, as sensory inputs that are in line with initial priors (low PE) imply more effective surprise minimization. This renders predictable stimuli as well as stimuli that allow for the resolution of PE and optimal model updating and learning as more positive than unpredictable stimuli. Furthermore, the concept of affective arousal is mirrored in the precision of PE, which is assumed to determine the strength of the subjective emotional experience. Thus, concerning the central components of affective state (valence and arousal), EDTs show high similarity with established approaches. Compared to IITs, EDTs don't restrict the relevance of PEs in determining affective valence to interoceptive processing. Rather, they focus on the global importance of PE, be it interoceptive or exteroceptive, in determining the ability to predict one's environment.

EDTs have further been extended to account for stable tendencies of affective experience in humans, i.e., affective traits. Clark et al. (2018) reasoned that since PE rates relate to the estimated momentary amount of environmental uncertainty and controllability, individuals will develop long-term expectations over the expected degree of these variables in future situations. These so-called hyperpriors will, just as normal priors, contain a content (expected valence) and precision (certainty of the predicted valence). From these two variables, the authors derived a two-dimensional classification scheme of mood which they also use to conceptualize affective traits of various psychological diseases. For instance, depression and mania are considered hyperprior states, in which either negative or positive valence (i.e., low/high predictability and low/high controllability) is predicted to occur with high precision[2].

[2] Importantly, the diagnostic criteria for the named diseases typically go well beyond a categorization of the disease as merely indicating a strong degree of any affective trait. Rather, they extend to deviances on a broad spectrum of psychomotor and neurocognitive functioning. However, it is a topic of an ongoing debate, whether to limit the characterization of patients with affective and anxiety disorders as individuals with high degrees of affective traits (depressiveness and trait anxiety) stands up to scientific scrutiny (Vazquez & Gonda, 2013).

Further, the authors consider trait anxiety as expecting negative results with low precision (i.e., high uncertainty). Note, however, that this account has been questioned by conceptualizing trait anxiety as 'learned uncertainty', thus, reflecting upon a disposition to expect uncertainty with high precision (McGovern et al., 2022). This approach of relating affective traits to the expected degree of controllability and predictability of future situations fits nicely with research on general predictors of well-being. Here, the experience of learned helplessness is a major contributor to the development of depression (Maier & Seligman, 1976) and self-efficacy (i.e., the belief over one's ability to influence the environment) is elevated in individuals with high wellbeing (Caprara et al., 2006).

Overall, both, IITs and EDTs, relate affective valence to a discrepancy between expected and experienced states, although with different foci on interoceptive and exteroceptive sensory streams. While EDTs appear to primarily focus on variables that in the literature would be considered as core affect and affective traits, IITs relate more strongly to classical notions of emotions (i.e., a particular cognitive appraisal structure that is aimed at explaining changes in somatosensory inputs). However, both theories tie negative valence to high rates of PE, which in PP runs contrary to the constraint of PEM. In PP, state affect can thus be considered to mirror the individual's need to adjust current strategies of PEM. As mentioned, PEM can be achieved through active and perceptual inference, with the latter one yielding a potential working principle of affective variables influencing perceptual inference processing.

2.4 A Potential Role for Affective Variables in Visual Perception

The last section described how different theoretical approaches within PP consider affective states and traits to be reflective of current and expected rates of PE. Simultaneously, this ties the proposed function that emotions hold in classical theories (e.g., provide information, response preparation and execution) to PEM. Negative affective states thus not only signal elevated PE, but also the necessity to adjust current strategies of PEM. First, consider the case of achieving PEM through instrumental active inference: noticing the signs of a fire in a building evokes rising PE, as it is considered a threat to survival and inherently uncontrollable.

This immediately triggers a preparatory somatic response (elevated heartbeat) which remains to be explained. From the external as well as the internal sensory information, one can now infer the most likely cause of the somatic changes, which is the emotion of fear. The negative valence of the situation then serves to motivate the individual to take a specific action (e.g., flight) that is expected to successfully reduce the cause of high PE and the threat to survival. Hesp et al. (2021) proposed a formalized model of such situations of emotional inference. They implemented the model in a simulated agent with a preferred state and a specified set of actions that it can take: a rat that is placed at the starting point of a T-maze with food at one of the end points with changing contingencies. The rat will get hungry over time and it can move either left or right. Trying the different behavioral options (moving left or right) will become associated with their potential to reduce (hunger related) rates of PE. This will in turn allow for the build-up of prior predictions over the potential of future behaviors to reduce PE (e.g.: "I will most likely find food if I go left"). The agent can then infer its valence state from prior precision of planned actions, where higher precision would signal the expectation that the action is likely to lead to PE reduction (in this case reduce the hunger). High prior precision with respect to an action that is predicted to reduce PE would thus be associated with positive valence and the subjective feeling of certainty.[3] Importantly, higher precision of planned actions is accompanied by higher reliance on prior knowledge in this scenario. However, it remains an open question whether a similar mechanism (positive state valence resulting in higher reliance on priors) can also be posited for perceptual inference.

To approach this question, it is useful to consider the degrees of freedom of a perceptual system in which PP is implemented, while bracketing out action as an inference mechanism. In this hypothetical scenario, neither the contents of sensory information nor the contents of priors can be freely adjusted by the individual, as the former is an environmental constant and the latter is calculated based on the perpetual evaluation of the former. However, both are weighted against each other in determining the most likely cause of current sensory inputs (PW). This process is reflective of the organism's best guess for the optimal solution to the

[3] Although the observable behavior of the agent in this paradigm would be equivalent to one that is driven by reinforcement learning, there are important differences concerning the emergence of subjective affective valence between the two frameworks. For a detailed discussion of this, see Friston et al. (2021).

trade-off between optimizing sensory precision through elevated attention and relying on prior knowledge about the most likely state of the environment. This process can therefore be considered flexible, and the respective weights can be adjusted depending on current PE rates (see Fig. 2). Negative (compared to positive) affective states could be assumed to shift perception towards higher weighting of sensory evidence instead of priors for two reasons. Firstly, as negative affect signals that a situation was either not predicted accurately or is judged to be uncontrollable, reliance on priors is unlikely to resolve the situation. Secondly, the precision of sensory data can temporarily be enhanced through attention, whereas prior precision, although it can be updated, is constrained by previous events. Reliance on sensory data, as well as heightened attention towards it, are likely to be more resource-intensive than reliance on prior knowledge. In this general trade-off, a negatively valenced situation is more likely to shift one's disposition to rely on the more resource-intensive, albeit more reliable, information source. Just as our fear of the bear will heighten our willingness to engage in a more resource-intensive behavioral fight-or-flight response. This line of reasoning led to the

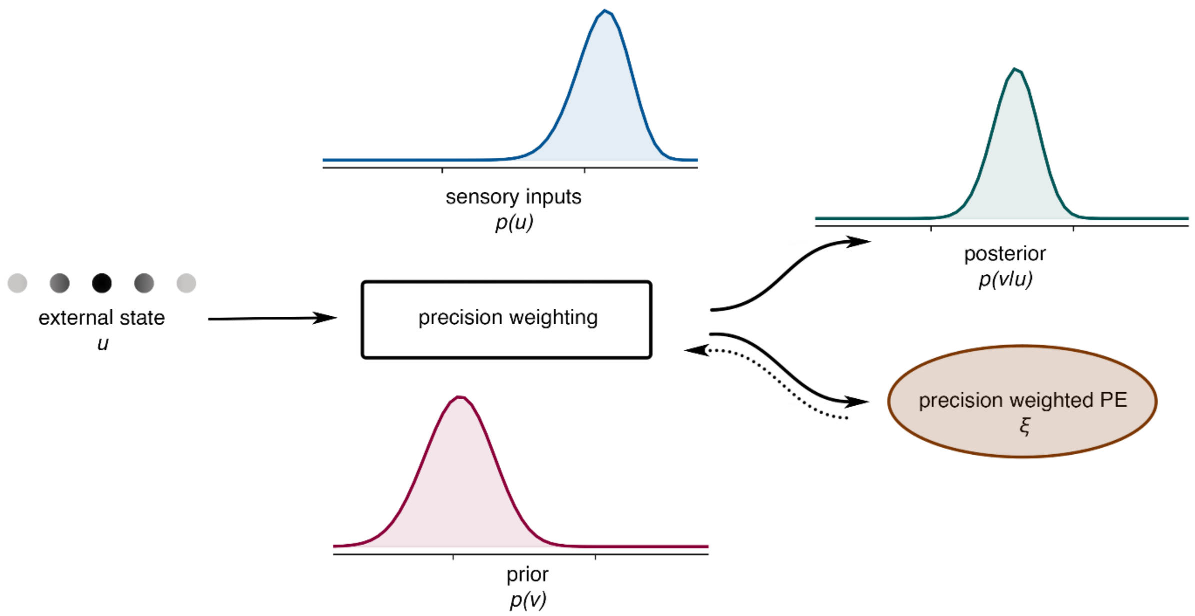

Figure 2: A simplified Bayesian updating scheme. The location (***v***) of a moving dot is inferred based on its luminance (***u***). During precision weighting, sensory inputs and prior predictions are combined with respect to their precision, resulting in a posterior (***p(v|u)***) and a precision-weighted prediction error (***ξ= Π(ε)***). In PP theories of affective experience, affective states result from current PE rates. The central hypothesis of this thesis is represented by the dotted line: PE, and therefore affective experience, could influence the weight that is ascribed to sensory inputs versus prior predictions during precision weighting. Further, the studies rest on the assumption that not only the PE arising from the current percept, but also that from previous percepts could affect PW. Note, that this scheme is highly simplified. It does not describe the temporal as well as the the hierarchical dynamics of this updating process. It also does not include processes of PEM like attention and action. For a comprehensible introduction into the differential equations of PP see Millidge et al. (2021).

central hypothesis of this dissertation, concerning the influence of affective state on visual perception: the balance of how much weight is ascribed to priors as opposed to sensory evidence in visual perception was assumed to vary with affective state. More specifically, negative valence was hypothesized to be associated with less reliance on prior knowledge and expectations.

Importantly, this proposed mechanism (a change of PW parameters through affective state) should be differentiated from another possible route of affective experience influencing visual perception, which is through modification of the content of priors (De Lange et al., 2018). Herein, an affective stimulus (e.g., a scowling face) could result in heightened attention towards it and update the possibility that the observer ascribes to the same or a similar event happening in a similar context. Given this update, the interpretation of any subsequent ambiguous stimulus (e.g., a shortly presented neutral face) could be shifted in the direction of the initial stimulus. Note, that this mechanism (prior modification) is in principle independent of affective valence and could be observed in any setup in which a sensory ambiguous stimulus is interpreted on the basis of prior knowledge (De Lange et al., 2018). Affect in this scenario would thus incidentally accompany a modification of subjective experience and not causally initiate it, as would be the case if affect were to change the weight of PW parameters. To distinguish both mechanisms experimentally, it would be important to render the stimuli that are to be evaluated as affectively neutral as possible. Further, in a mood induction paradigm, affect should be manipulated in a way that is semantically distant to the stimuli to be evaluated (e.g., if the response variable consists of participants' valence ratings of neutral faces, then faces should be avoided as mood induction stimuli).

There is an ongoing debate about how to best operationalize and measure visual PW in experimental tasks (Cretenoud et al., 2019, 2021; Tulver, 2019; Tulver et al., 2019). Accordingly, there is a wide variety in approaches that have been used previously to quantify PW (for an elaborated discussion on this, see section 4.2). In addition to this inconsistency in measuring approaches, only a few empirical studies are available to evaluate the hypothesis that state affect could shift the reliance on perceptual priors. Sheppard and Pettigrew (2006) showed that positive state affect correlated strongly (r=.80) with the time participants reported perceiving a coherent single pattern compared to two separate but overlaid line arrangements in a plaid motion rivalry task. This kind of stimulus can be considered bistable, and alternation rates were shown to strongly correlate with alternation rates in a binocular rivalry task (Sheppard & Pettigrew, 2006). PP accounts of bistability typically consider a change of perceived content as a specific case of PW (Hohwy et al., 2008; Weilnhammer et al., 2017). These findings therefore suggest that positive affect induces a bias towards a specific interpretation of the bistable stimulus, rendering it less susceptible to change due to accumulating contrary sensory evidence. However, it should be noted that the authors interpreted their findings in terms of lateralized differences in neuronal activity between both hemispheres, which has been associated with both affect and biased perception in plaid motion rivalry. Additionally, this result was limited to a small sample size of ten subjects and has not been replicated to the best of the author's knowledge.

Wilbertz et al. (2014) have further demonstrated that previously affectively neutral visual stimuli (Gabor patches of different orientations) dominated subjective perception during binocular rivalry after they had been tied to positive outcomes in a reward learning task. These results show that the valence of a stimulus (as opposed to its low-level features) can influence its stability, i.e., the threshold for competing sensory information to become dominant during binocular rivalry. However, as the authors note, this effect was likely mediated by attention, and it is generally in line with several studies showing that the affective valence of a stimulus significantly influences attentional engagement with it (Leite et al., 2012; Vogt et al., 2008) which in turn can elevate dominance duration during binocular rivalry (Hancock & Andrews, 2007). Moreover, affect in this study was elicited through the perceived visual stimulus itself, requiring at least partially completed perceptual processing of it in order to influence further affective and perceptual processing.

Further hypotheses can be derived about the potential role of affective traits in visual perception. As described in the previous section, several PP models of depressiveness unanimously characterize it in terms of strong and long-lasting prior assumptions about the valence of future situations (Chekroud, 2015; Clark et al., 2018; Kube & Rozenkrantz, 2020). Anxiety on the other hand has been described as either a marker of high uncertainty in prior predictions (Clark et al., 2018) or as predicting uncertainty (i.e., negative valence) of future events with high precision (McGovern et al., 2022). Concerning the clinically relevant expressions of depressiveness and anxiety, both disorders can be described in terms of behavioral and thought patterns that are resistant to change even in the face of contrary evidence (Kube & Rozenkrantz, 2020). It could thus be assumed, that stronger expressions of stable affective tendencies like depressiveness or anxiety are accompanied by stronger reliance on prior expectations compared to sensory evidence.

Browning et al. (2015) demonstrated that individuals with high trait anxiety had difficulties adapting to elevated volatility in a reward learning task, suggesting a bias towards previously learned contingencies. Although these findings point to a link between trait anxiety and higher reliance on prior knowledge and a disregard of contrary evidence, it remains unclear whether this general pattern of altered belief updating can be extended to low-level perception of affectively neutral visual stimuli. Jia et al. (2020) studied alternation rates during binocular rivalry of affectively neutral stimuli in two samples of patients with either generalized anxiety disorder (GAD) or major depression, compared to healthy controls. They found significantly elevated alternation rates in the GAD sample and significantly lowered rates in the depression sample. This can be interpreted as supporting evidence for the differentiation between the two illnesses in terms of their levels of prior precision, with elevated prior precision in depression and attenuated prior precision in anxiety (see section 2.3). However, both illnesses are accompanied by severe alterations of executive functioning and psychomotor responsiveness, potentially influencing response behavior independent from perceptual experience during the task (Iverson, 2004; Olatunji et al., 2011).

In summary, there are theoretical and empirical indicators that suggest that affective variables may have a causal role in visual perception through the modification of PW parameters. According to PP theories of emotional experience, state affect signals the need to change PW parameters in order to achieve long-term reduction of PE. If applied to perceptual inference, negative affect could result in a temporary shift towards a greater reliance on sensory data compared to prior expectations. In planning the dissertation studies, it was therefore hypothesized that negative state affect would be associated with a down weighting of prior information relative to sensory evidence. Affective traits, on the other hand, have been conceptualized differently in the literature. Some authors (e.g., Kube & Rozenkrantz, 2021) characterize affective traits generally as stable tendencies in which individuals do not appropriately integrate new information into pre-existing beliefs. Others attribute different patterns of belief updating to different forms of affective traits (Chekroud, 2015; Clark et al., 2018; McGovern et al., 2022). Given these somewhat conflicting conceptions, no specific a priori hypotheses were formulated regarding the specific role of different forms of affective traits in perceptual PW. The three papers in this dissertation explore various aspects of affective states and traits and their potential influence on visual perception. The following section summarizes the papers and their main implications for the idea that affective variables can influence visual perception through a change in PW parameters.

3. Summary of the Dissertation Studies

In this chapter, I will summarize the three dissertation studies and discuss their implications.

3.1 Trait Anxiety is Linked to Increased Usage of Priors in a Perceptual Decision Making Task

Affective traits such as anxiety, depressiveness or hypomania have been described in PP as stable tendencies to predict the valence (i.e., predictability and controllability) of future situations with high precision (Chekroud, 2015; McGovern et al., 2021). Trait anxiety specifically has been conceptualized as learned uncertainty, i.e., expecting low predictability with high precision (McGovern et al., 2021). Empirical evidence for this hypothesis partly comes from mood congruency effects, such as the finding that fear-related distractors yielded higher influence on individuals with high trait anxiety (Salahub & Emrich, 2020). Additionally, the hypothesis is supported by the finding that individuals with high trait anxiety are slower in adapting to changing environmental volatility in a reward contingency learning task (Browning et al., 2015). These results suggest that trait anxiety is characterized by aberrations in belief updating, resulting in preferential reliance on prior expectations over new, conflicting sensory evidence. However, considering both lines of evidence, it remains unclear whether this predisposition is limited to affective stimuli (fear-related or reward-signaling) and whether its influence extends to low-level contents of visual perception.

This preregistered study aimed to measure whether and to what extent participants' trait anxiety levels relate to how strongly they rely on prior predictions compared to available sensory evidence in a visual motion direction detection task. We therefore asked healthy participants (n=117) to judge the perceived motion direction in cued random dot kinematograms (RDKs). Cues could either be predictive (an arrow pointing either to the left or right) or neutral (an arrow pointing in both directions). Participants were informed that predictive cues depicted the correct motion direction in about 75% of all trials. Sensory uncertainty was manipulated by varying motion coherence levels at three approximated difficulty thresholds. These thresholds were individually determined by a staircase procedure, intended to result in accuracy levels of about 60%, 75%, and 90%. Trait anxiety levels were measured before the start of the experimental task using the Spielberger State-Trait Anxiety Inventory (STAI).

Results showed that trait anxiety was not associated with task performance, age or gender. However, individuals with higher trait anxiety values did show a higher usage of cues in the task. Contrary to prior expectations, this effect was not mediated by the degree of sensory uncertainty, i.e., the effect size did not significantly differ between the three motion coherence levels.

This finding demonstrated the presence of the hypothesized relationship between trait anxiety and reliance on prior expectations in a visual task involving affectively neutral motion stimuli. Although the study was limited to measuring the specific influence of anxiety, the results provide partial support for the conceptualization of affective traits in general as tendencies to place higher reliance on priors compared to sensory evidence. However, it can be questioned whether what was observed in this study is an adequate measure of perceptual precision weighting, i.e., whether relying on a cue in a two-alternative forced choice (2AFC) task can be equated with higher weighting of prior expectations in perceptual inference. This question is also directly tied to a common concern in CP studies, that is, whether response behavior directly reflects perceptual experience or whether what is observed is rather a reflection of post-perceptual judgment processes. In a previous study using a very similar task, de Lange et al. (2013) were able to show that pre-stimulus motion cues biased not only behavioral responses, but also neural activity, measured via magnetoencephalography (MEG), of the visual cortex prior and during stimulus exposure in the cue-congruent direction. It is thus likely that the influence of pre-stimulus cues in this task can be seen as an adequate method to induce prior expectations that directly influence processing of sensory information and therefore subjective perception.

This study therefore supports the idea that affective traits, specifically trait anxiety, can influence visual perception through a change in PW parameters. It adds to this idea by showing that higher reliance on priors in individuals with high trait anxiety is not limited to higher order beliefs about the world, but also extends to perceptual precision weighting. Additionally, this pattern was found in affectively neutral motion cues, suggesting that high prior precision is not limited to the valence of future situations (as suggested by Clark et al.,

2018) but rather constitutes a general strategy for reducing uncertainty across different situations. To extend these findings to other tasks of visual perception and to further explore the specific role of affective states, a second study was conducted which will be described in the following paragraph.

3.2 Negative Affect Impedes Perceptual Filling-In in the Uniformity Illusion

Valence of state affect has been hypothesized to originate from current estimates of PE reduction rates (Joffily & Coricelli, 2013; Van de Cruys, 2017). It has further been hypothesized, that this serves as an incentive to initiate a change of PEM strategies of belief updating and action sampling (Hesp et al., 2021). As PW within perceptual inference can be considered as a mechanism of PEM, it remains an open question whether central parameters of this mechanism could be altered through affective state. Prior studies have shown that positive compared to negative affect is associated with higher usage of prior knowledge in social judgement tasks (i.e., stereotyping; Bodenhausen, et al., 1994; Sheppard, et al., 1994). The aim of this study was thus to investigate whether similar effects can be found in a perceptual task and to test whether perceptual priors are more readily used if induced affect is positive compared to negative.

Visual PW in this study was operationalized by the probability and onset of occurrence of the uniformity illusion. In this task, participants were asked to fixate the center of an optical pattern which was surrounded by a similar peripheral pattern that showed slight differences to the center (e.g., in brightness). These differences were then experienced to dissipate as illusionary perception took effect (perceptual filling-in). This effect has been reasoned to result from a prior for uniformity of the visual field that is gaining dominance over low-precision sensory information from extrafoveal areas (Otten et al., 2017; Suárez-Pinilla et al., 2018). Due to generally lower visual acuity in this area, it has been proposed that it is especially susceptible to stronger influence of perceptual priors and therefore particularly suitable for studying effects of extraperceptual factors, such as affective state, on perceptual PW (Lammers et al., 2017).

Probability of uniformity and the time it took to occur in the stimulus were considered as a proxy measure for the influence of priors on perception. Positive and negative affect were induced before and during stimulus presentation via an auditory mood induction paradigm. To induce positive affect, harmonic pieces of music were played. To induce negative affect, while keeping low level features (such as pitch, or volume) constant, the same stimuli were scrambled (effectively rendering them as noise) and played to the participants. To rule out potential confounding influences of induced affect on non-perceptual factors that could potentially bias response behavior (e.g., higher physiological arousal leading to faster reaction times), we compared occurrence rates and onset times to the respective measures in a control condition. In this control condition, perceptual filling-in was simulated by fading-in of an actual uniform stimulus, so that experience of uniformity was the veridical percept but subjectively indistinguishable from illusionary perception. Trials were aborted if participants did not report uniformity within ten seconds after the stimulus fade-in was completed. The experiment was run in a student sample of n = 50. Sample size, hypotheses, and main statistical analyses were all preregistered.

Results showed a significantly higher probability of participants reporting to perceive uniformity in illusionary trials when they were in a positive, compared to a negative affective state. This effect was not present within the control condition, ruling out an influence of affect on general response behavior. However, there was no significant difference in reported onset times between the two mood conditions in illusionary trials. This was likely due to a lack of statistical power, since trials in which perceptual filling-in was especially impeded, the occurrence of uniformity was naturally less likely to be reported within the given time constraint. Since these trials were excluded from the onset time analysis, this pattern can likely be attributed to the absence of trials from the analyses in which the effect was presumably most present. If onset times for these excluded trials were set to the maximum trial length of ten seconds, the analysis showed significantly longer onset times when affective valence was negative. Note, that this is a common methodological approach in studies that rely on slow perceptual processes and in which, because of that, a significant proportion of the trials would otherwise have to be excluded (e.g., Stein et al., 2011, 2012).

These findings emphasize the significant influence of affect on the contents of visual perception. Perceptual filling-in, i.e., the enrichment of low-precision sensory perceptual contents with prior expectations on how these areas would presumably look if they were viewed foveally, was significantly less likely when participants were in a negative affective state. Thus, negative state affect likely signaled the necessity to base perceptual inference on less error-prone sensory evidence instead of perceptual priors. Since this influence of affect was not present in the control condition, this pattern was not due to a general influence of affect on response behavior or other non-perceptual factors. This finding supported the linking of state affect with alterations of PW and a concomitant alteration of subjectively experienced visual content. By way of conclusion, it provided evidence for the affective realism hypothesis and serves as a potential example of CP of vision through affect. To explore potentially confounding influences of the mood induction, a further study was planned to replicate the finding with respect to baseline state affect and in a different visual task.

3.3 Linking State and Trait Affect with Perceptual Stability During Binocular Rivalry

There are important differences in the conceptualization of affective states and traits within predictive coding models of emotional processing. Traits, such as depressiveness and anxiety, have been conceived as stable tendencies within the individual to have high certainty (i.e., precision) in prior assumptions, rendering these assumptions less prone to change through contrary evidence (Kube & Rozenkrantz, 2020). Affective states on the other hand have been assumed to serve as an indicator of momentary PE rates, providing a motivational basis for the organism to optimize current PEM strategies (Joffily & Coricelli, 2013). More specifically, negative state affect has been linked to less reliance on prior knowledge, both in high-level processing of social information such as stereotyping (Chartrand et al., 2006) but also in low-level perceptual processing (Study 2). Both, affective states and traits could therefore provide individual and somewhat conflicting contributions to PW. The exact nature of the relationship remains to be empirically explored.

One promising approach of measuring the potentially differential contributions of affective states and traits is bistable perception and specifically binocular rivalry. When current sensory inputs allow for more than one plausible interpretation (either due to stimulus ambiguity or due to different stimuli being presented separately to both eyes), one typically experiences alternations between the possible percepts over time. These alternations are typically interpreted in terms of an iterative process: the subjective percept, representing the current prior (i.e., the most likely interpretation of current sensory data), is challenged by an alternative interpretation, leading to gradually accumulating PE over time. Once PE precision is sufficiently high, the subjective percept switches to the alternative stimulus, which now becomes the most likely cause of sensory data and therefore the new prior (Weilnhammer et al., 2017, 2021). Putting higher weight on priors in this task will thus lead to higher perceptual stability. This stability can be operationalized as average phase durations but also as bias towards a particular variant of the two conflicting alternatives (dominance ratio).

Both measures (phase durations and dominance ratios) have been studied, often treated as independent measures, with respect to affective states and traits. Jia et al. (2020) found longer phase durations (i.e., stronger influence of priors) in participants with depression but shorter ones for patients with generalized anxiety disorder. Law et al. (2017) found trait anxiety and depressiveness both to be weakly positively correlated with average phase duration, partly contradicting the findings of Jia et al. (2020) with respect to anxiety. Law et al. (2017) also found no association of state affect with phase durations or dominance ratios. In contrast, Sheppard & Pettigrew (2006) found stimulus preference (i.e., stronger prior use) to positively correlate with positive affect. These inconclusive and partly contradictory findings were addressed in this preregistered study.

Participants (N=50) were exposed to two sets of affectively neutral stimuli in a binocular rivalry task. The first set of stimuli consisted of two Gabor patches of different orientations. The second set consisted of a male face that was depicted upright on one side of the screen and tilted upside down on the other side. Participants were asked to report perceptual alternations via button press. Button allocation and stimulus placement were randomized across trials. Prior to the task, negative affective traits and states were measured via questionnaires (PHQ-9, STAI, PANAS). In addition, affective state was manipulated through listening to 30 seconds of music (harmonic, noisy or no music; see Study 2) prior to each trial, resulting in three valence conditions (positive, negative and neutral). PW variables were operationalized as phase durations (longer durations equal stronger influence of priors) and dominance ratios (higher deviance from .5 indicated stronger influence of priors). Considering the findings of previous studies, we hypothesized positive state affect as well as trait depressiveness to be associated with higher prior use. We were agnostic on the role of trait anxiety, given the mixed pattern of previous findings on this topic (Jia et al., 2020; Kraus et al., 2021; Law et al., 2017).

Results indicated an influence of baseline positive affect on phase durations, with positive affect leading to longer phase durations compared to negative or neutral affect. This is suggestive of a stronger influence of priors and thus confirmed our preregistered hypothesis. Importantly, this association was not found when analyzing the effects of the mood induction. To further explore potential confounds with respect to the mood induction procedure, we carried out an additional exploratory analysis, that was limited to the first block of the experiment, thus ruling out carryover effects of induced mood states on to the next blocks. We still found no effect of induced state affect on phase durations, but dominance ratios indicated lower reliance on priors when induced mood was negative. We did not find any significant relationship between the measured affective traits and perceptual stability.

Overall, this pattern supports, with some limitations, a conceptualization of affective state valence as a corollary of PW, as it is conceptualized in binocular rivalry. Specifically, positive valence led to longer phase durations (i.e., higher prior reliance) and negative valence to attenuated bias in dominance ratios (i.e., lower prior reliance). However, given the mentioned inconsistencies (e.g., that only baseline but not induced positive state affect was related to phase durations) as well as methodological concerns (type I error inflation through the treatment of related outcome variables as independent), the interpretation and generalization of these findings should be carried out with caution.

Concerning the particular role of affective traits, we did not find a relationship between phase durations and our measures of trait affect. This runs contrary to previous findings in this domain. In study 1, trait anxiety was found to be associated with higher reliance on priors in a motion direction detection task. However, it is unclear whether the different operationalizations of perceptual PW in the two studies rely on the same underlying neural mechanism (see Section 4.2). Jia et al. (2020) found strong diverging effects of anxiety and depressiveness on phase duration, albeit in patient groups (major depression vs. generalized anxiety disorders). The study of Jia et al. did further not control for important confounding variables which have been shown to be altered in those patient groups, such as psychomotor agitation (Etkin et al., 2022; Walther & Morrens, 2015). Law et al. (2017) found that depressiveness and trait anxiety were both associated with lower phase durations in healthy participants. However, the observed effects were generally small and only found in particular stimulus sets and not others. In summary, the pattern of effects concerning the role of affective traits and their potential role in bistable perception remains yet unclear. A potential source of heterogeneity among the different studies is the use of different measures to operationalize perceptual stability in binocular rivalry.

To probe the relationship between both measures used in this study, we found a strong correlation (r=.54) between phase durations and dominance ratio in an exploratory analysis. This result is supportive of the notion that both measures indeed relate to a common underlying tendency within individuals to balance precision of priors and sensory evidence during binocular rivalry. However, it also calls into question the commonly used methodology of differentiating between both measures and treating them as independent variables in separate statistical analyses. Future research should attempt to extract a common factor underlying different measures of perceptual stability during binocular rivalry and relate individual values on that factor to measures of state and trait affectivity.

4. General Discussion

The notion of affective realism states that affective variables fundamentally shape our perception of the world. However, proponents of the cognitive impenetrability of perception notion have laid out a central argument against the affective realism approach to interpreting the broad range of findings that relate affective variables with changes in measures of perception (Firestone & Scholl, 2016; Pylyshyn, 1999). In this argument, perception serves the broad purpose of informing the observer as accurately as possible about changes in the environment. Perceptual processing that is dependent upon observer-based variables such as affect would defeat this purpose, as it would somewhat disconnect subjective perceptual experience from actual changes in the environment. However, according to PP models of visual perception as well as of affective states and traits, affective variables can indeed influence what we see. By determining the amount of PE that is experienced at any given moment in time, affective valence could shift the degree of reliance on prior knowledge and sensory evidence, respectively. This could provide an adaptive mechanism for shifting PW parameters in response to current PE rates and serve as an effective strategy of prediction error minimization. The aim of this thesis was to investigate whether such a link between affective states and traits and visual PW can be demonstrated empirically.

All three studies in this dissertation have found results that are indicative of affective variables being closely linked to parameters of visual precision weighting. Study 1 found that trait anxiety is positively correlated with the use of a predictive cue in a visual motion direction detection task. Study 2 found that induced positive, compared to negative, state affect led to higher rates of perceptual filling-in, indicating a stronger influence of prior knowledge on visual perception during positive affect. In study 3, we found positive affective valence to be associated with longer phase durations and thus stronger use of perceptual prior knowledge during binocular rivalry. However, the findings described above were partly inconclusive, and all three studies contained important limitations that must be considered.

4.2 Measuring Precision Weighting

One way of how the core idea of affective realism within a PP framework could be implemented, is through a shift in PW parameters that varies with affective state (i.e., rates of PE). In order to assess whether such a shift has actually occurred, all three dissertation studies attempted to quantify the parameters of PW and in turn relate them to measures of affective states and traits. However, one can question whether the described tasks represent valid measures of PW in the visual domain. Therefore, the following section focuses on the construct itself, difficulties in operationalizing it, and the implications that result from those difficulties for the interpretation of the findings of the three studies.

Precision weighting, i.e., the comparative weighting of precision estimates of priors and sensory evidence to determine the most likely cause of sensory signals, has been posited as a central mechanism of Bayesian inference within the PP account of perception (Bastos et al., 2012; Friston, 2005; Rao & Ballard, 1999). Since PW is assumed to be altered in some PP models of mental illnesses (e.g., Clark et al., 2018; Sterzer et al., 2018; Van de Cruys et al., 2014), there have been several attempts to experimentally measure it in individuals. Many of these studies aimed to quantify the degree to which priors can influence perception and related this measure to personality traits, the effect of specific interventions or symptom severity in clinical populations. For instance, Van de Cruys et al. (2018) studied the advantage that prior knowledge of the original stimulus provided in recognizing the same stimuli when they were rendered nearly unrecognizable (so called Mooney pictures) in autistic participants and healthy controls. Adams et al. (2004) measured the degree to which the general assumption that light usually comes from above ('light-from-above' prior) altered the likelihood of an ambiguous stimulus being perceived as illuminated from below or above and whether this could be changed through training. Aru et al. (2018) studied the influence of priors on perception by manipulating the probability with which a square stimulus is expected by participants, which was correlated to the probability of perceiving the stimulus even when it was absent. They related this measure of illusionary perception to autistic traits. Considering this broad range of experimental tasks that have been used to measure PW, one can conclude that there is no established consensus over how to best assess parameters of PW empirically.

This diversity of measures has sparked some debate over whether there is in fact a stable tendency within individuals to rely more strongly on prior knowledge and expectations or on new sensory evidence. In a recent multi-paradigm approach, Tulver et al. (2019) conducted exploratory factor analyses of participants' scores on five different visual tasks that have previously been used to quantify the effects of priors on perception. They did not find supportive evidence for the notion of a global, trait-like tendency to either rely on priors or sensory information across different tasks. Rather, they found a two-factor structure, which they interpret as reflecting individual differences concerning the influence of priors at different levels of the visual processing hierarchy. They state that this supports the notion that: "*[...] mechanisms underlying the effects of priors likely originate from several independent sources and that it is important to consider the role of specific tasks and stimuli more carefully when reporting effects of priors on perception*". This conclusion thus questions a premise that often underlies studies that attempt to experimentally operationalize PW, namely that a single task could provide an accurate measure of the reliance on priors versus sensory inputs throughout all levels of perceptual processing.

Differentiating between PW parameters at different levels of the processing hierarchy, as proposed by Tulver et al. (2019), has been suggested previously in different PP accounts of mental illness. For instance, Sterzer et al. (2018) proposed diverging influences of priors in psychosis, where low influence of priors in low-level perceptual processing would result in unrestricted noisy sensory signals and therefore hallucinations, whereas strong influence of priors at higher levels of cognition would cause strong, imperturbable beliefs (i.e., delusions). Stuke et al. (2019) tried to empirically validate this conception by conducting two highly similar decision making tasks, one perceptual and one cognitive, in which the influence of prior information on the current decision could be quantified. They indeed found delusion proneness correlated with lower reliance on priors in the perceptual task. However, they did not find a significant association of delusion proneness with prior use in the cognitive task. In fact, delusion proneness was negatively related to prior use in the same task in another study of the same group (Stuke et al., 2017). Thus, recent studies more and more build upon the premise that PW parameters may vary significantly within individuals depending on the level of processing.

However, there is insufficient empirical validation of this premise, let alone a guideline on how to best assess PW parameters at different levels of processing. Future research should address this concern by conducting a wide variety of tasks, ranging from low-level perception (such as brightness in the 'light-from-above' prior) to high-level cognitive reasoning, in a large sample and testing whether the implied factorial structure can be empirically confirmed. Building on such a body of work, one could further differentiate whether the influence of affective states and traits on PW in vision is restricted to only particular levels of processing. For instance, one could hypothesize that affective traits are most likely to be coupled to PW only at late stages of processing (Raftopoulos, 2014). This would be in line with the hypothesis that CP is possible only in late, but not early, stages of stimulus processing (Pylyshyn, 1999; Raftopoulos, 2019; Voltolini, 2020).

Considering that none of the three dissertation studies included neuroimaging data, it is only possible to speculate about where the respective phenomena originate within the visual processing hierarchy. Taking into account the broad variety of visual tasks that have been conducted in the different dissertation studies, as well as previous experiments that attempted to localize their neural underpinnings (e.g., de Lange et al., 2013; Lu et al., 2018; Suárez-Pinilla et al., 2018), a wide range of brain regions will have been involved in the decoding of the presented stimuli. Importantly, not every region that is somehow involved in stimulus processing is necessarily relevant to the question of PW measurement. It remains an open question of where, when and how exactly PW takes place on a neuronal basis.

In the case of binocular rivalry, PW has been conceptualized as a form of perceptual conflict resolution, which occurs when priors and sensory evidence diverge (Hohwy et al., 2008). Such a conflict could for instance arise at an early stage of stimulus processing where PE signals are accumulated and then passed on to higher levels of processing. Some authors have argued that it is at these higher levels where conflict resolution presumably takes place, and the resulting information in turn modulates activity in sensory areas via feedback connections (Qian et al., 2018; Weilnhammer, Fritsch, et al., 2021). Thus, a potential neural mechanism of how affect could influence perceptual PW is through the modulation of areas that are involved in the resolution of perceptual conflict (e.g., inferior frontal cortex (IFG)) by regions that are typically associated with core affect, such as the limbic system. For a detailed review on this topic and the involved brain regions, see Ray & Zald (2012). Importantly, it is unclear whether this mechanism that has been asserted to underlie binocular rivalry is also involved in other forms of perceptual conflict that are typically used as examples of perceptual PW.

Notably, all phenomena that have been described in the three dissertation studies rely on basic processes of visual perception, such as motion detection or resolving the discrepancy between two different inputs of the two eyes. Furthermore, all tasks have been previously used in studies that interpreted the outcomes in terms of the weight that is ascribed to priors and sensory inputs respectively in low-level vision (e.g., Otten et al., 2017; Stuke et al., 2019; Weilnhammer, Chikermane, et al., 2021). Thus, even if several questions on the neural basis and the experimental measurement of PW remain to be elucidated, the findings presented here provide a valuable source in the search for experimental paradigms that assess PW in individuals as well as potential extraperceptual processes that influence PW.

In conclusion, it appears that the modulation of PW through affect is a feasible and plausible mechanism underlying the observed effects. However, given the lack of scientific consensus over appropriate experimental measures of PW, it becomes necessary to consider alternative explanations of the effects observed in the three dissertation studies.

4.1 Measuring Subjective Perception

As outlined in section 2, a significant part of the debate over CP concerns the issue of measuring subjective perceptual experience. This issue is often exemplified by a distinction between perception and judgment (e.g., Firestone & Scholl (2015)). In this classical distinction, perception is considered to be informed by sensory evidence, while judgment is informed by the contents of perception as well as prior knowledge. Therefore, judgment can only ever occur after perceptual processing has identified a stimulus to a degree that enables its further evaluation. In a typical perceptual task, a given stimulus is presented for a particular time span after which participants are asked to make a judgment on a low-level feature of it (e.g., the color of a flower). Importantly, as Firestone & Scholl (2015) pointed out, this judgment could also be made on any other stimulus-related feature that would typically not be considered to be of a perceptual nature (e.g., the assumed region of origin of the flower). Thus, demonstrating that any observer-based variable (such as affective valence) can explain variance in perceptual ratings cannot be considered as conclusive evidence for CP, as the same pattern could stem from an influence of affect on high-level, deliberative judgments.

To address this concern, Firestone & Scholl (2015) proposed an "overgeneralization test": this test consists of showing that any extraperceptual observer-based variable has influence not only on perceptual ratings, but also generalizes to clearly non-perceptual constructs. As an example they take a prior study design that demonstrated that conservatives judge the skin tone of Barack Obama to be darker than liberals do (Caruso et al., 2009). They extend this task and show that conservatives also judge a picture of Obama showing him with devil's horns to be more representative of him as one with a halo. The authors thus conclude, that the initially observed finding is best explained by political affiliation affecting judgment processes rather than subjective perception of skin tone. One could demonstrate genuine CP by showing that a participants' descriptions of a stimulus are selectively altered for low-level perceptual ratings but not for any non-perceptual judgment measure. However, one can come up with a scenario in which such a pattern would occur but which would not be considered a clear-cut case of CP. For instance, consider a study in which the affective state of participants would alter their judgment of the colorfulness of a flower, but it would not influence their judgment of the supposed place of origin. Such a distinction could likely stem from affective status selectively influencing some categories of judgments but not others. Thus, the overgeneralization test might falsely suggest the occurrence of CP, even if subjective perceptual experience remains unchanged. However, depending on the particular task being conducted, it appears useful to consider potential control conditions and sanity checks to ensure that the observed responses reflect actual perceptual experience rather than post-perceptual judgments. In the three studies of this dissertation, we used different experimental paradigms to address this general concern over what level of processing is potentially affected by affective states and traits.

In study 1, participants judged the motion direction of a RDK after they received a predictive arrow cue that indicated the most likely direction of the RDK. One could argue that the predictive arrow merely influenced a high-level cognitive judgement of the participants' best guess over what the most likely direction would be. In this scenario, the results would not be suggestive of altered perceptual PW, but would be limited to showing that more anxious individuals were more susceptible to this kind of external information. A useful experimental condition to control for such post-perceptual effects would have been to present the arrow after the RDK. However, the presence of both effects (altered perceptual PW and post-perceptual cognitive judgements) is not mutually exclusive and both could be present in high trait anxious individuals. Furthermore, de Lange et al. (2013), in a very similar experimental design, found that predictive auditory direction cues altered pre-stimulus MEG activity in the visual cortex that correlated with post-stimulus motion direction judgements. Even if no predictive cue was presented, pre-stimulus activity correlated significantly with the subsequent direction choice. This effect was stronger for trials with low motion coherence (i.e., low precision sensory evidence). It is therefore likely that what was observed in study 1 was indeed a modification of prior expectations through the arrow cue, which made perception more likely to shift towards the expected direction. Further validation for this interpretation of the findings could be gathered by replicating the design in an MEG setup, measuring whether trait anxiety correlates with pre-stimulus MEG activity that predicts subsequent motion direction choice. However, it is important to note that even such a finding would not be unequivocal proof that it was indeed subjective perception that was altered. Participants could still have deliberately committed to a particular motion direction prior to stimulus onset, i.e., have made a non-perceptual judgement.

In the second study, participants were asked to report the experience of a visual illusion, indicating the likelihood and speed at which perceptual filling-in occurred. These illusions provide an interesting case for the measurement of subjective perception, as cognitive judgments of stimulus characteristics are somewhat decoupled from one's perceptual experience of it. To correct for potential influences of induced affective valence on response behavior, we included a perceptually similar control condition in the study. In this condition, the endogenous filling-in of the periphery was mimicked by actual changes depicted on the monitor. By showing that induced affect did not influence response behavior in the control condition, we were able to argue that it was not response behavior itself that was altered (e.g., faster button presses due to higher arousal in the negative condition). However, it is possible that participants indirectly noticed differences between the conditions, even though they were generally not aware of them. For instance, during illusory perception, participants were significantly less likely to report uniformity than in the control condition, since uniformity did not rely on perceptual filling-in in the control condition. Therefore, an alternative interpretation of the findings could be that affective valence differentially impacted the decision threshold to report uniformity in the case of an ambiguous percept. When uniformity was unambiguous, however (either due to strong illusory perception or because it was the veridical percept), this threshold remained unaffected. To address this objection, one could modify the control condition so that the degree of uniformity varied from trial to trial, rather than complete uniformity being depicted in all control trials. However, if induced affect indeed makes perceptual filling-in more likely, this effect would also be present in the control condition in trials where differences between the center and periphery, although gradually reduced, are still present. It would thus become difficult to differentiate between veridical and illusionary uniformity in this scenario. Another way of ensuring that the observed effect was indeed of a perceptual nature, would be to measure the experience of uniformity through a no-report procedure. For that, one would first have to find a distinct psychophysical corollary of the experience of uniformity (e.g., pupil dilation or altered BOLD signal in a particular brain region) that is unaffected by emotional experience. For instance, DeWeerd et al. (1995) measured single cell activity in extrastriate neurons whose activity accelerated during perceptual filling-in until it plateaued at a rate that was similar to when the complete stimulus was presented and no filling-in took place. By demonstrating that induced affective valence would alter the probability of experiencing uniformity on such a no-report measure would provide additional evidence that the effect is indeed attributable to changes in perceptual processing.

In the third study, participants performed a binocular rivalry task in which their perceptual stability was related to measures of affective state. Here too, one can question whether the results are attributable to actual changes in subjective perception or to a shifting of behavioral reporting thresholds. For instance, one could argue that affect altered the threshold to report a clear percept although the actual perception was still mixed, leading to an inflation of reported changes of perception. However, given that the task in this study was of a continuous nature and typically several perceptual alternations were reported during one trial (as opposed to only one as in study 2), such effects should cancel out over the course of multiple consecutive alternations.

In conclusion, although there is room for debate on whether the described effects reflect genuine changes of perceptual experience, the three studies taken together are supportive of the notion that affective variables can change the contents of visual perception. As outlined in the introduction, the assumed mechanism for how such a change of perception could occur is through shifting the balance of PE parameters. The following section will focus on whether this can indeed be plausibly inferred from the reported findings.

4.3 Alternative Explanations of the Observed Effects

The effects that have been described in the three dissertations studies have been interpreted to result from an affect induced shift of PW parameters. As such a shift would be considered as an example of the CP of visual perception, it appears useful to refer to the broad discussion on this topic in the literature on CP in the search for alternative mechanisms to explain the observed effects. Cermeño-Aínsa (2021) summarized three general alternative mechanisms that have been used to explain empirical findings that have been brought forward as examples of CP. The first category are influences on post-perceptual judgement processes. Their potential occurrence as well as experimental precautions that have been taken in the dissertation studies to lower their influence have been discussed in section 4.1.

The second category Cermeño-Aínsa (2021) described are top-down effects *within* the perceptual processing hierarchy, i.e., information over the whole stimulus that causes a shift in the perceived low level features of the stimulus (e.g., the banana shape of a grey stimulus leading to it being perceived as slightly yellow). Given that such a shift would be caused by gathering of information within the visual system, functional encapsulation of information processing would remain intact. In the context of this thesis, this confound is functionally equivalent with what was referred to in section 2.4 as prior modification. Here, the content of prior expectations, and therefore the subjective experience of related stimuli, would vary as a function of affective states and traits. The last category of effects that Cermeño-Aínsa (2021) specified is modulation of attention. He argues that differences in locus of attention or speed of attention shifting would alter sensory inputs, but not the way with which they are processed or perceived. Given the various intricate interdependencies between affective states and traits and attention, this category appears especially important when considering alternative explanations for the effects described in the dissertation studies.

Importantly, all three categories are difficult to separate from one another in the assessment of specific examples of experimental studies that claim to demonstrate genuine effects of CP. For instance, in another study (unpublished data), participants were asked to judge the motion direction of a bistable rotating sphere stimulus. We found that participants reported the stimulus to spin rightwards for significantly longer time than leftwards when induced affective valence was positive compared to negative. This could be considered a direct effect of affective valence on motion perception. However, movements from the left to the right have been shown to be evaluated as more positive than movements to the left (Egizii et al., 2018; Milhau et al., 2013). The effect could thus be explained by positive affect modulating the probability with which a positive stimulus is predicted to occur. This would be comparable to effects of cuing (i.e., a preferential processing of stimuli that are expected) rather than to a global shift of PW parameters. Hence, all used stimuli should be evaluated with respect to their potential to elicit affective reactions in participants to rule out prior modification and attention shifting as mechanisms of action. In what follows, I will discuss the three paradigms (cued RDKs, UI, and binocular rivalry) and whether modulation of prior content or attention dynamics could potentially account for the effects that were observed.

In study 1, several participants reported motion direction detection in the RDK stimuli as inherently frustrating. Considering the high sensory uncertainty of the RDK stimuli (motion coherence was adjusted so that average accuracy levels were 25% above chance), it is conceivable that participants experienced them as inherently negative. Furthermore, trait anxiety has been associated with the construct of 'intolerance of uncertainty' (IU; Jensen et al., 2016). IU in turn has been shown to correlate with risk-averse decision-making and behavior that is expected to reduce uncertainty (Carleton et al., 2016; Jacoby et al., 2013; Jensen et al., 2016). Individuals with high trait anxiety could therefore have been inclined to avoid the source of uncertainty (the RDK stimulus) and could have diverted attention away from it. By way of compensation, they would have focused on the informational source that was about as reliable as the RDK but that comprised far less sensory uncertainty (the arrow cue). Such trade-offs of attentional resources could be studied with the help of event-related potentials (ERPs). In tasks with two or more consecutively presented stimuli, an often-observed pattern is that ERP markers of late attentional engagement (such as the P300 or the late positive potential (LPP)) are negatively correlated, i.e., that high engagement with a given stimulus predicts low engagement with the subsequent one (e.g., Weinberg & Hajcak, 2011; Zizlsperger et al., 2014). To test whether a comparable mechanism has contributed to the effect observed in study 1 (i.e., an attentional trade-off between engagement with the cue vs. the RDK), the design should be repeated with parallel EEG recordings. The relationship between cue and stimulus elicited ERPs could then be analyzed with respect to a potentially modulating role of trait anxiety. However, an attenuated ERP response to a stimulus caused by high attentional engagement with a previous stimulus has been reported to be accompanied by a slowing down of reaction times (e.g., Most et al., 2007; Weinberg & Hajcak, 2011). Therefore, if such a postulated attentional trade-off had occurred in study 1, one would expect trait anxiety to have been positively correlated with RTs. However, no significant association of RTs and trait anxiety was found in the analysis. Nevertheless, asymmetric attentional engagement with cues and RDK stimuli, varying as a function of trait anxiety, should not be ruled out as an alternative mechanism to explain the observed effect and further experiments controlling for that factor should be conducted.

Likewise, there are alternative ways of explaining the mechanism behind the effect found in study 2 (reduced perceptual filling-in when affective valence was negative), several of which are related to attention. Firstly, affective valence has consistently been associated with the breadth of attentional focus. Specifically, more positive affective states have been found to correlate with a wider scope of attention (Hüttermann & Memmert, 2015; Moriya & Nittono, 2011; Rowe et al., 2007; although see also Gable & Harmon-Jones, 2008) which experimentally translates to higher accessibility of peripherally presented information. To date, there have been no studies on the influence of attentional scope on the likelihood of perceptual filling-in in the UI. However, Levinson & Baillet (2022) found that greater border eccentricity (i.e., a wider center) was associated with a higher likelihood of perceptual filling-in as well as reduced onset times. Thus, with more conflicting sensory information available from the periphery, one would expect lower occurrence rates and longer onset times of illusionary uniformity. It would therefore be somewhat counterintuitive for a wider attentional scope to lead to enhanced perceptual filling-in in the UI. However, De Weerd et al. (2006) showed that selective attention towards a stimulus set (red or green discs placed randomly in a visual noise pattern) increased the probability of perceptual filling-in of stimuli in that set, replacing them with the noise pattern. Higher attention towards the periphery through a generally wider scope (induced by positive affect) could therefore increase the probability of perceptual filling-in of the periphery in this illusion, as found in study 2. One way to account for this potential confound would be to modify stimulus features (border eccentricity, shape and size of the center) to make perceptual filling-in of the center about as likely as perceptual filling-in of the periphery (see Levinson & Baillet, 2022). This way, a wider attentional scope should not necessarily lead to enhanced perceptual filling-in of the periphery. Another possibility would be to ask participants to explicitly attend to the periphery while maintaining foveal fixation at the center of the stimulus. If it is indeed attention drawn towards the periphery that mediates the speed of perceptual filling-in in the UI, then this intervention should cancel out the effects of the wider attentional scope that accompanies positive affect.

Another way in which attention could have influenced the results would be if there were different attention shifting dynamics present that varied with affective valence or arousal levels. Carver (2003) posits that positive affect generally serves as a sign that one could "attend something else". The often-reported broadening of attentional scope would then allow for a reorientation to stimuli outside of the current attentional focus. One could hypothesize, that this could be accompanied by generally altered rates of attention shifting, depending on the current mood state. As attentional focus has been shown to significantly influence the probability of perceptual filling-in (De Weerd et al., 2006), attentional shift rates could have similar effects. There appears to be only limited empirical research on whether attentional shifting varies with affective state. However, it is at least conceivable that affective states impact attentional shifting speed and must therefore be considered as a potential confound. To adjust for possible effects of attention shifting, experimental checks could be implemented to ensure fixed attentional engagement with the center of the stimulus (e.g., by having the color of the fixation cross change at random intervals and asking participants to count the changes). In addition to the distribution pattern of attention across the visual field, another confound could be the overall amount of attention that participants were directing towards the visual stimulus. Since the musical mood induction in this study was played during visual stimulus presentation, the mood induction stimuli could have functioned as auditory distractors, drawing away attentional resources and slowing down visual perception (Dunifon et al., 2016). Importantly, this would only be a relevant confound if the attentional engagement with the musical stimulus differed by valence condition. There is some evidence that this could be the case, as ERP indexes of attentional engagement (N1/P2) have been shown to be elevated when auditory sequences were harmonic and judged as more aesthetic compared to disharmonic (Sarasso et al., 2019). Notably, Sarasso et al. further reported slowed motor responses for aesthetic judgment responses when stimuli were harmonic compared to disharmonic. On the one hand, this suggests another potential mechanism for how the effect of study 2 could be explained without referring to altered PW parameters (affect influencing the speed of motor responses). On the other hand, the effect reported by Sarasso et al. (2019) is contrary to what was observed in study 2, since positive affect was associated with faster perceptual filling-in and therefore faster motor responses. This therefore strengthens the notion that the reported effect was not a result of altered motor responses.

Besides attentional mechanisms, modification of prior content should also be considered as an alternative explanation for the observed effect in study 2. This would mean that the different percepts (veridical experience of different center and periphery vs. illusionary uniformity) would be associated with different features of the mood induction stimuli, such as the idea that a uniform visual field is experienced as more harmonious and predictable than a disrupted one. Occurrence of a uniform visual field would then be predicted with a higher likelihood based on the previously perceived harmonic music. The observed effect would then best be described as a modulation of prior content within the perceptual hierarchy (as described in category 2 of pitfalls by Cermeño-Aínsa (2021)). Effects of this category function by updating expectations and increasing the probability of perceiving the expected stimulus. Importantly, such modulations are neither dependent on affective state nor on any other extraperceptual process.

Modification of prior content is also an important potential confound in study 3 (higher perceptual stability during binocular rivalry when affective valence was positive). While there is little reason to assume that the valence of Gabors with opposing orientations would be different, an upright face could be experienced as more predictable and therefore more positive. Sun et al. (2016) found that a wider attentional scope, which is often associated with positive affect, leads to preferential processing of upright but not tilted faces during continuous flash suppression. This effect could increase the likelihood of an upright face dominating binocular rivalry when state affective valence is positive. Given the high correlation between dominance ratios and phase durations, this would also likely influence analyses of phase durations. However, both reported effects of state affect (on phase durations and dominance ratios) were found in both sets of stimuli. It is therefore unlikely that modification of prior content (i.e., upright faces are perceived as more positive and will therefore be perceived with higher likelihood when state affective valence is positive) caused the observed effects in study 3.

The binocular rivalry paradigm is further susceptible to influences of attention and other processes that underlie cognitive control. In a series of studies, Lack (1978) demonstrated that participants had a certain amount of control over reported phase durations and dominance ratios if they were asked to do so. Thus, they reported being able to deliberately switch between perceiving both presented stimuli. Importantly, this result is based on subjective ratings in response to an explicitly stated goal (e.g., to slow down or accelerate alternation rates) and is therefore highly susceptible to effects of participants wanting to produce results that they assumed were demanded of them. However, several studies have demonstrated that the degree of voluntary control participants can exert varies between different forms of multistable perception (Meng & Tong, 2004; van Dam & van Ee, 2006; van Ee et al., 2005). Note that binocular rivalry in these studies consistently allows for the least amount of voluntary control compared to other forms of multistable perception. Nevertheless, these findings suggest that compliance effects cannot be the only source of the effects described by Lack (1978). In a review article on this topic, Paffen & Alais, (2011) conclude that "voluntary control over binocular rivalry is possible, yet limited". They further posit that deliberate control over alternations in binocular rivalry can be best explained through contrast enhancement of the stimulus that one chooses to draw attention to. To consider this mechanism an important confound, one would again have to argue that one of the variants in the two stimulus sets would be attended to with a higher likelihood due to altered affective state, which has been discussed in the previous paragraph. Importantly, different affective states could influence the degree to which participants want to comply with the demands of the experimental task. However, task instructions were formulated neutrally: participants were asked to report perceptual alternations when they appear. No incentive was stated to report particularly few or many alternations. In summary, deliberate manipulations of perceptual alternations during binocular rivalry are possible, albeit considering the experimental design of study 3, unlikely to have contributed to the observed effect in a significant way.

4.4 Conclusion and Outlook on Future Research

I started this dissertation by presenting the affective realism hypothesis of perception (Anderson et al., 2012; Siegel et al., 2018; Wormwood et al., 2019). Briefly summarized, this view states that „Feelings do more than influence judgments of what you have seen; they influence the actual content of perception." (Siegel et al., 2018). If this hypothesis were to be verified, it would have wide-ranging implications for competing views on the flow of information within the brain. Fridman et al. (2019) further argued that the implications of this view extend beyond academic debates and should inform policy making and legal assessments of people who make perceptual judgments in highly emotional situations. Considering these far-reaching consequences, empirical assessments of this claim should be subjected to close scientific scrutiny.

Given that affective realism would, by definition, constitute an unequivocal case of the penetrability of perception, many of the pitfalls that have been put forward in the CP debate can be equivalently applied when evaluating the validity of affective realism. The CP debate has been characterized by seemingly irresolvable disagreements over the boundaries between perception and cognition as well as over the measurement of subjective perception, so much so that it has been called to be "at a dead end" (Cermeño-Aínsa, 2021). Several researchers have called for a reappraisal of the debate through the use of a common framework, predictive processing, that includes accounts for perception, cognition, and affect (Cermeño-Aínsa, 2021; Hohwy, 2017; Litwin, 2017; Marchi, 2020). Applying this framework to the debate has several crucial implications. Most importantly, in PP, sensory information is always evaluated with respect to prior knowledge and expectations, since both sensory and prior information are weighted by their respective precision estimates (PW). Priors develop through Bayesian perceptual learning and are therefore mostly well-adjusted in their content and precision to our sensory environment. PW will thus mainly become measurable in edge cases of perception, where priors significantly diverge from sensory evidence and are encoded with relatively high precision with respect to sensory information. Therefore, the question of whether and how subjective perceptual experience can be influenced by observer-based, extraperceptual variables, approached from a PP point of view, translates into the question of what variables could potentially shift the balance between priors and sensory inputs.

Thus, a potential mechanism for how affective realism could manifest itself in visual perception would be if affective experience shifted the weight that is assigned to priors and sensory information. Indeed, PP accounts of affective states have characterized affect as an adaptive feedback signal indicating current PE rates (i.e., whether priors can accurately predict current sensory inputs; Joffily & Coricelli, 2013; Van de Cruys, 2017). In the case of high PE, experienced valence would be negative, and perhaps priors should have less influence on information processing, as prior predictions failed to accurately predict the current state of the world. In addition, based on clinical conceptions of affective and anxiety disorders, affective traits have been conceived as stable tendencies of individuals reflecting the degree to which new information is incorporated into an existing worldview. This line of reasoning led to the central research question of this thesis: do affective states and traits influence the parameters of perceptual precision weighting? The empirical findings presented in the three dissertation studies provide a good starting point for evaluating this hypothesis.

Considering the role of affective traits, study 1 found that trait anxiety predicted the degree to which individuals rely on prior information in a perceptual decision making task. However, neither trait anxiety nor depressiveness were related to perceptual stability during binocular rivalry, another paradigm that has been used to quantify parameters of PW. The reasons for this inconsistency in results could be manifold. It could be due to differences in statistical power (study 1 included more than twice the number of participants than study 3) or due to differences in what was measured during the task. It is possible that affective traits only affect processing at a specific level of the processing hierarchy, and that studies 1 and 3 measured PW at different levels of that hierarchy. For example, affective traits may only have an influence on higher levels of information processing. This idea is consistent with the observation that affective disorders are typically associated with distorted patterns of thinking and decision making, rather than with perceptual aberrations such as hallucinations (although see (Baethge et al., 2005; De Weerd et al., 2006). This would suggest that an effect of affective traits is more likely to occur in a task of perceptual decision making, where higher level reasoning and judgment processes are used to a greater extent, than in a binocular rivalry task, where low-level stimulus features are more likely to shape perception.

This notion that affective traits could only affect PW at higher levels of processing would also address an apparent contradiction in the findings: if trait anxiety indeed correlate with a global tendency to rely on priors (study 1), this would contradict the result that negative state affect was found to be associated with lower reliance on priors (studies 2 and 3), as trait anxiety is characterized by the regular occurrence of negative affective states. However, if affective states and traits were to affect PW at different levels of the processing hierarchy, this could explain the diverging pattern by assuming that the tasks used measured PW at different stages of processing. However, the results presented in studies 1 and 3 do not provide conclusive evidence to support the existence of such a hierarchical relationship between affective traits and altered visual PW at late stages of processing.

In order to further clarify this question, future research should avoid specific pitfalls and adjust for as many of the potential confounds that have been outlined in this section as possible. Firstly, an effect of affective traits is more likely to be found in tasks that rely on higher level cognitive decision making. If low-level perceptual PW is indeed affected by affective traits, the effect is likely to be small and will be found more pronounced in participants with high levels of the affective trait in question. However, studies with samples that include severe cases of affective and anxiety disorders would have to account any abnormalities in psychomotor functioning in these populations. Thus, studies should include large samples and screen for clinical cases of severe affective disorders. Ideally, multiple tasks should be conducted, all of which should have been evaluated beforehand with respect to the level of processing at which they measure PW. Furthermore, stimuli should be selected to be as affectively neutral as possible. No-report paradigms in which participants are not incentivized to achieve a specific goal (such as achieving high accuracy) should be preferred over classical AFC tasks. For instance, there has been recent research on visually evoked ERPs during binocular rivalry in an attempt to extract reliable no-report estimators of perceptual alternations (Laukkonen et al., 2022).

Concerning the role of affective states, a potential influence on low-level visual PW can be assumed with somewhat less caution. Study 2 showed a significant influence of induced mood on the likelihood and speed of perceptual filling-in, with more positive valence being associated with higher rates of illusionary perception. In accordance with this, study 3 found that more positive baseline affect was correlated with longer phase durations during binocular rivalry. Combined, these results support the notion of stronger reliance on priors in visual perception when affective valence is positive as compared to negative. This notion links established conceptions of affective states as functional adaptations (Keltner & Gross, 1999) with contemporary models that conceive them to function as a signal during Bayesian inference (Seth, 2020). In this view, affective states serve as a feedback mechanism, signaling the degree of prediction error that results from current strategies of PEM (Chetverikov & Kristjánsson, 2016). In turn, the individual would become incentivized to adjust current strategies of PEM. In terms of perception, this would entail reliance on more resource-intensive but less error-prone strategies (i.e., low reliance on prior predictions) when affective valence is negative.

However, considering the methodological confounds, the partly inconsistent findings across tasks as well as several alternative explanations for the effects that have been gathered, one should be cautious in asserting certainty over this putative role of affective state in visual perception. Future research concerning this question is, just as described for the role of affective traits, dependent upon the initial development of a common methodology concerning the measurement of PW at different levels of the visual processing hierarchy. Once such a methodology has been established, more empirical evidence can be gathered concerning the role of affective state in visual PW. Likewise, the other methodological recommendations (large samples of healthy participants, multiple tasks, affectively neutral stimuli, no-report paradigms) also apply for the study of affective state and its involvement in visual PW. Mood induction paradigms should be used as well as measures of baseline affective state. While mood induction compared to baseline measurements likely leads to more variance of affective state and allows for within-subject measurements, it also potentially interferes with perceptual processing (e.g., through altering attention allocation dynamics) and therefore introduces experimental confounds. Likewise, baseline measurements are likely to lose explanatory power over time, as participation in most experimental tasks can influence the current affective state. Future research should also focus on potentially diverging contributions of affective valence and affective arousal in the visual domain, as has been observed in the auditory domain and speech recognition (Citron et al., 2014; Kuperman et al., 2014).

Besides the intensively outlined confounds, alternative explanations, and calls for caution in interpreting the results, this dissertation provides a valuable contribution to the study of affective experience and its potential involvement in visual perception. On a theoretical level, it postulates a plausible working mechanism of how affective realism could be implemented in a system underlying the principles of predictive processing. In terms of empirical findings, all three studies were preregistered, gathered experimental data from a substantial number of participants, and took various precautions to ensure valid inferences about their central assertions. Thus, the findings constitute a relevant part in the body of research on this intricate yet captivating topic.

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Appendix

Original Publication of Study 1

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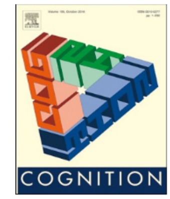

Trait anxiety is linked to increased usage of priors in a perceptual decision making task

N. Kraus[a,b], M. Niedeggen[b], G. Hesselmann[a,*]

[a] *Psychologische Hochschule Berlin (PHB), 10179 Berlin, Germany*
[b] *Freie Universität Berlin, 14195 Berlin, Germany*

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ABSTRACT

Current predictive processing accounts consider negative affect to result from elevated rates of prediction error, thereby motivating changes in the degree with which prior expectancies and sensory evidence influence our perceptions. Trait anxiety is associated with the amount of negative affect a person is experiencing and has been linked to aberrant strategies in decision making and belief updating. Here, we assessed the degree to which induced prior expectancies influenced motion judgements in a simple perceptual decision making task in 117 healthy participants with varying levels of trait anxiety. High trait anxious individuals showed increased usage of priors, independent from the amount of sensory uncertainty that was perceived. This finding demonstrates aberrant strategies of belief updating in anxiety even in evaluating nonthreatening visual motion stimuli, and thus suggest an influential role of affective traits in processes of perceptual inference.

1. Introduction

Predictive processing accounts of human brain functioning conceive perception as a form of statistical inference learning (Friston, 2012). In this process, an observer would be able to infer the causes of current sensations. It is hypothesized to achieve that by constantly matching prior predictions with sensory inputs and weighting both with the certainty that is ascribed to them, a process typically described as precision weighting. Parameters of precision weighting (i.e., to what degree priors and sensory data are relied on) will crucially shape the contents of perception (de Lange et al., 2018) and therefore determine the level of confidence that can be put into current perceptions. Accordingly, those parameters will be informed by the amount of prediction error that is encountered when model predictions are compared with sensory inputs.

It has recently been argued that the amount of prediction error (PE) that is experienced equates to the emotional valence that is ascribed to a situation (Van de Cruys, 2017). This idea of emotions as emerging from deviations of observations from expectations has also been brought forward outside of predictive processing as a unifying approach to theories of affective arousal (Proulx et al., 2012). Following that line of reasoning, states of high predictability and controllability would be perceived as inherently positive, states with low predictability and controllability as negative (please note though, that there is an ongoing discussion about how stimulus predictability relates to likability, see for example Gold et al., 2019). Clark et al. (2018) extend this framework from short-term fluctuations of emotional status being evoked by current rates of PE to more trait-like features of affective experience. They argue that humans will, based on prior experience, develop what they call hyperpriors, i.e. long-term estimates of their expected emotional status. These hyperpriors would enable individuals to predict the degree of controllability and predictability of their environment across multiple situations and therefore reduce overall uncertainty. Those predictions would furthermore inform momentary emotional experience, resulting in the emergence of moods (i.e., long-term averages of emotional states). Depending on their predictive content and precision, they could take several different appearances. For example, an imprecise, negatively valenced hyperprior would entail the prediction of aversive events with high uncertainty, resulting in overly strong attempts to reduce uncertainty, which would psychologically manifest itself as trait anxiety (Clark et al., 2018).

It is important to note that both conceptualizations (those of state-like as well as of trait-like features of affective experience), focus primarily on a unidirectional relationship between perception and emotion, in that they conceive emotions as resulting from differences between experienced and predicted sensory inputs. In predictive processing, agents will nevertheless strive to reduce rates of PE and can do so via two essential mechanisms (Friston, 2012). The first one

* Corresponding author.
E-mail address: g.hesselmann@phb.de (G. Hesselmann).

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consists of altering sensory inputs by actively engaging with the environment and thereby aligning it with prior predictions (active inference). This, on a behavioral level, would equate to the notion that emotions motivate behavior (Scarantino, 2017) and it has been proposed that affective disorders can be conceptualized as a self-evidencing cycle of aberrant predictions leading to maladaptive behavior (Clark et al., 2018). The second mechanism would be to refine model predictions based on current sensory evidence, so that subsequent perception results in less PE (perceptual inference). Whether emotions can have a direct influence on perception has been intensely debated (see for example Firestone & Scholl, 2016; Zadra & Clore, 2011). One conceivable mechanism for this could be that affect influences parameters of precision weighting, i.e. adding or subtracting weight from either priors or sensory information in perceptual inference.

Applying this line of thinking to the conceptualization of affective traits from Clark et al. (2018), individuals high in trait anxiety will render their beliefs about the environment as well as future outcomes as imprecise. In order to counter this inherently negative state of uncertainty, they will try to resolve uncertainty either on a behavioral (e.g. by avoidance) and possibly also on a perceptual level. We can point to several findings, which show trait anxiety being linked to aberrant patterns of behavior (Struijs et al., 2018), cognitive appraisal strategies (Everaert et al., 2018), allocation of attention (Abend et al., 2018) and learning rates (Browning et al., 2015). One needs to keep in mind, though, that these findings are limited to high-level cognitive processes and were measured in tasks with potentially threatening or aversive stimuli. In order to detect potential differences in perceptual inference that relate to the degree of trait anxiety, we carried out a perceptual decision making task in which the degree of sensory evidence could be varied and prior expectations could be induced via cues. We were thus able to relate variance in trait anxiety levels of healthy participants with parameters of precision weighting in a non-threatening environment.

In our task, participants were operating around their individually determined perceptual detection threshold. In the absence of behavioral or attentional strategies that could resolve uncertainty during this task, we hypothesized that participants with higher trait anxiety would show increased usage of cued expectations in making their decision. We hypothesized further, that this effect would be especially pronounced in conditions of high sensory uncertainty.

2. Methods

2.1. Sample

131 participants were recruited from the general population (n = 67) as well as from a student pool (n = 64) and received either monetary compensation or course credit. Inclusion criteria were the absence of any previously diagnosed psychiatric (e.g. anxiety disorder) or neurological illnesses as well as normal or corrected to normal vision. Participants were excluded from the sample when they failed to score above chance level of 50% in the initial practice phase of the experiment (n = 13), indicating difficulties with one or more of the essential task requirements (i.e., detecting coherent motion in a shortly presented Random Dot Kinematogram (RDK)). Participants were further excluded when their accuracy rates in the main task did not show a monotonic increase as a function of motion coherence, indicating that more sensory evidence did not improve participants' task performance (n = 1). This exclusion criterion was implemented in order to ensure that participants' decision in the task was at least in part informed by the visual evidence presented to them (Lufityanto et al., 2016). The final sample therefore consisted of 117 participants (76 female; age mean = 28.7, SD = 12.2). Justification for the sample size can be found in point 2.3. To check whether excluded participants differed concerning their trait anxiety score, we compared them with included participants with a two sided Welch *t*-Test for independent samples with unequal variances. Results do not suggest a difference in trait-anxiety scores ($t(20.07) = 0.34$, $p = 0.736$). We carried out the same procedure for participants age and again found no significant differences ($t(20.78) = -0.48$, $p = 0.634$). To further check for possible differences concerning the gender of included and excluded participants, we carried out Pearson's Chi-squared test with Yates' continuity correction and also did not find a significant difference ($\chi^2(1) < 0.001$, $p = 1$).

Informed written consent was obtained from all participants after they received a detailed written description of the study. All investigations have been conducted according to the principles expressed in the Declaration of Helsinki and have been approved by the local ethics committee at the Psychologische Hochschule Berlin (PHB). Trait Anxiety was assessed through the State–Trait Anxiety Inventory (Spielberger, 1983). Those excluded did not differ significantly from included participants concerning gender, age or trait anxiety scores.

2.2. Stimuli and experimental procedure

Participants were asked to judge the global motion direction (left or right) of RDKs which were displayed on a 24″ LCD screen (Acer KG241, 75 Hz). RDKs were generated and presented with the Psychtoolbox for Matlab (Brainard, 1997) and consisted of 200 white dots (0.1° in size) moving in a black circular aperture (9° in diameter, speed 6°/s) for 500 ms. To prevent participants from following single dots and potentially perceive consistent motion in them, per frame a new, randomly chosen set of dots (corresponding to the motion coherence level) was determined to consistently move into the target direction, while the other dots moved randomly. Additionally, dots were removed from the aperture after five frames and replaced by a new dot at a random position inside the aperture. Before dot presentation an arrow pointing either to the left or to the right (predictive cue, 2/3 of all trials) or to both directions (neutral cue, 1/3 of all trials) was presented for 500 ms. In case of a predictive cue, the arrow direction was either congruent (valid cue, 75% of the trials) or incongruent (invalid cue, 25% of the trials) with the subsequent target direction. Participants were explicitly informed about these contingencies beforehand. Participants were asked to judge the motion direction as well as their subjective certainty in the decision on a continuously adjustable response bar (Fig. 1). The participants were asked to express their certainty in a decision by moving a red vertical line either close to the center (low certainty) or to the periphery of the response bar. Responses were prohibited to fall directly in the middle of the response bar (i.e., left-right forced choice task).

To get acquainted with the task, participants completed 20 trials in the beginning of the experiment in which all cues were neutral, stimuli were presented until a decision was made, motion coherence levels in a high range (between 50% and 80%), and feedback on the correctness of the decision was presented at the end of every trial. After the training period, participants completed 300 neutrally cued trials in which individual motion coherence thresholds were determined that were intended to correspond to accuracy rates of about 75% through a stepwise staircase procedure. The determined motion coherence.

threshold functioned as intermediate level of sensory uncertainty in the subsequent trials. The threshold was then divided by two as well as multiplied by two in order to function as low and high levels of sensory uncertainty, respectively (de Lange et al., 2013). When participants failed to achieve accuracy rates above chance level of 50% during this phase, they were excluded from further data collection. The main session consisted of 450 trials with equal probability of all three previously determined motion coherence levels. Participants could choose whether to pause the experiment at any given point, but trials before and after a pause were excluded from data analysis.

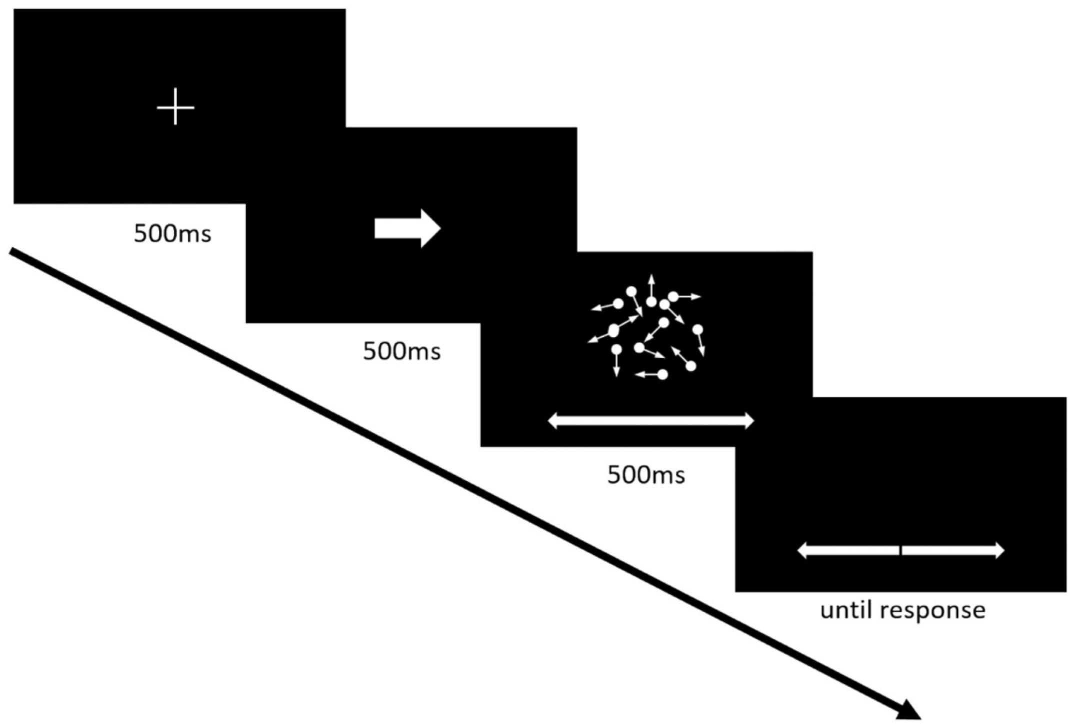

Fig. 1. Experimental Paradigm: Sequence of one trial with a fixation cross, a predictive arrow cue, random dot stimulus and response bar.

2.3. Preregistered research hypotheses, sample size and data analyses

Data acquisition, intended sample size and analyses were preregistered (https://aspredicted.org/blind.php?x=mz3dh2). We specifically predicted that in a task of perceptual decision making when the amount of available sensory information was experimentally reduced, the influence of prior expectations (induced via cues) on decisions would increase, as was demonstrated by de Lange et al. (2013). We further hypothesized that this effect would be especially pronounced in highly trait anxious individuals, which would equate to a three-way interaction effect of influence of cues, level of sensory information and level of trait anxiety on accuracy rates of perceptual decisions. In order to test these hypotheses, we chose for a generalized mixed regression analysis with Laplace approximation of likelihood (lme4 package for R-Studio, Bates et al., 2015) for binary outcome data (i.e., global motion direction correctly identified or not). Accuracy was herein predicted by motion coherence level (numeric) and cue validity (categorical, contrasts set to invalid vs. neutral and valid vs. neutral), varying across participants and trials, as well as trait anxiety scores (numeric) varying across participants. To account for cross-level interactions, numeric predictors were mean-centered. We report results in the form of Wald *Z*-Tests, as recommended by Bolker et al. (2009). In order to ensure that the measured effects are not influenced by differences in learning rates between participants (e.g., cues gaining influence later in the experiment when their predictive value has been experienced), trial number was added as a numeric predictor in the model.

In a more exploratory analysis a similar GLMM was calculated for subjective certainty ratings. We did not preregister specific hypothesis about possible effects on subjective certainty ratings. Since high trait anxious individuals are assumed to experience higher uncertainty in inferring the underlying causes of sensory inputs and possibly compensating for that uncertainty by changing parameters of perceptual or active inference, we were agnostic to whether we would find altered ratings of subjective certainty in a perceptual decision.

In order to determine an adequate sample size, we specifically focused on a study with a comparable task and research hypothesis. Stuke et al. (2018) measured the relationship of delusion proneness (measured via PDI questionnaire) and usage of priors in RDKs. They first determined an individual coefficient representing the magnitude of influence prior expectations had on a perceptual decision. They then correlated this coefficient with participants' PDI scores and found a small effect ($r_p = -0.243$, $p = 0.012$) in a sample of 106 participants. Given the similarities of the experimental variables and statistical techniques applied, we anticipated a comparable sample size in order to find the hypothesized effect. In order to prevent unnecessary resource spending and testing capacities, we decided to preregister a sequential testing procedure, in which data analysis only began once data for the first 25 participants had been collected. This analysis consisted of a simplified Bayesian model of our final analysis (mixed ANOVA, treating motion coherence as a factorial variable) which was conducted via JASP (JASP Team, 2020) and was repeated in regular intervals of every five newly tested participants. Testing was preregistered to be terminated when the Bayes factor for our research hypothesis (interaction effect of trait anxiety, cue validity and motion coherence) reached a value above 10 or below 0.1 or when sample size reached $n = 100$. This procedure was specifically implemented in order to get an estimate of whether further testing was necessary in order to verify or falsify the research hypothesis. Note, that in order to compute valid measures of effect sizes and significance after data collection was completed, data was analysed in a more traditional frequentist approach described above.

Due to fortunate testing circumstances we were able to acquire 17 additional participants to improve the overall statistical power. Because of the preregistered maximum sample size of 100, all analyses were repeated with a reduced data set of only the first 100 participants. There were no differences in result patterns concerning the significance of effects in this secondary analysis. All data and analysis scripts can be found via https://osf.io/27xy9/.

3. Results

3.1. Influence of motion coherence, cues and trait anxiety on accuracy

In trials with neutral cues, participants on average achieved

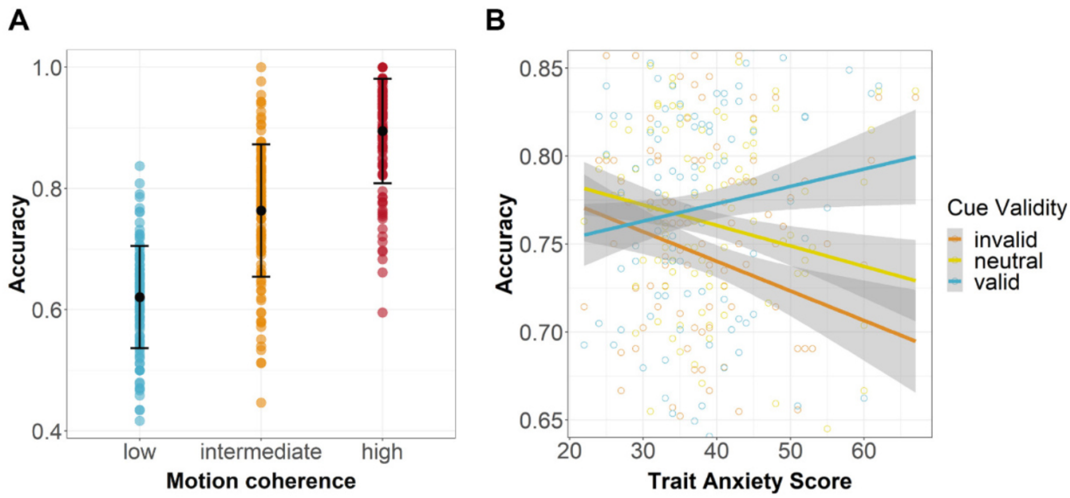

Fig. 2. Results (n = 117). A. Mean accuracy rates (± 1 SD) in neutrally cued trials depending on motion coherence levels. Dots represent the achieved accuracy of individual participants in one of the motion coherence conditions. B. Effect plot with mean (± 1 SD) accuracy rates depending on cue type as well as trait anxiety score, averaged over all motion coherence levels. Dots represent the achieved accuracy of individual participants in one of the cueing conditions (indicated by dot color).

accuracy rates of 65.63% when motion coherence was low, 76.62% when it was intermediate and 89.73% when it was high (Fig. 2a). Results of logistic regression analysis show a main effect of motion coherence on accuracy rates (β = 0.828, SE = 0.030, z = 26.84, p < 0.001), with higher levels of motion coherence leading to higher accuracy rates. This demonstrates that the chosen staircase procedure to determine motion coherence levels resulted.

in adequate difficulty levels, preventing possible ceiling or floor effects, thereby allowing for a potential effect of cue validity on accuracy to show.

Trait anxiety scores ranged from 22 to 67 with a mean of 38.91 (SD = 9.23). Trait anxiety itself did not yield a significant main effect on accuracy rates (β = −0.003, SE = 0.005, z = −0.62, p = 0.537). To ensure that this was not due to trait anxiety already having influenced performance when individual motion coherence thresholds were determined, additional correlation analysis was carried out. There was no significant correlation between the intermediate motion coherence level (determined to lead to about 75% task accuracy) and trait anxiety scores (r_s = −0.007, p = 0.942).

Cue validity had a significant effect on accuracy rates with valid cues showing a significant improvement (β = 0.093, SE = 0.040, z = 2.37, p = 0.018) and invalid cues showing a significant reduction of accuracy rates in comparison to neutral cues (β = 0.102, SE = 0.034, z = 3.06, p = 0.002). Contrary to our expectation, the effect of cue validity did not significantly vary between different levels of motion coherence (valid cues: β = −0.027, SE = 0.021, z = −1.26, p = 0.210; invalid cues: β = 0.022, SE = 0.025, z = 0.86., p = 0.388). Since this effect has been reported in a study with very similar task demands (de Lange et al., 2013) we carried out further statistical analysis. We applied the same statistical test used in the study by de Lange and colleagues (3 × 3 rm-Anova) to our data and found a significant interaction effect of cue type and motion coherence level (F (4, 464) = 2.7, p = 0.029) on accuracy.

The effect of cue validity was modulated by the level of trait anxiety (Fig. 2b), depicting a positive relationship between trait anxiety and the influence of cues on decisions. This was significant only when contrasting valid with neutral cues (β = 0.011, SE = 0.004, z = 2.49, p = 0.013) and failed to reach significance when contrasting invalid with neutral cues (β = 0.007, SE = 0.004, z = 1.90, p = 0.058). Contrary to the preregistered hypothesis, this effect was also not dependent on the level of motion coherence (valid cues: β = 0.001, SE = 0.002, z = 0.55, p = 0.582; invalid cues: β = 0.003, SE = 0.003, z = 0.98, p = 0.329). In order to ensure that the observed effects are not explained by differences in learning rate between participants, we added the trial number as a predictor to the GLMM. There was no significant main or interaction effect with any of the other predictors, suggesting that the observed effects were independent from the elapsed experimental time.

3.2. Subjective certainty ratings and response biases

Visual inspection revealed a non-normal distribution of subjective certainty ratings, since participants tended to report maximum certainty. This was illustrated by the fact that only 1.51% of all trials were answered with a rating analogous to between 90% and 99% certainty but in 11.26% of all trials participants reported maximum certainty. We therefore aggregated the data per participant and condition (cue validity and motion coherence level) before subjecting it to the regression analysis. Results showed the only significant effect on certainty ratings to be motion coherence (t(115.07) = 9.383, p < 0.001).

In order to study the described response bias, we carried out an additional exploratory GLMM analysis with the same variables as in the previous analyses (cue validity, motion coherence and trait anxiety) predicting whether trials were answered with a maximum reported certainty. This analysis showed a significant main effect of motion coherence (β = 0.961, SE = 0.134, z = 7.14, p < 0.001), but no significant main or interaction effects with cue validity or trait anxiety (all p-values > 0.1).

4. Discussion

The presented results suggest an association between trait anxiety and elevated influence of priors in perceptual decision making. The observed effect demonstrates a possible link between anxiety and aberrant patterns of belief updating in a task that focuses on perceptual decisions and is not based on reward learning or possibly anxiety provoking stimuli (Aylward et al., 2019; Browning et al., 2015; Kube & Rozenkrantz, 2020). This adds to current theoretical predictive processing accounts of emotional experience in general and trait anxiety specifically (e.g., Clark et al., 2018; Joffily & Coricelli, 2013; Van de Cruys, 2017). As mentioned, these models focus on emotional experience resulting from elevated or attenuated levels of perceptual prediction error. The findings presented here encourage a broader understanding of affect in predictive processing theories, in that they suggest affective experience not only as resulting from perception (Chetverikov & Kristjánsson, 2016; Erle et al., 2017), but potentially also influencing parameters of precision weighting and therefore subsequent perceptual inference.

Negatively valenced states in general have been conceived as resulting from the inherent unpredictability and uncontrollability of a currently perceived situation. Trait anxiety in particular has been hypothesized to occur when long term expectations about future states render them as negatively valenced, but with low precision (Clark et al., 2018). Due to the innately aversive nature of this, humans will try to reduce uncertainty by adjusting parameters of current inference modes (active or perceptual). Pathological anxiety could thus become especially apparent, when confronted with a source of irreducible uncertainty, individuals nevertheless attempt to engage in uncertainty reduction (Grupe & Nitschke, 2013). The presented results could indicate a similar attempt to reduce uncertainty by adjusting parameters of perceptual precision weighting.

Prior research that relates personality traits or psychopathologies with potentially aberrant aspects of predictive processing (e.g., Heinz et al., 2019; Seriès, 2019; Stuke et al., 2018; Van de Cruys et al., 2014) often proposed specific mechanisms of action, concerning how identified alterations in predictive processing would relate to the observable psychological correlates (i.e. the failure to attenuate the precision of sensory information based on priors leading to false inferences and delusional thinking). In attempting to do this for the case of trait anxiety it is important to note that, in this particular experimental setup, the predictive value of priors was kept at a fixed amount (75%) over all trials, with only sensory information allowed to vary between different levels of certainty. Within this specific design, it is thus only possible to show aberrant weighting of priors under varying degrees of sensory certainty, not the other way around. Moreover, if trait anxiety does reflect the tendency to adjust current modes of inference in order to reduce uncertainty, the specific adjustments made could be varying across tasks. This becomes apparent when looking at behavioral strategies of trait anxious individuals dealing with situations of uncertainty (e.g. overly excessive engagement in the form of rumination vs. avoidance behavior).

Contrary to prior expectations, the observed interaction effect of trait anxiety and cues was restricted only to valid cues and did not reach significance when contrasting invalid cues with neutral ones. This could suggest varying influence of priors on decision making, dependent on the degree of experienced prediction error (i.e., discrepancy between cued expectation and sensory information) in individuals with higher levels of trait anxiety. Also contrary to preregistered hypotheses, the described effect was independent of the degree of sensory uncertainty, hence we did not find a significant interaction effect between cue validity, trait anxiety and motion coherence. This could suggest a tendency of trait anxious people to put higher reliance on priors, independent of the amount of sensory uncertainty. However, note that within the chosen statistical method (GLMM) our study in general failed to replicate the effect of higher reliance on cues when sensory information was downgraded, independent of trait anxiety. Since this mechanism of precision weighting has previously been shown in cued RDKs by de Lange et al. (2013) it seems necessary to elucidate the reasons for its absence in the current data.

For this purpose we applied the same statistical method (rm-Anova) as used by de Lange et al. (2013) to our data and found a significant interaction effect between cue validity and motion coherence. It is therefore highly likely that the observed differences in effect patterns are at least in part attributable to differences in statistical methods (i.e., mean-averaging, treating motion coherence level as factorial, considering trait anxiety as a predictor). Furthermore, it is important to note that the influence of priors on decision making in the mentioned study has overall been higher, conceivably due to differences in cue type (motion word instead of arrow), shorter presentation time of cues (200 instead of 500 ms) and longer fixation intervals between cue and motion stimuli (between 800 and 1300 ms instead of none), possibly leading to increased attention on and processing of the cues.

Note further, that in a recent study which investigated the suggestibility to different optical illusions across individuals, Tulver et al. (2019) did not find reliance on priors to correlate across different tasks. This raises the general concern of whether parameters of precision weighting can be considered as a stable, trait-like feature of human visual perception at all, or whether paradigms that have been used to quantify these parameters so far (e.g., RDKs, optical illusions, bistable perception) fail to measure these parameters validly. It becomes therefore especially important to consider potential limitations in the studied paradigm concerning its internal validity. In the task presented here it is unclear whether the observed influence of motion cues reflects higher level cognitive processes (i.e., paying closer attention to task instructions or the tendency to align one's decision with presumed task demands), or whether the effect was of a perceptual nature (i.e., the cue set up an expected motion direction which influenced subsequent perceptual processing). In a study with a very similar task, de Lange et al. (2013) found that a presented verbal motion cue induced significant changes in pre-stimulus MEG activity over visual cortex, correlating with post stimulus decisional biases. These findings suggest that the motion cues in this paradigm actually influence perceptual processing of subsequently presented visual stimuli. Nevertheless, one has to be cautious in inferring assumed changes of perceptual processes from behavioral choice data.

In this regard, the presented results provide preliminary empirical evidence for an influential role of affective traits such as anxiety in processes of perceptual inference and encourage further research studying potential links between different traits and their relation to parameters of precision weighting. Considering our study's limitations, further research in which both the informational value (i.e., predictive power) of priors as well as the certainty of sensory evidence can be manipulated across different tasks will be necessary. Future studies will need to further elucidate whether there are stable alterations of precision weighting parameters relating to trait anxiety.

Relevance

This study is the first linking trait anxiety with increased usage of priors in a perceptual decision making task. This suggests a role of affective traits in perceptual processing.

CRediT authorship contribution statement

N.K., M.N. & G.H. designed the research, N.K. conducted the research, N.K. analysed the data, N.K., M.N. & G.H. wrote the manuscript.

Declaration of competing interest

None.

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Negative affect impedes perceptual filling-in in the uniformity illusion

N Kraus [a,b,*], M Niedeggen [b], G Hesselmann [a,*]

[a] Psychologische Hochschule Berlin (PHB), 10179 Berlin, Germany
[b] Freie Universität Berlin, 14195 Berlin, Germany

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ABSTRACT

The notion of cognitive penetrability, i.e., whether perceptual contents can in principle be influenced by non-perceptual factors, has sparked a significant debate over methodological concerns and the correct interpretation of existing findings. In this study, we combined predictive processing models of visual perception and affective states to investigate influences of affective valence on perceptual filling-in in extrafoveal vision. We tested how experimentally induced affect would influence the probability of perceptual filling-in occurring in the uniformity illusion (N = 50). Negative affect led to reduced occurrence rates and increased onset times of visual uniformity. This effect was selectively observed in illusionary trials, requiring perceptual filling-in, and not in control trials, where uniformity was the veridical percept, ruling out biased motor responses or deliberate judgments as confounding variables. This suggests an influential role of affective status on subsequent perceptual processing, specifically on how much weight is ascribed to priors as opposed to sensory evidence.

1. Introduction

Whether low-level perceptual processes could in principle be influenced by extraperceptual states such as personality traits or someone's mood has been intensely debated during recent years (Firestone & Scholl, 2016). The influence of a broad variety of constructs on perceptual processing, ranging from language comprehension (Meteyard et al., 2007) to recall of moral values (Banerjee et al., 2012), subsumed under umbrella terms such as cognition or top-down effects, have been brought forward to demonstrate the notion of cognitive penetrability. In this paper, we specifically focus on the potential influence of mood and emotional states on visual perception.

Criticism of studies claiming to demonstrate examples of cognitive penetrability in this domain have been manifold. A major concern has been the specific mechanism leading to the observed influences of affect on perception, i.e., whether the observed effect is an actual influence of one's emotional status on low-level perceptual processing and not instead a result of altered attentional focus or an influence of emotion on post-perceptual judgement processes (Valenti & Firestone, 2019). The debate has thus been shaped by different conceptualizations of the defining features of perception. In predictive processing theories, perception is conceived as a hierarchically organized Bayesian updating scheme, in which the hidden causes of sensory inputs are inferred by integrating current sensory evidence into prior knowledge and predictions (Walsh et al., 2020). In contrast to classical feedforward models of visual perception (e.g., DiCarlo et al., 2012), these models presuppose the constant influence of high-level predictions on low-level processing

* Corresponding authors.
E-mail addresses: n.kraus@phb.de (N. Kraus), g.hesselmann@phb.de (G. Hesselmann).

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of sensory information and therefore on subjective experience. Following this line of reasoning, it would not appear valid to assume a clear-cut functional differentiation between early, purely data-driven, perceptual processing and subsequent stages of processing involving memory and affective appraisal (Cermeño-Aínsa, 2021). It is further important to note, that in this framework, modulations of low-level features of visual stimuli do not occur as the result of deliberate cognitive intentions to do so, as it is implied in narrow definitions of cognitive penetrability (e.g., Lammers et al., 2017).

However, predictive processing models do suggest that parameters of precision weighting (i.e., how much weight is ascribed to priors and sensory evidence, respectively, in current perceptual experience) crucially determine the contents of perception (de Lange et al., 2018), and that those parameters are flexible in nature. One variable that has been hypothesized to influence parameters of perceptual precision weighting is emotional status (Kraus et al., 2021). Emotional status has been hypothesized to equate to currently experienced rates of prediction error (PE, Joffily & Coricelli, 2013; Van de Cruys, 2017), so that negative affect is elicited in the case of high environmental uncertainty. This in turn has been implied as the key mechanism in determining precision weighting parameters in extraperceptual processes such as learning and action selection (Clark, 2018; Friston et al., 2015; Hesp et al., 2021). In the case of action, as a reaction to high rates of PE, the resulting negative affect would serve an incentivizing function, motivating the agent to choose behavioral strategies that are expected to effectively minimize PE in the future (Friston et al., 2015). We propose a similar mechanism in perceptual processing, where high rates of environmental uncertainty lead to negative affect, which in turn leads to a change of perceptual precision weighting parameters.

As a possible reason for why there is a lack of conclusive evidence on the potential influence of affective valence (or other extraperceptual constructs) on low-level perceptual processing, Lammers et al. (2017) emphasize that research in this area has primarily focused on the processing of foveally-presented stimuli. High visual acuity in this region as well as the high demand for attention, which is inherent in most experimental settings, could lead to elevated reliance on sensory information as opposed to priors. Furthermore, strong influence of priors has been shown to result from low rates of sensory precision in perceptual decision making (de Lange et al., 2013). If one's goal is to observe differences and measure variance in visual perception that is potentially caused by extraperceptual factors, this would be especially hard to accomplish when reliance upon sensory evidence is generally heightened, as is the case in foveal perception.

Lammers et al. therefore propose the use of visual illusions happening in the peripheral visual field in order to study cognitive penetrability. Since perifoveal acuity is substantially diminished, peripherally perceived contents are especially prone to perceptual distortions of shape, size and sharpness, modifying stimulus characteristics in a way that is to be expected when the same stimuli are viewed foveally (Baldwin et al., 2016; Valsecchi et al., 2018). A similar effect can be observed in the uniformity illusion (Otten et al., 2017). In this task, by fixating one's gaze on a visual pattern, physically present differences between central and peripheral areas of the pattern dissipate, so that centrally presented stimulus features are appearing to be uniformly distributed throughout the whole stimulus (Fig. 1). Different possible mechanisms have been brought forward in order to explain this phenomenon (see for example Knotts et al., 2019), but a common interpretation is that instead of continuously relying upon low precision sensory information from the periphery, a prior for visual uniformity gains influence on subjective experience over time (Suárez-Pinilla et al., 2018). As the perceptual prior is rendered more precise, resulting rates of PE will accumulate correspondingly, culminating in a switch of conscious perception.

Considering the high susceptibility to shifts from sensory to prior-based perception in perifoveal vision and the hypothesized influence of emotional status on parameters of perceptual precision weighting, we decided to test the influence of positive and negative mood on susceptibility to the uniformity illusion. Specifically, we hypothesized that lowering the predictability of a passively

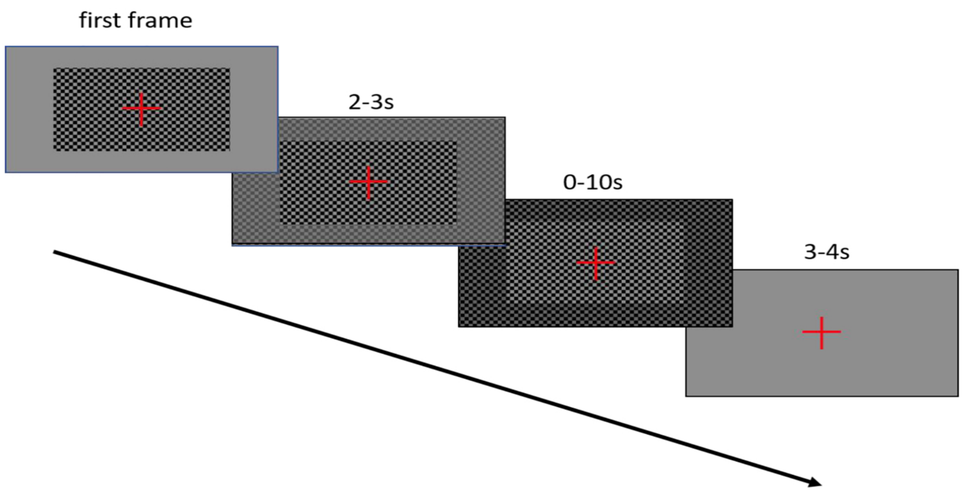

Fig. 1. Experimental paradigm: In the first frame of every trial, only the central patch and the fixation cross were depicted with a grey periphery. Within 2–3 s the corresponding peripheral patch was faded in. After the fade-in completed, participants could indicate to experience visual uniformity within 10 s, after which the trial was automatically aborted.

perceived musical stimulus would induce a negatively valenced status in participants, indicated by lower subjective valence ratings as well as higher levels of both subjectively experienced and physiological levels of arousal. We further hypothesized that in the studied paradigm, that compared to positive, negative affect will lead to a downweighing of prior precision in order to effectively reduce PE, which in turn will lead to reduced occurrence rates and longer reported onset times of visual uniformity.

2. Methods

All experimental procedures, sample size, research hypothesis as well as statistical analyses were preregistered prior to data collection and can be accessed via https://aspredicted.org/6876p.pdf. All collected data, visual stimuli as well as the analysis script are publicly available under https://osf.io/7y9bx/?view_only=3bbd1d56f4ea4d52b95c4d2c61f2a8dc.

2.1. Sample

The sample consisted of 57 participants who were recruited from the general population as well as from a student pool. Participants received either monetary compensation or course credit. Due to technical errors during the stimulus presentation (n = 6) and feelings of nausea during the experiment (n = 1) seven participants had to be excluded, resulting in the final preregistered sample size of 50 (32 female, age = 30.28, SD = 12.72). Due to technical errors during EDA-sampling, skin conductance data of 4 participants could not be recorded, which is why all EDA analyses are restricted to a sample of n = 46. Informed written consent was obtained from all participants after they received a detailed written description of the study. The experiment has been conducted according to the principles expressed in the Declaration of Helsinki and has been approved by the local ethics committee at Psychologische Hochschule Berlin (PHB).

2.2. General procedure

Participants were seated in front of a 24″ LCD screen (Acer KG241, 75 Hz) in a dimly lit room. They were asked to place their head on a chinrest 45 cm in front of the screen, so that horizontally the monitor covered 61.2° of the visual field and 36.8° vertically. After getting acquainted with the task in five demonstration trials, a calibration of the eye tracker took place. Afterwards, two experimental blocks followed consisting of at least 84 trials each, half of which were consisting of illusionary and the other half of control stimuli, presented in randomized order. Before and during the two blocks participants' mood was manipulated by listening to either harmonic or stressful musical stimuli. This resulted in two experimental blocks of different affective valence (positive and negative), of which the order was randomized across participants. In total, the experiment lasted between 33 and 45 min.

2.3. Mood induction

In order to induce positive affect, participants were asked to choose their preferred piece of music out of five preselected harmonic stimuli. All stimuli were instrumental and polyphonic, ranging between 90 and 105 bpm. Stimulus volume was set individually to a level comfortable for the participant. Building on the premise that preference to a musical stimulus is determined by its predictability and information content (Gold et al., 2019; Koelsch et al., 2019), we hypothesized that negative affect would be induced by significantly increasing the unpredictability of the piece of music. In order to achieve that while holding low-level features (such as volume, pitch and tempo) of the musical stimulus constant, stimuli were cut into short pieces (ranging between 150 ms and 300 ms) and afterwards rearranged in random order. The two resulting musical stimuli were then played to the participants in a baseline period of 45 s prior to the respective experimental blocks and were then continued during the task. The order of stimulus valence conditions was randomized across participants.

Participants listened to the respective stimuli on Sennheiser HD-25-1 II headphones for 45 s prior to the experimental block in order to assess their emotional reaction to it. For that, they rated their affective valence as well as their arousal level on the respective scales of the Self-Assessment Manikin (SAM, Bradley & Lang, 1994) before and after the listening period. Furthermore, in order to measure participants' physiological arousal level during the task, electrodermal activity was measured. For this purpose, two Ag/AgCl electrodes filled with a 0.9% saline electrode paste were attached to the thenar and the hypothenar of the participant's non-dominant hand, leaving it on a hand rest. Online data collection was sampled with 500 Hz and a constant voltage of 0.5 V. For offline data analysis, Ledalab software package for Matlab (version 3.4.9.; Benedek & Kaernbach, 2010) was used to downsample the data to 50 Hz and to apply a continuous decomposition analysis (CDA) to it. As a proxy measure for tonic arousal during the task, the amount and amplitude of non-stimulus related skin conductance responses (NS.SCR, Boucsein et al., 2012) were measured within the first 10 min of every experimental block with a threshold of 0.01 μS.

2.4. Visual stimuli

14 different stimuli were created using basic visual template patterns in Adobe Photoshop CC (Version 21.0.3, Adobe Systems, San Jose) in which a central patch (65% of display size) differed either in hue, brightness or contrast from the periphery (see Fig. 1). Per block, every stimulus was presented six times, half of the time as illusionary and the other half as a control stimulus with no differences between central and peripheral patches, resulting in 84 trials per block. After the initial presentation of the central patch, the periphery was faded in within 2–3 s. Participants were asked to indicate visual uniformity by pressing a button with their dominant hand -

however, they were explicitly encouraged to wait until the trial ended if they perceived no visual uniformity. If participants did not indicate uniformity within 10 s after the fade-in, the trial was aborted. In accordance with best practice guidelines for data collection for LMMs (Meteyard & Davies, 2020) recommending at least 30 trials per experimental condition, further trials were added if participants did not meet this criterion at the end of the block. Due to the long lasting aftereffects of the visual stimuli, the intertrial intervals were ranging between 3 and 4 s.

In order to ensure near equality of the perceptual experience in illusionary and control trials, participants were held naïve to the presence of control trials and were prevented from actively noticing the absence of differences in the depicted patterns by online fixation control. For that purpose, participants wore a head-mounted, mobile, video-based eye tracker developed by Pupil Labs (Berlin, Germany; Kassner et al., 2014), with a 30-Hz sampling rate and a gaze accuracy of 0.8° (Ehinger et al., 2019). Trials were immediately aborted if gaze position deviated more than 3.5° from the centrally presented fixation cross and were repeated at a random position of the remaining block. A 9-point calibration of the eye tracker was performed prior to both experimental blocks.

2.5. Statistical analysis

Effectiveness of the musical mood induction was assessed by calculating a difference score per participant between SAM ratings of valence and arousal pre and post music listening. Difference scores were then compared between the two valence conditions with t-tests for dependent samples. Tonic arousal level was measured by amount and mean amplitude of NS.SCRs within the first 10 min of both experimental blocks. Both measures were mean averaged per participant and valence condition and then compared via t-tests for dependent samples.

Suggestibility to the illusion can be operationalized as whether participants reported to perceive uniformity or not. In order to test whether this was predicted by trial type (control and illusionary) and emotional status (positive and negative) we computed a generalized linear mixed effects model for binomial outcome distributions. Within this model we defined stimuli nested within participants as random effect terms to account for potentially high variability in outcome measure caused by different stimuli. Suggestibility can further be operationalized by reaction time (RT) after which uniformity was reported. This analysis was preregistered to consist of a linear mixed-effect model (LMM) of untransformed reaction times, again with the predictors emotional status and trial type as fixed effect predictors, and stimuli nested within participants as random factors. However, preliminary data analyses suggested that the requirement of homoscedasticity was not met within the calculated model and further that the onset times were skewed to the right (skewness = 1.14). The main analysis was thus changed accordingly to a generalized linear mixed-effects model (GLMM) with an assumed gamma distribution of the dependent variable following the recommendations of Lo & Andrews (2015). To further account for the skewed onset time data, post-hoc t-tests for dependent samples were applied to median, rather than mean values. In order to specifically test the implications of our hypotheses (affect having an influence on response behavior in illusionary but not control trials) post-hoc tests of interaction effects in both analyses were applied within the two valence conditions to test for differences between the respective trial type conditions (illusionary and control).

3. Results

3.1. Mood induction

Participants rated their affective valence and arousal level on a 9-point Likert scale of the SAM before and after listening to the mood inducing musical stimuli. Mean valence and arousal ratings before listening were 6.44 and 3.32 (with higher values indicating

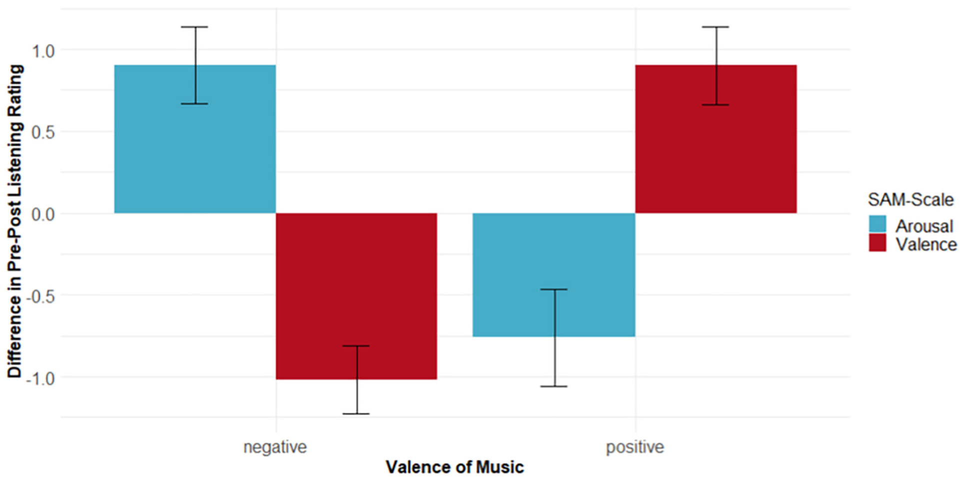

Fig. 2. Average difference between ratings of emotional status (valence and arousal) prior and after listening to the positive and negative Music. Bars represent 95% confidence intervals.

more positive affect and higher arousal). Valence ratings were on average 1.02 points lower after listening to the stressful and 0.90 points higher after listening to the harmonic music. Arousal ratings were on average 0.90 points higher after listening to the stressful and 0.76 points lower after listening to the harmonic music (Fig. 2). To assess whether these changes reached statistical significance, we computed difference scores of SAM ratings for every participant between pre and post the respective listening periods. The individual difference scores were then compared between the different valence conditions with t-tests for dependent samples. Results show a significant decrease of subjective affective valence scores after listening to the stressful music, compared to the harmonic music (t (49) = −5.72, $p < .001$, d = −1.22), whereas subjective arousal ratings were significantly increased by the stressful music (t (49) = 4.13, $p < .001$, d = 0.88). Tonic arousal levels during the task were operationalized as NS.SCR events within the first 10 min of both experimental blocks. Neither amount of NS.SCR (t (45) = 1.00, $p = .322$, d = 0.30) nor mean amplitudes (t (45) = 0.02, $p = .988$, d = 0.01) differed between positive and negative mood conditions.

3.2. Suggestibility to the uniformity illusion

Across all conditions, participants reported uniformity in 91.00% of all trials (97.56% in control and 84.01% in illusionary trials; Fig. 3) with a median response time of 2.51 s (2.15 in control and 3.30 in illusionary trials; range from 0.68 to 5.17; measured from the completion of the fade-in; Fig. 4). To test whether suggestibility to the illusion varied we first tested whether the proportion of trials in which uniformity was reported significantly differed between experimental conditions. We therefore conducted a GLMM for binomial outcome distributions with stimuli nested within participants defined as random effect terms and the predictors mood (positive, negative) and trial type (control, illusionary). Trial type significantly influenced average reporting rates, with control trials leading to higher rates of reported uniformity than illusionary trials (χ^2 (1) = 41.38, $p < .001$). Mood did not yield a significant main effect on uniformity rates (χ^2 (1) = 3.00, $p = .083$) but there was a significant interaction of mood and trial type (χ^2 (1) = 9.68, $p = .002$). Further examination of the interaction effect with post-hoc t-tests of reporting rates aggregated per participant and experimental condition showed that while mood did not significantly influence reporting rates in control trials (t (49) = −0.76, $p = .450$, d = −0.15) reporting rates were significantly lower for illusionary trials when participants were in a negative compared to in a positive emotional state (t (49) = −2.04, $p = .047$, d = 0.23; Fig. 3).

In a next step, influence of trial type and mood on RTs were analyzed in GLMMs for gamma distributions with stimuli nested within participants as random effect terms. In order to account for the uneven occurrence distributions over the different experimental conditions (see former analysis), reaction times in trials in which no uniformity was reported within the predetermined time period were set to the maximally allowed response duration of 10 s, a procedure frequently used in datasets where conscious perception of a visual stimulus is restricted to a predetermined time interval (Stein et al., 2011, Stein et al., 2012). The analysis yielded a significant main effect of trial type (χ^2 (1) = 103.18, $p < .001$) with illusionary trials leading to longer reaction times (Fig. 4). There was no main effect of mood (χ^2 (1) = 3.06, $p = .080$) but a significant interaction effect of mood and trial type (χ^2 (1) = 5.43, $p = .020$). Further examination of the interaction effect with post-hoc t-tests of median onset times per participant and experimental condition showed that while mood did not significantly influence reporting times in control trials (t (49) = 0.86, $p = .394$, d = 0.08) median reporting times were significantly higher for illusionary trials when participants were in a negative compared to in a positive emotional state (t (49) = 2.44, $p = .018$, d = 0.30; Fig. 4).

In a second step, in order to examine a potential influence of the unevenly distributed occurrence rates between the different experimental conditions on this effect, we excluded trials in which no uniformity was reported and repeated the analysis. Results from this analysis suggested a significant main effect of trial type (χ^2 (1) = 64.04, $p < .001$) with illusionary trials leading to longer reported

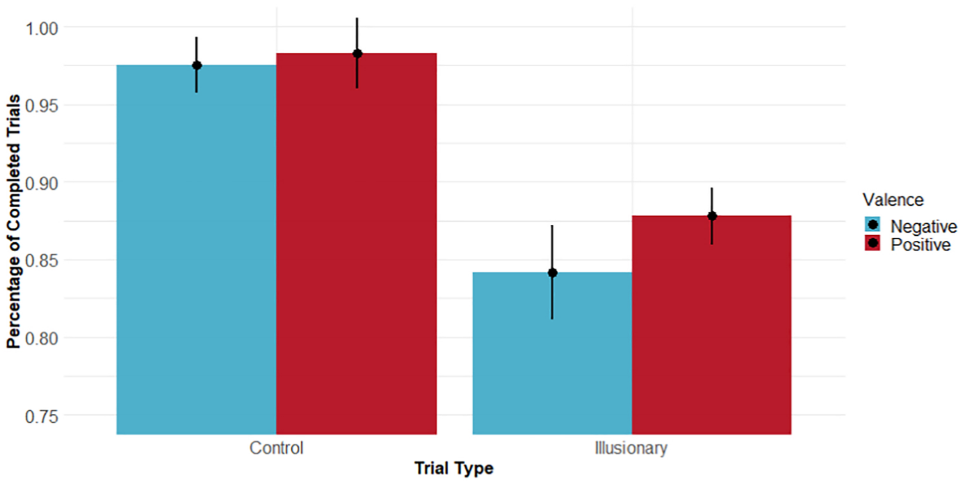

Fig. 3. Mean percentage of trials (+/- 95% confidence intervals) per condition in which uniformity was reported. While within the control condition there was no significant difference between positive and negative emotional states, in the illusionary condition, uniformity was reported more often when affective status was positive (87.79%) compared to negative (84.15%).

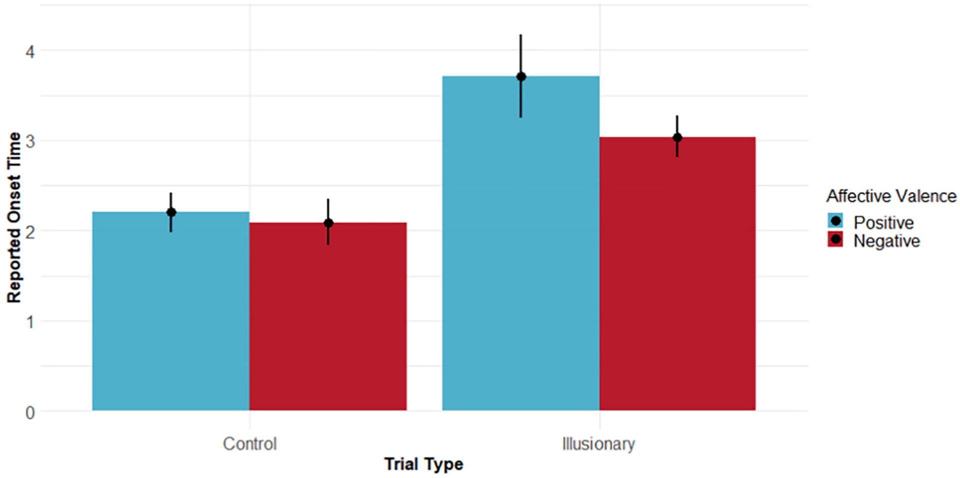

Fig. 4. Median onset times (+/- 95% confidence intervals) per condition in which uniformity was reported. While within the control condition there was no significant difference between positive (2.09 s) and negative (2.20 s) emotional status concerning onset times, in the illusionary condition, uniformity was reported significantly earlier when affective status was positive (3.04 s) compared to negative (3.71 s).

onset times of uniformity. There was neither a significant main effect of mood (χ^2 (1) = 1.52, p = .217) nor a significant interaction effect of mood and stimulus type on reported onset times (χ^2 (1) = 2.81, p = .094).

4. Discussion

In this study, participants reported to experience a uniform visual field in the uniformity illusion with a higher probability when affective valence was positive compared to negative. This effect was limited to illusionary trials in which perceptual filling-in was necessary to create visual uniformity and not present in control trials, where experience of a uniform visual field was the veridical percept. This indicates that when asked to report their subjective perceptual experience, affective status in this paradigm did not influence response behavior in participants per se. Rather, the results point to a selective influence of affective status on the probability of perceptual filling-in taking place in the uniformity illusion.

Perceptual filling-in in this illusion can be explained in the context of predictive processing theories of perception. It is herein suggested to result from a perceptual prior for uniformity of the visual field gaining influence on perception while low-precision sensory information from the periphery gets disregarded over time (Otten et al., 2017; Suárez-Pinilla et al., 2018). Affect, however, has been hypothesized to result from high rates of PE in those theories (Van de Cruys, 2017), motivating changes in strategies of active inference (i.e., behavior; Hesp et al., 2021) and potentially also perceptual inference (i.e., parameters of perceptual precision weighting; Kraus et al., 2021). Here, we successfully induced negative affect in participants by increasing the unpredictability of a musical stimulus. This reduced the influence of perceptual priors in subsequent visual processing without influencing motor and response behavior in a nearly perceptually equal control task.

Negative affect has been shown to induce a more bottom-up focused processing style, increasing attentional focus to details and in general to reduce the influence of prior knowledge and expectations in evaluative and deliberative judgements such as stereotyping (for a review, see Lerner et al., 2015). The presented results suggest a similar effect of emotions on low-level perceptual processing, where perceptual priors are less likely to influence subjective experience when affective valence is negative compared to neutral or positive. Note that in the used mood induction paradigm, although participants reported a significant influence of the musical stimuli on their subjective levels of arousal immediately after first listening, skin conductance levels of tonic arousal did not differ between the conditions. This is likely due to long-term habituation effects of physiological arousal to aversive musical stimuli (Mutschler et al., 2010). Furthermore, the musical stimuli influenced both variables typically subsumed as defining affect (valence and arousal). From the research design used in this study, it is thus difficult to differentiate conceivably diverging contributions of valence and arousal to the effect of affect on perceptual precision weighting.

Looking at the temporal dynamics of the observed effect pattern, two aspects are important to consider. Firstly, there was a main effect of stimulus type on onset times, pointing to shorter onset times in control compared to illusionary trials. Since individual variance was still considerably large and both conditions were subjectively indistinguishable, it is unlikely that a potential effect of affect on onset times in the control condition did not reach significance due to different average onset durations. However, future research should further explore this possibility by altering the visual parameters of the control condition, thereby matching it with illusionary trials with respect to onset times as well as occurrence rates.

Secondly, considering the relatively long time that it can take for the illusion to take effect, it is reasonable to assume that in trials in which participants did not report uniformity, the effect would have occurred at some point after the given time constraint. We therefore chose to set onset times in these cases to the maximum trial length in the first step of analysis. However, if those trials were excluded in a second step, the effect of affective status on onset times did not reach significance. In their initial description of the uniformity illusion, (Otten et al., 2017) found a similar effect pattern of discrepancy between occurrence rates and onset times, where analyses of onset times were less likely to indicate significant differences between experimental conditions. This likely results from the exclusion of trials in which illusionary perception was weak from reaction time analyses but not from occurrence rates analyses, depriving the former of statistical power. However, future research should further study the assumption that illusionary perception will set in eventually and the potential existence of critical periods for perceptual filling-in.

In the cognitive penetrability debate it has been discussed where and when in the processing of sensory information extraperceptual factors could potentially influence perception (e.g., Cermeño-Aínsa, 2021), with some authors arguing for cognitive penetrability being possible only in late, but not early vision (Raftopoulos, 2017). While the timing of the effect observed in our experiment points to a late stage of visual processing, the cortical localization of perceptual filling-in is yet unclear. Suárez-Pinilla et al. (2018) studied the orientation of visual aftereffects in the uniformity illusion, which is based on physical rather than illusionary orientation, and conclude that processes underlying the illusion are not to be expected to originate from primary visual cortex. Note however, that several neuroimaging studies have located neuronal activity correlating to perceptual filling-in phenomena in cortical areas as early as V1 (Hsieh & Tse, 2010; Sasaki & Watanabe, 2004; Weil et al., 2008).

Negative affect did only influence response behavior when uniformity was resulting from perceptual filling-in and not when a perceptually similar experience was created in the control condition. Further, since participants were prevented from becoming aware of the different stimulus types, we can conclude that affect did not influence deliberative judgements of participants or globally bias their motor responses. Instead, the observed effect pattern suggests a selective influence of mood on perceptual filling-in and therefore low-level perceptual processes. Specifically, negative affect in this task led to increased reliance on sensory information respective to priors. Considering the results of previous studies, it is unlikely that this relationship between negative affect and reduced influence of priors holds true across different experimental paradigms. Kraus et al. (2021) have for example found that trait anxiety in participants was linked to increased usage of previously presented cues instead of stimulus characteristics when asked to judge the direction of a motion stimulus. However, Jia et al. (2020) have found shorter phase durations (i.e., less influence of perceptual priors) in bistable vision for patients with generalized anxiety disorder.

Considering these in part opposing effects of different forms of negative affect on perception in different tasks, one should be cautious when inferring a consistent relationship between negative affect and parameters of perceptual precision weighting – e.g., it leading to a global downweighing of priors relative to sensory evidence. In predictive processing theories, affect is conceived as currently experienced rates of PE. Actively changing sensory inputs so that they are more congruent to one's predictions by different behavioral strategies (active inference) has been suggested as the main mechanism by which humans achieve minimization of prediction errors (PEM) over time (Friston et al., 2011). PEM has therefore been suggested to be the driving force behind action selection (Friston et al., 2015): In case of high environmental uncertainty, an agent will choose the behavioral strategy that is expected to reduce uncertainty most effectively. We therefore propose that just as different behavioral strategies can, depending on the situation, lead to a reduction of experienced uncertainty (e.g., approach and avoidance behavior), the same could be true for perception. The experience of affective valence would then serve an incentivizing function, motivating specific adjustments in parameters of perceptual precision weighting that are expected to hold the highest probability of minimizing PE in subsequent experience. In the task presented here, ascribing high precision to the prior for uniformity leads to higher rates of PE, since it is inconsistent with sensory information. When experiencing excessive rates of PE resulting from negative affect, a downweighing of perceptual priors would be an effective strategy of PEM and lead to impeded perceptual filling-in in the uniformity illusion. One implication of this conceptualization is that the contingency between strategies of perceptual precision weighting and prediction error dynamics are task specific and that participants will learn to apply more effective strategies over time. In order to elucidate this question, in an exploratory analysis we found that in the present dataset, the link between negative affect and reduced perceptual filling-in appears to become stronger over the time course of the experiment (see supplements).

Overall, our results are in line with a predictive processing approach to cognitive penetrability, wherein current prediction error rates and therefore affective status can influence the respective weighting of priors and sensory evidence in current perceptual experience. Further, our study encourages the use of peripheral vision as well as perceptual filling-in phenomena as a promising method to further study the temporal and structural dynamics of affective status as an influential variable in cognitive penetrability.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.concog.2021.103258.

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Original Publication of Study 3

Kraus, N., & Hesselmann, G. (2022). Affective States and Traits and Their Influence on Perceptual Stability During Binocular Rivalry [Manuscript submitted for publication]. Retrieved from psyarxiv.com/enq8t

Abstract

Affective states and traits have been associated with different measures of perceptual stability during binocular rivalry. Diverging approaches to measuring perceptual stability as well as to examination of the role of affective variables (baseline affective state vs. mood induction; clinical vs. sub-clinical expressions of affective traits) have contributed to an inconclusive pattern of findings. Here, we studied the influence of affective traits (depressiveness and trait anxiety) and states (positive, negative and neutral; manipulated with a musical mood induction paradigm) on different measures of perceptual stability (dominance ratios and phase durations) during binocular rivalry. Healthy participants (N=50) reported alternations in a biased perception condition, during which one stimulus was more likely to be perceived than its counterpart (upright vs. tilted face), and in a control condition, in which both stimuli (Gabors of different orientations) were equally likely to be perceived. Baseline positive state affect significantly predicted longer phase durations during neutral viewing conditions, whereas affective traits did not yield any such effect. Furthermore, in an exploratory analysis, induced negative affect attenuated stimulus related bias in predominance ratios. Overall, we found a strong correlation between both measures of perceptual stability (phase durations and dominance ratios). Our findings thus question the distinction between different measures of perceptual stability during binocular rivalry and highlight the role of affective traits in its formation.

Introduction

When the brain is confronted with ambiguous sensory inputs, what typically happens is a back and forth switching between the plausible alternatives in subjective experience (e.g., when viewing the Necker cube). This phenomenon of multistable perception has been frequently used to study a potential link between perceptual experience and other mental variables that are typically considered to be independent of perception. Findings suggest influences from a diversity of extraperceptual constructs such as creativity, conscientiousness or autistic thinking style on temporal dynamics during multistable perception (Dunn & Jones, 2020; Jannis, 2013; Wiseman et al., 2011). All of these finding have been intensively discussed in the general debate over the cognitive penetrability of perception (CP, Macpherson, 2012), in which several researchers have questioned the possibility of extraperceptual variables ever being able to change what or how we see. Rather, they suggest, the described findings are best understood by extraperceptual variables influencing response behaviour or allocation of attention, but not perceptual experience per se (Firestone & Scholl, 2016).

A major candidate in the race over mental processes that could penetrate visual perception has been emotional experience in the form of affective states and traits. Several authors have argued for the *affective realism* hypothesis, wherein the influence of emotional variables would not be limited to guiding attention allocation. Rather, affective realism proposes that affect continually shapes current perceptions, including those of affectively neutral stimuli (Anderson et al., 2012; Siegel et al., 2018; Wormwood et al., 2019). Although several studies showed that stimulus valence influences perceptual processing of it (i.e., the probability of the stimulus being perceived and not its competitor; Alpers & Gerdes, 2007; Alpers & Pauli, 2006), this is usually not considered as an example of CP, as it is not an observer based variable influencing subjective experience, but a feature of the stimulus itself. However, these biases have been shown to be amplified in affective and anxiety disorders (Anderson et al., 2013; Gerdes & Alpers, 2014).

Notably, alternation rates (i.e., how often perception switches between both stimulus variants in a given time interval) during binocular rivalry have been shown to be significantly altered in those disorders not only with respect to aversive stimuli, but also in affectively neutral stimuli like gratings (Jia et al., 2015, 2020; Vierck et al., 2013). In a study of Jia et al. (2020)

different types of affective traits correlated with alternation rates during binocular rivalry. The average phase duration (i.e., the time it takes for perception to switch to the previously neglected stimulus variant) for affectively neutral gratings was almost twice as long in depressed subjects as it was in highly anxious subjects. However, results of these studies have been partly conflicting. For example, alternation rates in depression have been attenuated in some studies (Jia et al., 2015, 2020) but not in others (Miller et al., 2003; Vierck et al., 2013). Furthermore, it remains unclear whether the described effects are indeed attributable to altered emotional experience and not to some third variable that is also affected in patients. For example, processes like attention shifting and intentional control can crucially determine phase durations during rivalry (Lack, 2019) and have been shown to be altered in affective and anxiety disorders (Hsu et al., 2015).

Until now, only limited research has been conducted on potential influences of affective states and traits on rivalry dynamics of affectively neutral stimuli in healthy participants. Sheppard & Pettigrew (2006) found a strong correlation ($r = .8$, $p < .005$) between positive state affect and dominance ratio (i.e., the proportion of total viewing time with which a particular stimulus variant was perceived) of the two competing percepts during plaid motion rivalry. However, this result is based on a small sample size of only ten participants. Nevertheless, similar results have been reported in a study by Pettigrew & Carter (2002) in which positive mood state correlated positively with disappearance phases during motion induced blindness, a phenomenon that is typically considered as a form of bistable perception. In an experiment that was primarily aimed at studying how different stimulus features affect phase durations, Law et al. (2017) found a negative correlation of trait anxiety and depressiveness and average phase duration in a sample of healthy participants. However, the correlations were small (r`s = 0.22-0.27) and were found to be significant only in some stimulus variants but not in others. The study also did not find any significant correlation between subjective mood state and phase durations or predominance ratio of both stimulus variants, challenging the aforementioned results. Overall, research on the relationship of affective state and traits and altered processing of affectively neutral stimuli during bistable perception has yielded conflicting results, making further research worthwhile.

Here, we wanted to investigate a potential relationship of affective states and traits with different measures of perceptual stability in healthy participants during binocular rivalry. Based on the findings of Jia et al. (2020) we hypothesized that phase durations of affectively neutral stimuli would correlate positively with depressiveness and negatively with trait anxiety. Furthermore, based on Pettigrew & Carter (2002) and Sheppard & Pettigrew (2006), we expected state affective valence to alter the predominance ratio of the competing stimuli during binocular rivalry. More specifically, since our previous study (Kraus et al., 2022) indicated a potential link of positive affect and stronger reliance on priors in visual perception, we reasoned that positive affect would increase pre-existing biases and negative affect would reduce the same biases.

Methods

All experimental procedures, sample size, research hypothesis, exclusion criteria as well as statistical analyses were preregistered prior to data collection and can be accessed via aspredicted.org/S9J_TR9. All collected data, visual stimuli as well as the analysis script are publicly available under https://osf.io/2gyvu/.

Sample

The sample consisted of 59 participants who were recruited from a student pool as well as the general population and received either monetary compensation or course credit. Due to technical errors during the stimulus presentation (n=2), reported mixed percepts in more than 20% of the time (n=2) and less than 15 reported alternations in any of the experimental conditions (n=5), nine participants had to be excluded, resulting in the final preregistered sample size of 50 (33 female, 43 right-handed, age=27.94, SD=10.99). All participants had normal or corrected-to-normal visual acuity. Informed written consent was obtained from all participants after they received a detailed written description of the study. The experiment has been conducted according to the principles expressed in the Declaration of Helsinki and has been approved by the local ethics committee at Psychologische Hochschule Berlin (PHB).

General Procedure

Participants were seated in front of a 24" LCD screen (Acer KG241, 75Hz) in a dimly light room. They were asked to place their head on a chinrest 60 cm in front of the screen, watching through a stereoscope (Screenscope, LCD version). Questionnaires measuring affective traits depressiveness (PHQ-9, Kroenke et al., 2001), anxiety (STAI-T, Spielberger, 1983) as well as momentary positive and negative affect (PANAS, Watson et al., 1988) were completed by the participants before introduction to the experimental task. During a practice run, participants were verbally instructed to report any change of their current percept via button press. They were further informed of the possibility to report a mixed percept if no stimulus variant appeared to reach clear dominance over the respective other. One experimental block consisted of eight trials, in each of which two competing stimuli were presented for 90 seconds. The three experimental blocks differed by valence (positive, negative, neutral) of the mood induction, which consisted of 30s of listening to an acoustic stimulus prior to every trial (see next paragraph). In total, the experiment lasted between 50 and 60 minutes.

Auditory Mood Induction

The mood induction paradigm was adapted from our previous study on the relationship of affect on visual perception (Kraus et al., 2022). The paradigm is derived from the premise that preference to a musical stimulus is determined by its predictability and information content (Gold et al., 2019; Koelsch et al., 2019; Kraus, 2020). In order to induce positive affect, participants were asked to choose their preferred piece of music out of five preselected harmonic stimuli. All stimuli were instrumental and polyphonic, ranging between 90 and 105 bpm. To induce negative affect while holding the low-level features of the acoustic stimulus (such as volume, pitch and tempo) constant, the predictability of the piece of music was significantly reduced. This was achieved by separating the stimulus into short sound bites (ranging between 150ms and 300ms) and playing them in random order. Kraus et al. established that listening to both stimulus variants (harmonic and scrambled) leads to significant changes of reported affective valence. Since parallel auditory stimulation has been shown to influence phase duration during binocular rivalry (Borojevic, 2012), the acoustic stimuli were played before and not during visual stimulus presentation. Auditory stimuli were played on Sennheiser HD-25-1 II headphones. The order of stimulus valence conditions was counterbalanced across participants.

Visual Stimuli

Stimulus presentation and response detection were controlled using the PsychToolbox software package (Brainard, 1997) for Matlab (R2019b, MathWorks Inc., USA). Two sets of visual stimuli were presented to participants through a stereoscope at a size of 3.5° visual angle on a grey background. Stimulus sets were selected for in a pilot experiment to evoke either balanced perception of both stimulus alternatives or to induce a consistent bias towards one stimulus variant over the other, while ensuring equal low-level visual features between stimulus variants. The first stimulus set consisted of diagonally oriented Gabor patches (-45° and 45° from vertical; frequency = 6 cycles/°) which resulted in equal reported perception times of both stimulus variants during the pilot experiment. The second stimulus set consisted of an upright and a tilted face, which in the pilot experiment led to the upright face being reported to be perceived in about 60% of the time. To account for possible biases of eye dominance or preference toward a specific response button, side of stimulus placement on the screen as well as button assignment (i.e., assignment of perceived stimulus variant with the right or left arrow key) were randomized across trials within a block. Before every trial, participants received a visual description of which stimulus set they are going to see and the specific button assignment for that particular trial.

Statistical Analysis

In a first step, participants who reported mixed percepts in more than 20% of the time (n=2) were removed from the dataset. For all further analysis, time periods in which subjects reported to see a mixed percept were excluded from the analysis. Furthermore, we excluded all responses that indicated a stable percept of over 30 seconds (0.47% of all responses), since a typical phase duration spans between 2 and 10 seconds and particular long intervals could indicate low attention to the task (Zhang et al., 2011).

We preregistered the main analysis to consist of a generalized linear mixed effect model (GLMM) in which phase durations during neutral mood are predicted by stimulus set (faces, Gabors) and four questionnaire values (PHQ-9, STAI, PANAS scales positive and negative affect). Phase durations were assumed to follow a gamma distribution (Carmel et al., 2010). However, regression diagnostics indicated non-normality of residuals. We therefore compared model fits of four potential parametric distributions (normal, lognormal, Weibull, gamma; fitdistr package for R, Delignette-Muller & Dutang, 2015) to the observed phase duration values, which favoured the lognormal distribution. We changed our analyses accordingly to a linear mixed effects model of logarithmized phase durations, resulting in normality of residuals.

To test a potential influence of induced affect on dominance ratio, we calculated the proportion of time with which one stimulus variant was reported to be seen per condition (stimulus set and music valence). We then computed a repeated measures ANOVA on those proportion values including the predictors stimulus set (Gabors, faces) and music valence (positive, neutral, negative). Normal distribution of values by condition was checked with Shapiro-Wilk test. If sphericity was observed (indicated by Mauchly's sphericity test), we report ε as well as Greenhouse-Geisser corrected p-values.

Results

Phase durations in general followed a right skewed distribution with an average median of 3.39s (Fig. 1). Mixed percepts were generally rare (5.13% of all responses), accounting for 4.38% of all viewing time. A normal distribution for all questionnaire values was confirmed by Shapiro-Wilk tests.

To test for a potential influence of affective states and traits, a mixed effects regression model was calculated in which phase durations of trials with neutral valence were predicted by four questionnaire values (STAI-T, PHQ-9, PANAS-P, PANAS-N, each mean-cantered) as well as stimulus type (gabors, faces). Note, that in the preregistration process we planned this model to consist of untransformed phase durations, assuming they would follow a gamma distribution (GLMM). However, since regression diagnostics indicated a better fit of the observed durations to a log-normal distribution (see Methods section), we changed this analysis to a LMM of log-transformed phase durations. Stimulus type yielded a significant influence on phase durations (χ^2 (1) = 11.16, p < .001). Specifically, Gabors were associated with lower phase durations than faces (2.68 vs. 3.18s median duration, see Fig. 1). Contrary to our expectation, affective trait scores of depressiveness or anxiety did not show any significant relationship with phase durations (PHQ-9: χ^2 (1) = 1.42, p = .233; STAI-T: χ^2 (1) = 0.02, p = .889).

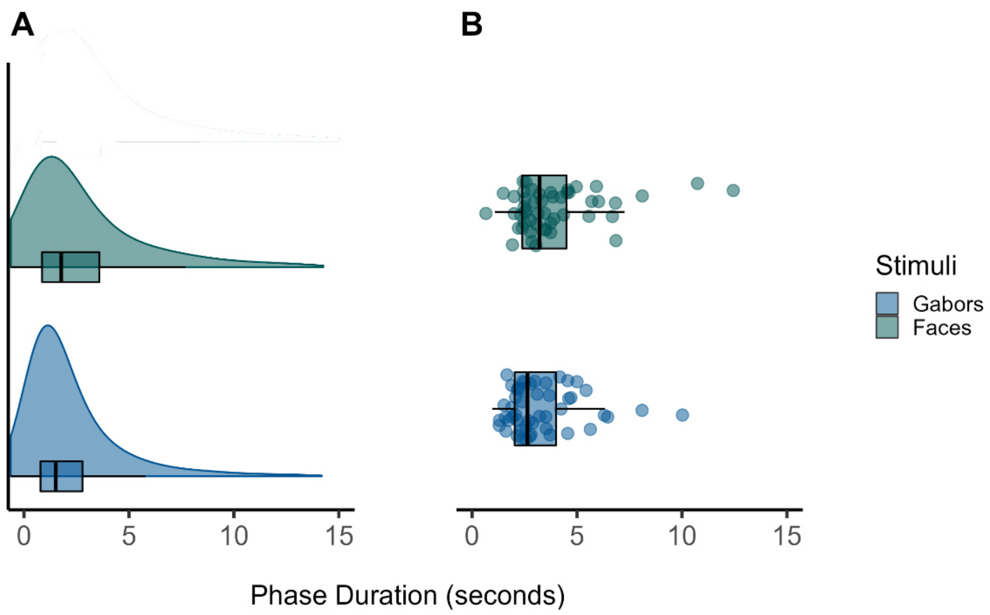

Figure 1: A) Density distributions by stimulus of phase durations (in seconds) and corresponding boxplots of all given responses (n=27145). **B)** Individual median values of participants by stimulus type and a corresponding boxplot

Positive state affect (as measured by PANAS P-scale) did show a positive relationship with phase durations (χ^2 (1) = 6.76, p = .009, Fig. 2), whereas a negative, albeit not significant trend, was measured concerning negative state affect (PANAS-N: χ^2 (1) = 3.06, p = .080). Importantly, given the nature of both variables, they were highly correlated (r = -.700), and should thus not be considered as independent predictors of phase durations. In order to further explore a potential relationship between state affect and phase durations, in an additional exploratory (i.e., not preregistered) analysis, we extended the analysis to the full dataset and added valence of the mood induction condition as a fixed effect predictor. However, music valence did not turn out to be a significant predictor of phase durations (χ^2 (2) = 2.52, p = .284) and it did not interact with stimulus type (χ^2 (2) = 1.38, p = .503).

The second preregistered main analysis was aimed at probing a potential link between music valence and preferential processing of a particular stimulus variant. For this, dominance ratios were calculated per experimental condition (stimulus type and music valence) and participant. To determine an estimate of individual bias towards a particular stimulus variant, we calculated difference values of dominance durations from .5 (i.e., the value to be expected if no bias was present). The resulting bias values were then predicted within a repeated

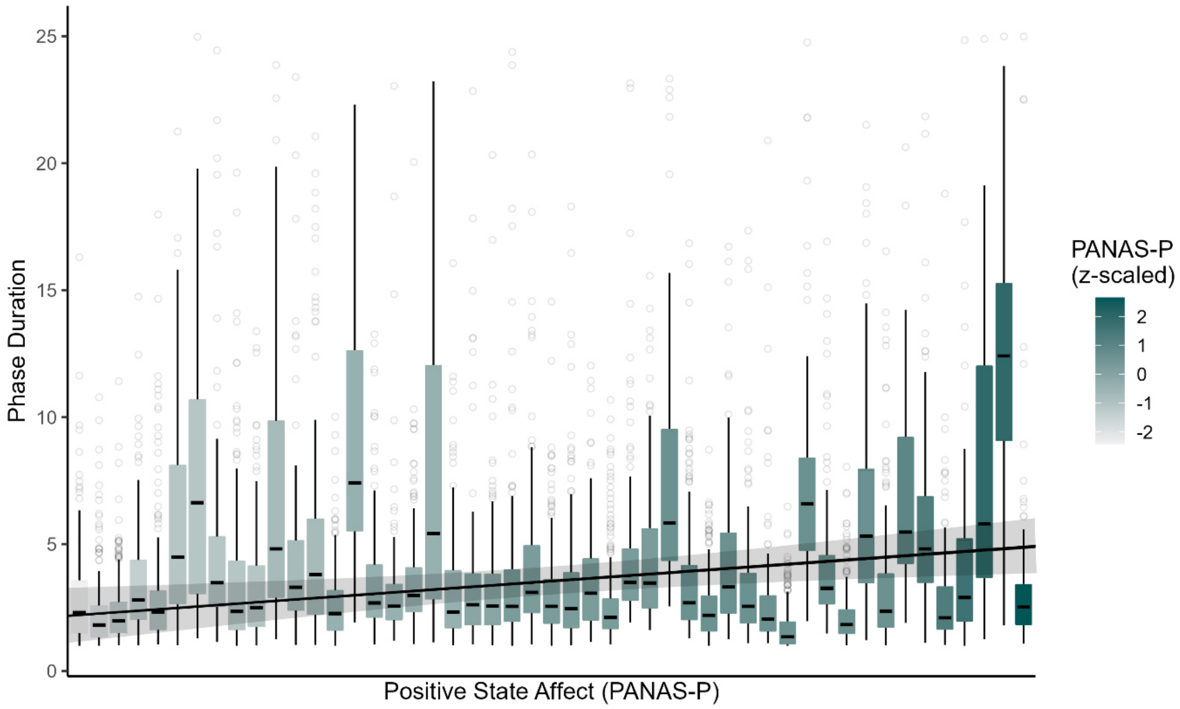

Figure 2: Boxplots of phase durations during neutral trials by participant, ordered along the x-axis by PANAS value (indicated by color gradient). Further depicted is a regression line and 95% confidence interval. Note, that the regression slope is calculated under the assumption of a linear progression of PANAS-P scores from lowest to highest observed value. However, some participants had equal PANAS-P values, which leads to slight deviations between phase duration values predicted by the LMM model and the plotted values of the regression line.

measures ANOVA by stimulus type (Gabors, faces) and musical valence (negative, neutral, positive). As expected, stimulus type yielded a significant influence on bias values (F(2, 49)=25.39, p <.001, η_p^2=.11). While there was a significant bias towards a particular stimulus variant in the face condition (upright face reported 56.75% of the time, SD=8.32), this was not the case for Gabor stimuli (leftward tilted Gabor reported 50.16% of the time, SD=4.39). However, music valence did not show a significant influence on bias values (F(2, 98)=2.55, p=.083, η_p^2=.01), and there was no significant interaction effect of music valence and stimulus type (F(2,98)=0.89, p =.355, η_p^2=.00; ε =.89; see Figure 3). In order to control for potential carryover effects of the mood induction (i.e., negative mood in one block influencing designated neutral mood in the following block) we carried out another exploratory analysis in which we limited the analysed data to only the first experimental block. Note, that since order of music valence was counterbalanced across participants, it was hence treated as a between-subject predictor in this analysis. Using this approach, stimulus type, (F(1, 47)=22.13, p < .001, η_p^2=.20), as well as music valence (F(2, 47)=5.07, p=.010, η_p^2=.09) yielded significant effects on bias values. Both factors did not significantly interact (F(2, 47)=2.73, p=.076, η_p^2=.06).

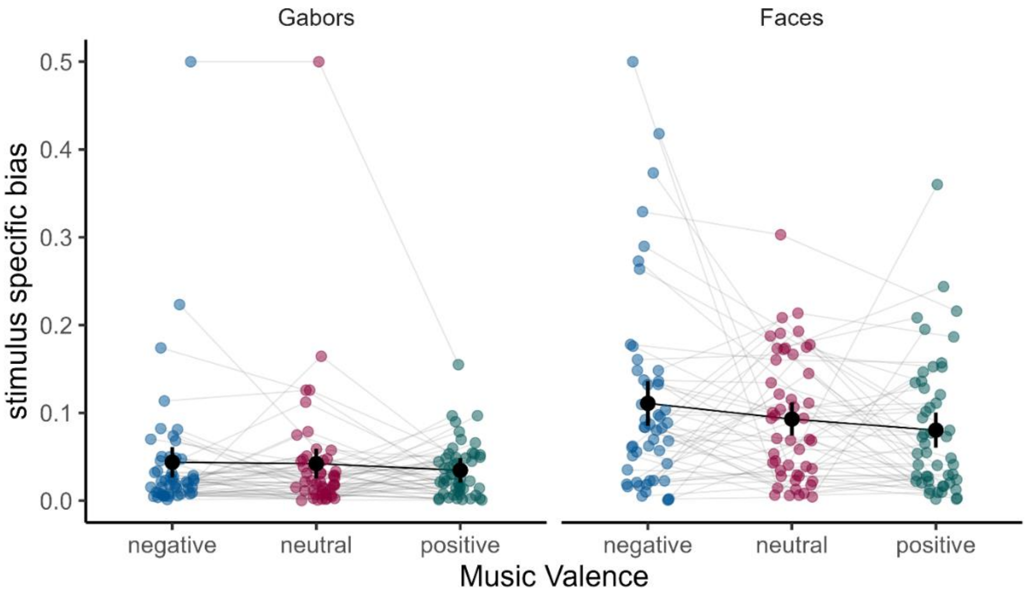

Figure 3: Average bias towards a specific stimulus variant per participant and experimental condition (music valence and stimulus type), as measured by difference from an unbiased (i.e.,50:50) proportion of both stimulus variants. Black bars represent group averages as well as 95% confidence intervals for within subject designs. The face stimulus, compared to the gabors, induces variant specific biases, since upright faces are preferentially perceived when competing with tilted faces. This effect is however not moderated by induced affective valence.

Pairwise post-hoc unpaired t-tests revealed that bias of participants in the negative condition was significantly lower than in the neutral ($t(31)= -3.32$, $p = .002$) and in the positive condition ($t(31)= -2.27$, $p = .030$). Values for the positive and the neutral mood condition did not differ significantly from one another ($t(32)= -0.99$, $p = .331$; see supplementary Figure S1).

In a last step, to better understand the relationship between the different measures of perceptual stability in our dataset, we computed bias scores and median phase durations across all stimuli and valence conditions per participant and correlated them. There was a significantly positive correlation ($r(48)=.54$, $p < .001$). This correlation remained significant even when the analysis was conducted separately for both stimulus types.

Discussion

The aim of this study was to further examine the potential relationship between affective states and traits to different measures of perceptual stability during binocular rivalry, given that previous research has yielded an overall inconclusive pattern of results. Here, we found that the two analysed measures of perceptual stability followed a pattern to be expected in a binocular rivalry task in healthy participants. Phase durations were generally right skewed, most values fell into a range between 2 and 10 seconds. We further found that stimulus type yielded a significant influence on phase durations, i.e., differently oriented Gabors tended to alternate faster than differently oriented faces. This effect may be caused by differences in low-level features or differences of familiarity between the stimuli, as both have been shown to affect phase durations (Blake & Logothetis, 2002; Yu & Blake, 1992). We also found stimulus type to have influenced dominance ratios, i.e., stimulus orientation affected the likelihood of a particular stimulus variant to be perceived significantly higher in faces than in Gabors, as was intended in order quantify stimulus specific bias.

Importantly, the two measures of perceptual stability in our study, could, in principle, be independent from each other (i.e., one could hold the amount of perceptual alternations in a given time constant but change the ratio with which both variants are perceived and vice versa). While many studies (e.g., Anderson et al., 2013; Law et al., 2017; Vierck et al., 2013), including ours, rest on this assumption of independence and treat both measures as outcome variables in separate statistical analyses, our results emphasize their interdepended nature. Hence, in a critical evaluation of the presented results, we suggest a categorization of them as different measures of perceptual stability during binocular rivalry.

Contrary to our hypotheses as well as previously described findings, affective traits did not significantly predict variance in phase durations. Importantly, the design of this study differed to previous ones in two ways. Firstly, previous studies have mostly focused on affective stimuli, e.g., bistable point walkers that could be perceived as either walking towards or away from the observer (Van de Cruys et al., 2012). The results could therefore stem from well-established differences in attention allocation, i.e., more socially anxious people will draw more attention towards the more anxiety provoking stimulus variant (e.g., a walker that is approaching the participant). Since our stimuli were deliberately chosen to be affectively neutral, such attentional biases will not have had substantial impact on alternation rates. Secondly, studies that have shown alternation rates to be elevated even when stimulus valence was neutral all showed this effect in clinical populations (Jia et al., 2015, 2020; Vierck et al., 2013; Xiao et al., 2018). Since in all the studied disorders (generalized anxiety disorder (GAD), major depression, bipolar disorder, schizophrenia) psychomotor, as well as cognitive functions, have been shown to be impaired (Etkin et al., 2022; Walther & Morrens, 2015), this is an important potential confound to be considered. However, Jia et al. (2015, 2020) have included catch trial conditions (trials in which both eyes receive the same input and perceptual alternations thus are the veridical percept), to control for potential behavioural differences of reporting current percepts and have not found significant differences between the groups. Furthermore, other authors (e.g., Vierck et al., 2013; Xiao et al., 2018) have included different tests of psychomotor functions and cognitive processing in order to rule out that differences in these constructs play a moderating role in explaining group differences in perceptual alternations. Nevertheless, it is conceivable that potentially important variables in which the diagnostic groups differed (e.g., susceptibility to mixed percepts or tendency to report them), were not considered as possible confounds in the experimental designs.

Notably, Jia et al. (2020) have found diverging directions of influence of anxiety and depression, i.e., depression was correlated with fewer perceptual alternations, whereas anxiety was correlated to more. Such effects are unlikely to occur in the general population, as trait anxiety and depressiveness usually are highly correlated, which in the case of our study is reflected by the multicollinearity of the regression model. For the purpose of their study, Jia et al. (2020) differentiated between GAD and depression patients, two disorders of which some comorbidity estimates reach up to 70% (Kessler et al., 1999). It thus seems unlikely that the effects described in their study are attributable to separate and opposing effects of different affective traits on perceptual stability. Rather, they might stem from a highly selective sampling process in which two characteristics that are usually highly interdependent were separated. Thus, several of the previously reported effects of affective traits on phase durations are best explained by attentional mood congruency biases of participants and selection biases concerning the participant sample. So far, only one study has found a statistically significant (positive) correlation between alternation rates of neutral stimuli and affective traits in a sample of healthy participants (Law et al., 2017). However, the effect sizes were comparably small and findings were inconsistent across different stimulus categories.

We further analysed affective state and its relationship with predominance ratios. In our preregistered main analysis, we did not find a significant effect of one’s affective status on preferential processing of a particular stimulus variant, adding to a generally inconsistent pattern of results. There are two previous studies that support said potential influence during perceptual rivalry with moderate to strong effect size estimates. Pettigrew & Carter (2002) found a positive relationship between positive state affect with the proportion of time that dots were perceived as compared to not perceived during motion induced blindness (MIB). Although the authors conceive MIB as a form of perceptual rivalry and both phenomena resemble each other in their temporal alternation dynamics, it has been disputed whether their appearance underlies a common neural mechanism (Jaworska & Lages, 2014). Sheppard & Pettigrew (2006), showed a strong influence of positive affect measured at the beginning of the experiment on the predominance proportion of the two potential stimulus interpretation during plaid motion rivalry (PMR). They further showed strong correlations ($r=.84$, $p < .001$) of alternation rates during binocular rivalry and PMR, suggesting an underlying common mechanism contributing to both phenomena. However, in contrast to our study, both studies focused on baseline affective state without manipulation of participants' mood.

In our dataset, baseline affective state did show a significant positive relationship with phase durations, suggesting an enhancing effect of positive affect on perceptual stability. Importantly, we have manipulated participants affective state and did not correct for potential carryover effects (e.g., through pauses between blocks). To rule out such carryover effects, we carried out an additional exploratory analysis which only included the first valence block. The results of this analysis found negative affect leading to less bias towards a particular stimulus variant. Taken together, both analyses indicate that affective states affect perceptual stability during binocular rivalry with respect to their valence. While we found higher baseline positive affect to be associated with longer phase durations, induced negative affective valence was related to attenuated bias towards a particular stimulus variant. This relationship is congruent with our preregistered hypotheses and with recent research from our group which demonstrated reliance on priors during a task of perceptual filling-in to be associated with induced affective valence (Kraus et al., 2022).

Furthermore, the presented findings are in line with an affective realism approach to the debate over cognitive penetrability of perception, in which the affective state of an observer is taken into account in the perception of its environment (Wormwood et al., 2019). This is especially noteworthy, since in the outlined experimental design all stimuli were affectively neutral and the results stem from a sample of the general population. Neither attention mediated mood congruency effects nor selective sampling and confounding characteristics of clinical populations are thus likely explanations of the described findings. Nevertheless, given their inconsistent nature (e.g., only negative but not positive induced mood leading to changes in dominance ratios), these results are to be interpreted with caution.

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Deutsche Zusammenfassung

Die Beziehung von Wahrnehmung und emotionalem Erleben wird in etablierten psychologischen Theorien traditionell als einseitig aufgefasst. Genauer gesagt, konzeptualisieren diese Theorien Emotionen als basierend auf bestimmten Wahrnehmungsinhalten. Diese Wahrnehmungsinhalte wiederum werden als unabhängig von personenzentrierten Variablen wie dem affektiven Erleben oder der Stimmung verstanden. Der in diesem Ansatz implizierte zeitliche Ablauf von Verarbeitungsschritten erscheint intuitiv korrekt, da die Wahrnehmung eines Reizes als notwendige Voraussetzung verstanden werden kann, damit dieser eine emotionale Reaktion hervorrufen kann. Dementsprechend sollte unsere Wahrnehmung eines Reizes nicht durch die emotionale Bewertung des Reizes beeinflusst werden. Trotz dessen lassen aktuelle Modelle mentaler Verarbeitung ein bidirektionales Verständnis von Interaktionen zwischen affektivem Erleben und Wahrnehmung zu.

In der vorliegenden Dissertation wird ein generelles Modell mentaler Verarbeitung (engl.: Predictive Processing) sowie dessen Anwendung in den Bereichen der visuellen Wahrnehmung und des affektiven Erlebens beschrieben. Basierend auf diesen theoretischen Überlegungen wird im Anschluss ein hypothetische Beziehung zwischen beiden Konstrukten abgeleitet. Diese postulierte Beziehung eröffnet die theoretische Möglichkeit der Beeinflussung von subjektiver visueller Wahrnehmung durch affektive Variablen. Im Anschluss werden die drei Dissertationsstudien beschrieben und zusammengefasst, welche unterschiedliche Aspekte positiven und negativen affektiven Erlebens sowie deren Auswirkungen auf Phänomene der visuellen Wahrnehmung empirisch untersuchen. Abschließend werden die Implikationen dieser empirischen Befunde auf den Diskurs um mögliche Auswirkungen affektiver Variablen auf die visuelle Wahrnehmung näher beschrieben.

Alle durchgeführten Experimente waren darauf ausgerichtet, mögliche Zusammenhänge zwischen affektiven Variablen und Parametern der perzeptuellen Abwägung (engl.: Precision Weighting) zu untersuchen. Bei diesem im Predictive Processing angenommenen grundlegenden Vorgang der visuellen Wahrnehmung werden eigene Erwartungshaltungen mit sensorischen Informationen auf Grundlage der jeweiligen Konfidenz in die Information abgewogen. In Studie 1 wurden die ProbandInnen gebeten, die Richtung eines präsentierten visuellen Stimulus einzuschätzen. Die Ergebnisse der Studie zeigten, dass sich Individuen mit höherer genereller Ängstlichkeit stärker auf einen prädiktiven Hinweisreiz verlassen als auf die tatsächlich präsentierte sensorische Evidenz. Die Ergebnisse von Studie 2 zeigten, dass induzierter negativer Affekt die Wahrscheinlichkeit illusorischer Wahrnehmungsinhalte in der sogenannten Uniformity Illusion verringerte. Dies legt den Schluss nahe, dass der Einfluss von Erwartungshaltungen durch negative Valenz des affektiven momentanen Erlebens herabgesetzt wird. In Studie 3 beeinflusste das momentane affektive Erleben die perzeptuelle Stabilität während binokularer Rivalität. Insbesondere positives affektives Erleben vor Experimentalbeginn war assoziiert mit niedrigeren Alternierungsraten, wohingegen während des Experimentes induzierter negativer Affekt mit verringerter Präferenz gegenüber spezifischen Stimuli einherging. Alle Studien wurden mit affektiv neutralen Stimuli und in Stichproben gesunder ProbandInnen durchgeführt. Die Ergebnisse basieren also wahrscheinlich nicht auf Unterschieden in der Aufmerksamkeitslenkung oder allgemein veränderten Verarbeitungsprozessen in klinischen Populationen.

Zusammenfassend sprechen diese Ergebnisse für einen möglichen Einfluss des affektiven Erlebens auf die visuelle Wahrnehmung. Die Ergebnisse heben die spezifische Rolle der Valenz des momentanen affektiven Erlebens hervor, wobei negative Valenz mit verringertem Einfluss von Erwartungshaltungen assoziiert war. Einen signifikanten Einfluss überdauernder affektiver Persönlichkeitszüge wie Depressivität oder Ängstlichkeit hingegen konnte über die verschiedenen Studien hinweg nur in Teilen gezeigt werden. Während Ängstlichkeit negativ mit der Tendenz korrelierte, neue sensorische Evidenz in der perzeptuellen Entscheidungsfindung zu berücksichtigen, konnte kein solcher Zusammenhang während binokularer Rivalität gezeigt werden. Eine Interpretation der Ergebnisse erscheint bei angenommener Unabhängigkeit von perzeptueller von affektiver Verarbeitung schwierig. Dementgegen erscheinen sie größtenteils kongruent mit einer Predictive Processing Auffassung von Emotions-Wahrnehmungs Interaktionen. Bei diesem Ansatz gehen sich verändernde Vorhersagefehlerraten mit Fluktuationen des momentanen affektiven Erlebens einher und regen eine Anpassung von Parametern der perzeptuellen Abwägung an. Die

Studien zeigten jedoch lediglich begrenzte Evidenz für die Konzeptualisierung von affektiven Persönlichkeitszügen als langanhaltende Tendenzen dafür, neue sensorische Informationen in aktuelle Wahrnehmungsinhalte zu integrieren. Aus den Ergebnissen ergeben sich wichtige Implikationen für unterschiedliche Vorstellungen von momentanem affektiven Erleben und affektiven Persönlichkeitszügen, deren Rolle in der perzeptuellen Verarbeitung, sowie für verwandte Themen wie die generelle Debatte über die Beinflussbarkeit von Wahrnehmung durch non-perzeptuelle Variablen.

Anteilserklärung

Studie I: Kraus, N., Niedeggen, M., & Hesselmann, G. (2021). Trait anxiety is linked to increased usage of priors in a perceptual decision making task. *Cognition*, *206*, 104474. (Study I)

- Entwicklung der Konzeption (mehrheitlich)
- Literaturrecherche (mehrheitlich)
- Versuchsdesign (mehrheitlich)
- Datenerhebung (in Teilen)
- Datenauswertung (mehrheitlich)
- Ergebnisdiskussion (mehrheitlich)
- Anfertigung der ersten Version des Manuskripts (mehrheitlich)
- Einreichung des Manuskripts und Korrespondenz (in Teilen)
- Überarbeitung des Manuskripts (mehrheitlich)

Studie II: Kraus, N., Niedeggen, M., & Hesselmann, G. (2022). Negative affect impedes perceptual filling-in in the uniformity illusion. *Consciousness and Cognition*, *98*, 103258.

- Entwicklung der Konzeption (mehrheitlich)
- Literaturrecherche (mehrheitlich)
- Versuchsdesign (mehrheitlich)
- Datenerhebung (in Teilen)
- Datenauswertung (mehrheitlich)
- Ergebnisdiskussion (mehrheitlich)
- Anfertigung der ersten Version des Manuskripts (mehrheitlich)
- Einreichung des Manuskripts und Korrespondenz (mehrheitlich)
- Überarbeitung des Manuskripts (mehrheitlich)

Studie III: Kraus, N., & Hesselmann, G. (2022). Affective States and Traits and Their Influence on Perceptual Stability During Binocular Rivalry [Manuscript submitted for publication]. Retrieved from psyarxiv.com/enq8t

- Entwicklung der Konzeption (mehrheitlich)
- Literaturrecherche (mehrheitlich)
- Versuchsdesign (mehrheitlich)
- Datenerhebung (in Teilen)
- Datenauswertung (mehrheitlich)
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- Einreichung des Manuskripts und Korrespondenz (mehrheitlich)
- Überarbeitung des Manuskripts (mehrheitlich)

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Nils Kraus

Berlin, 13.01.2023

Eidesstattliche Erklärung

Eidesstattliche Erklärung nach § 7 Abs. 4 der Gemeinsamen Promotionsordnung zum Dr. phil. des Fachbereichs Erziehungswissenschaft und Psychologie der Freien Universität Berlin vom 8. August 2016:

Hiermit erkläre ich, dass ich die vorliegende Dissertation selbstständig verfasst und ohne unerlaubte Hilfe angefertigt habe. Alle Hilfsmittel, die verwendet wurden, habe ich angegeben. Die Dissertation ist in keinem früheren Promotionsverfahren angenommen oder abgelehnt worden.

Nils Kraus

Berlin, 13.01.2023

Due to privacy concerns, the curriculum vitae has been removed from the online version of the dissertation.

List of publications

Kraus, N., (2020). The joyful reduction of uncertainty: Music perception as a window to predictive neuronal processing. *Journal of Neuroscience*, *40*(14), 2790-2792. https://doi.org/10.1523/JNEUROSCI.0072-20.2020

Kraus, N., Niedeggen, M., & Hesselmann, G. (2021). Trait anxiety is linked to increased usage of priors in a perceptual decision making task. *Cognition*, *206*, Article 104474. https://doi.org/10.1016/j.cognition.2020.104474 (Study 1)

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