Hearing while feeling: Affective influences on auditory perception

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Summary and Discussion

Perception is often understood as a direct and true reflection of our outer world. The plausibility of this view, however, has been challenged on various grounds. Information we receive through our senses is often incomplete or ambiguous and therefore needs to be combined with other available information to form a percept (e.g., Bruner & Goodman, 1947; Kersten & Yuille, 2003; McClelland et al., 2014). In addition, neurostructural and neurophysiological findings as well as recent predictive coding models of brain function are in agreement with the notion that information (e.g., perceptual, cognitive and affective information) is integrated at all levels of processing, including perceptual levels (e.g., see Angelucci et al., 2002; Markov & Kennedy, 2013; Ninomiya et al., 2012 [neurostructural]; Gilbert & Li, 2013; Rauss et al., 2011 [neurophysiological]; Clark, 2013; Lupyan, 2015a [predictive coding]). It has been argued that affect is an important and pervasive source of information, which changes how the brain processes incoming sensory information and informs conscious perception (e.g., E. Anderson et al., 2011; Asutay & Västfjäll, 2012; Barrett, 2017b; Barrett & Bar, 2009; Barrett & Bliss-Moreau, 2009; Meier et al., 2007; O'Callaghan et al., 2017; E. H. Siegel & Stefanucci, 2011; E. H. Siegel et al., 2018; Stefanucci et al., 2011; Stefanucci & Storbeck, 2009).

Several studies have investigated the idea that affect impacts basic perception in the visual domain, but only a few looked at affective influences on basic auditory perception (Asutay & Västfjäll, 2012; E. H. Siegel & Stefanucci, 2011;

Weisz et al., 2007). Previous research did show clear dependencies between affective state, affective quality, and affect disposition on the one hand and annoyance responses towards sounds on the other hand (Bartels et al., 2015; Crichton et al., 2015; Job, 1988; van Kamp et al., 2004; Miedema & Vos, 2003; Västfjäll, 2002; Västfjäll et al., 2003). These findings clearly demonstrate that affect can influence the way in which we experience sound. However, an annoyance response encompasses much more than auditory perception alone (e.g., it has a strong evaluative component to it as well). Therefore, inspired by these findings and by indications that affect impacts basic perception, we set out to explore affective influences on more basic aspects of sound experience.

The central issue of this thesis thus concerned the extent to which relatively basic auditory perception and processes are associated with affective states and traits. More specifically, it examined affective influences on pitch shift perception and masked auditory sensitivity. In our research we took efforts to avoid pitfalls common in studies about top-down effects on perception (see the Introduction chapter for a review of these pitfalls). The first section of the current chapter will provide an overview of the findings and conclusions of each of the four empirical chapters of this thesis. The second section will discuss general implications and limitations of our findings, thereby taking into account some of the pitfalls, and provide suggestions for future research. The last section of this chapter will provide an overall summary and conclusion of this thesis.

6.1 Overview of Empirical Findings

This thesis contained four empirical chapters. The current section will summarize each of these chapters.

Chapter 2: Effects of Mood on Pitch Shift Perception

To examine affective influences on auditory perception, in Chapter 2 we compared pitch shift perception between participants in a happy mood and a sad mood. We used tone pairs with an ambiguous pitch shift direction. That is, the pitch could be heard as going upward or downward in pitch from the first to the second tone depending on which of two pitch cues the participants used. We found a small, but significant, effect of mood on pitch shift judgment: Listeners in a sad mood judged tone pairs with ambiguous pitch shifts more often as downwards than happy listeners. This effect was not conditional on the response labels (“UP” or “DOWN”) of the buttons that the participants used to indicate pitch shift direction, which suggests that it was a genuine effect on pitch shift judgment and could not be attributed to response selection bias caused by an affective mapping effect (see Eder & Rothermund, 2008; Lavender & Hommel, 2007). The findings of Chapter 2 thus suggest that auditory perceptual judgment can be subject to affective influences, which is consistent with the idea that affect pervades our experience of the auditory world.

The findings are in line with several theories, such as the affect-as-information account of mood congruent judgments (Schwarz & Clore, 2007, 1983), or the notion that affective feelings activate conceptual metaphors that bias perception (Crawford, 2009; Meier & Robinson, 2004; Weger et al., 2007). Furthermore, we suggested that biased competition mechanisms (Desimone & Duncan, 1995) in the brain may have enhanced perception of the mood congruent pitch shift. However, the findings of Chapter 2 cannot answer the question at what level of processing biasing takes place and whether perception proper and/or perceptual judgment (assuming these can be separated) are affected by mood. Specifically, the possibility cannot be excluded that participants (consciously or unconsciously) adopted a more lenient criterion for judging pitch shift as upwards than as downwards in a happy state compared to a sad state or vice versa. In Chapter 3 and 4 we therefore did not attempt to measure perceptual bias but used a performance-based task measuring auditory sensitivity to minimize possible contamination by changes in the decision criterion.

Chapter 3: Inconsistent Effects of Mood on Sensitivity to Masked Sounds

In Chapter 3 we explored affective influences on auditory perception by comparing the masked auditory threshold, which is a measure of auditory sensitivity, between listeners in an anxious, sad, happy, or calm mood. This allowed us to disentangle possible effects of pleasure from effects of arousal on the masked auditory threshold and to check for interaction effects between these two dimensions of affect. Furthermore, we employed a 2IFC task to measure the masked auditory threshold, which yields a relatively unbiased measure of sensitivity in noise.

We investigated the effect of the pleasure and arousal dimension of mood on the masked auditory threshold in two experiments. In Experiment 1 the mood induction procedure was accompanied by affective music, while in Experiment 2 the mood induction procedure was accompanied by affective pictures. In Experiment 1 listeners in low arousal (calm and sad) moods had on average a lower masked auditory threshold, thus higher sensitivity, than listeners in a high arousal (happy and anxious) mood. Additional (polynomial regression) analysis suggested a curvilinear relation between subjectively experienced arousal and threshold, which reflected that listeners who reported very low subjective arousal or very high subjective arousal had higher thresholds (lower masked sensitivity) than listeners with a more intermediate (optimal) level. The presence of a curvilinear relationship is in line with theories about the relation between arousal and performance in general (Aston-Jones & Cohen, 2005; Easterbrook, 1959; Kahneman, 1973).

However, despite successful mood induction, arousal did not have the same effect in Experiment 2. In Experiment 2, the effect of arousal on the masked auditory threshold did not reach significance but in fact showed a trend in the opposite direction to the effect of Experiment 1. The inconsistent findings of the two experiments could not be explained by a curvilinear relation between subjective arousal and threshold across the two experiments. These results thus indicate that the effect of arousal on auditory masked sensitivity may depend on the modality of the mood inducing stimuli. We can only speculate about the exact cause of this dependency. We carefully matched sound level of the musical pieces used for the mood induction across mood conditions. It is thus unlikely that differences in sound level have caused differences in the threshold between low and high arousal conditions in Experiment 1. However, it was not possible to control for all other acoustic properties of the music, such as tempo, mode (minor, major) and other spectral properties because these properties are essential for giving the music its affective quality. Therefore, these acoustic differences, which were not an issue in Experiment 2, may have driven the effects in Experiment 1 (and not Experiment 2). To the best of our knowledge, such effects of music on the threshold have not been reported in the literature before. It may be of interest to explore such effects in future research. Furthermore, in addition to the difference in possible impact of acoustic properties, there were other differences between the experiments. The effect of the mood induction on subjective arousal tended to be more extreme in the pleasant conditions elicited by the music-based than by picture-based induction, which may have contributed to the discrepancy in findings between the two experiments. Also, more complex interactions between modality of mood-induction and elicited mood may have occurred. For example, attention may have been more focused on the auditory domain after music-based than picture-based mood induction, which may have had different consequences for the effects of arousal in each experiment.

The discussion of Chapter 3 provided several suggestions for further research into the dependencies between affective state and auditory sensitivity, some of which will be discussed below. In Chapter 4 we also further investigated the relationship between auditory sensitivity and affect. However, in contrast to Chapter 3, we looked at affect as disposition (trait) rather than state, because it has long been suggested that there is a link between perceptual sensitivity and dispositions such as affective reactivity to stimuli.

Chapter 4: The Relationship Between Trait Reactivity and Perceptual Sensitivity

In Chapter 4 we examined the relation between (auditory and general) sensitivity to weak stimuli and self-reported reactivity to strong stimuli. Several theorists have suggested that sensitivity and reactivity are two sides of the same coin (Aron & Aron, 1997; Eysenck, 1967; Nebylitsyn et al., 1960), while others argue that they are independent characteristics (Ellermeier et al., 2001; Evans & Rothbart, 2008). As we reviewed in Chapter 4, previous studies yielded inconsistent results regarding this matter. Those studies only considered reactivity in terms of the individual tendency to experience unpleasant affect (punishment reactivity) resulting from strong sensory stimulation. In our study we also took into account the individual tendency to experience pleasant affect (reward reactivity) resulting from strong sensory stimulation. We included this additional measure of reactivity based on predictions following from the neurobehavioral framework of the Predictive and Reactive Control Systems (PARCS) theory (Tops et al., 2010, 2014).

We found that self-reported as well as objectively assessed sensitivity to weak stimuli was associated with self-reported punishment and reward reactivity to strong stimuli. Importantly, however, these relationships only became apparent when the reactivity measures were controlled for each other, indicating a mutual suppression effect. The fact that previous studies did not take this suppression effect into account may explain the inconsistent results of these studies.

The findings of Chapter 4 thus suggest that sensitivity to weak stimuli and reactivity to strong stimuli are related tendencies, but this relationship may be obscured if punishment and reward reactivity are not both taken into account, which is in line with PARCS theory. Auditory sensitivity in noise thus seems associated with affect dispositions, specifically those concerning reactivity to strong environmental stimuli. Another relevant type of affect that may in part determine the auditory perception of environmental stimuli is the affective quality of those stimuli themselves. In the Chapter 5 we examined a method that could aid in studying how basic processing of auditory stimuli is influenced by their affective quality.

Chapter 5. Evaluative Conditioning as Method to Avoid Confounding by Low-Level Perceptual Feature Differences

In Chapter 5 we examined whether evaluative conditioning (EC) could be used to create changes in the affective quality of short environmental sounds. Through EC a stimulus can acquire positive or negative affective value by pairing it with another positive or negative stimulus respectively (De Houwer et al., 2001; Hofmann et al., 2010; Levey & Martin, 1975). EC effects have been demonstrated for various types of stimuli under various conditions but have been hardly studied in the auditory domain. Therefore we examined whether EC effects and its properties are generalizable to the auditory domain. This also allowed us to assess whether EC could be helpful in studying effects of affective quality on basic sound perception. Differences in affective quality of environmental sounds (e.g., the sound of a baby crying or a bird singing) is frequently accompanied by differences in low-level features of these sounds (e.g., frequency components and amplitude), which may confound effects of affective quality on basic auditory perception. Evaluative conditioning may allow manipulation of the affective quality of a stimulus, while its physical properties remain the same. EC as a tool to study processing of affective environmental sounds should enable changes in valence in both negative and positive directions. Furthermore, these changes in affective quality should be genuine and not attributable to demand effects, and, to make it suitable for psychophysical and psychophysiological studies, applicable to short sounds and lasting over repeated presentation of these sounds in the absence of unconditioned stimuli. These properties were investigated in two studies.

In Experiment 1, neutrally evaluated short (< 400 ms) environmental sounds were repeatedly paired with positive, negative, or neutral words during an evaluative conditioning phase. Next, affective quality of the sounds was assessed by means of direct subjective ratings as well as by an affective priming task. The latter is an indirect measure of affective quality of which the outcome is relatively difficult to voluntary control for participants. We found affective priming effects on this task for sounds with a pre-existing positive or negative affective quality. This showed that the affective priming task, which was originally designed for visual stimuli, indeed reflected affective evaluation of short affective sounds. The results regarding the affective quality of the conditioned sounds were as follows: Affective priming effects in the expected direction were found for sounds that had been paired with positive or with negative unconditioned stimuli. The sounds had thus acquired the expected affective quality through EC and this quality was relatively automatically reflected in behavior. The subjective ratings reflected the EC effect only for sounds paired with negative words. Experiment 1 thus demonstrated that EC brought about genuine changes in affective quality in the negative direction, and to a lesser degree in the positive direction.

In Experiment 2, we investigated to what extent the EC effect for environmental sounds was a lasting effect. In this experiment an evaluative conditioning phase was followed by a substantial number (40) of extinction trials in which the conditioned sounds were presented in absence of the unconditioned stimuli while repeatedly asking people to rate the affective valence of the sounds. The results of this experiment largely replicated the EC effects on subjective ratings found in Experiment 1 but in this case the pairing with positive unconditioned stimuli also yielded a near significant EC effect. Furthermore, the second experiment indicated that the acquired affective quality remained present over a substantial number of extinction trials. The sizes of the EC effects were however numerically smaller at the end of the extinction phase than directly after the EC phase. Those findings suggests that EC as a method is suitable for applying enduring affective changes and can be used for psychophysical and psychophysiological studies, which require repeated presentation of (conditioned) sounds in absence of the unconditioned stimuli. However, since the effects were less pronounced after the extinction phase, compared to directly after conditioning, it may be advisable to add reconditioning phases after repeated conditioned stimuli-only presentations.

Taken together, EC induced genuine and lasting changes in affective quality of short environmental sounds in negative and, albeit subjectively to a lesser extent, positive direction. These findings show the potential of employing EC as a method to avoid confounding by low level sound features when studying auditory processing and perception of affective sounds: It enables employment of short acoustically identical stimuli that have acquired different affective valence for different individuals.

A point of concern for the use of EC may be that findings regarding processing of sounds with acquired valence do not apply to other affective sounds. Some researchers argue that biologically relevant stimuli, such as snakes and spiders, are processed more efficiently than stimuli that have acquired their emotional value through learning, such as knives and guns (Öhman & Mineka, 2001). This point should not discourage one to use EC. In fact EC will allow comparing auditory processing of biological and learned affective sounds. Furthermore, many stimuli we encounter have acquired their emotional value over life (Juslin & Västfjäll, 2008; Rozin & Millman, 1987). A full understanding of emotional sound processing is thus best served by also studying stimuli with acquired valence. EC is thus a valuable tool in the study of affective sounds processing.

6.2 Taking Stock and Moving Forward (II)

Now that the empirical findings of this thesis have been summarized in the previous section, the current section will evaluate these findings in the light of the penetrability debate. Furthermore, the current section will assess what may be inferred from these findings regarding our responses to the day-to-day auditory environment. This section will also address several important limitations of the studies presented in this thesis and explore how we can move forward from here to learn more about the integration between auditory perception and affect.

Implications for the penetrability debate

As discussed in the Introduction chapter of this thesis there has been a long-standing debate about the degree to which perception can be modulated by cognition or affect. This so-called penetrability debate formed an important background for understanding the theoretical relevance of our overall research question. The current thesis cannot, and also did not aim to, provide a final answer to this debate, which may be unsurprising given the fact that the debate has been running for over more than a century. The discussion below will however provide some reflection on how the findings of this thesis may (and may not) contribute to the penetrability debate. Please refer to the Introduction chapter for a discussion about the difficulty to define what the concepts of "penetrability", "affect" and "auditory perception" exactly entail. The following sections will evaluate our findings against specific requirements for penetrability that have been set by some authors (Firestone & Scholl, 2016; Pylyshyn, 1999) and will delineate between "perceptual" and "decision" processes based on the framework of signal detection theory (Green & Swets, 1966).

Alternative explanations

In order to demonstrate that affect penetrates perception one should be able to exclude possible alternative explanations for effects of affect on measurements of perception. First, the affect manipulation should only create the intended affective differences between conditions, and not other differences that may impact auditory processing, such as acoustic auditory feature differences. This point has already been discussed above in the overview of Chapter 3 and 5. Second, differences in outcomes of perceptual tasks between affect conditions should reflect differences in perceptual and not in non-perceptual processes. In fact, most of the pitfalls mentioned by Firestone and Scholl (2016, particularly #2, #4, #5 and #6, see Introduction chapter) refer to this latter requirement. However, as argued in the Introduction chapter, certain attention and memory processes in fact seem to be integral to perceptual processing, and may be exempt from this requirement. In order to demonstrate affective penetrability of (early) perceptual processing, one should thus rule out that affect modulated judgment (pitfall #2) or response (pitfall #3) instead of perceptual processes. As expounded in the Introduction chapter, we took several measures to abate the influence of task demand and response bias on the results. These measures make it unlikely that the effects found can be attributed to these factors. Effects on judgment as alternative explanation for affective modulation of perception, however, could not be ruled out in all chapters. In Chapter 2 we explicitly attempted to measure bias in perceptual experience using an appearance-based measure. Both decisional and perceptual biases would be reflected in the outcome of this measure (see Introduction chapter and further below for explanations). Therefore, as mentioned, we could not exclude the possibility that the biasing effect we found of mood on pitch shift judgment was an effect on judgment rather than on perceptual processes. By contrast, in Chapter 3 and 4 we measured auditory sensitivity using a task that minimized contribution of judgment bias and the task outcome thus more likely reflected perceptual processes only. In Chapter 3, however, affective state did not unequivocally cause changes in auditory sensitivity. In Chapter 4 we did find a relation between affective disposition towards strong environmental stimuli and auditory sensitivity. However, the study design of Chapter 4 was correlational and therefore the findings of this study do not allow conclusive statements about the causal nature of the relationship between affect disposition and auditory sensitivity. In fact, based on PARCS theory and previous studies we hypothesized that both outcomes may be (partly) driven by activity of the salience network, which does not seem to suggest a direct effect of affect on early perception.

Together the findings presented in these three chapters do not provide sufficient basis to conclude (nor refute) that affect penetrated early auditory processing in a strict sense. This is not to say that our findings are not meaningful or do not provide any contribution to the penetrability debate. The summary below will elaborate further on this point, but first the discussion will focus on another aspect of penetrability: semantic relatedness.

Semantic relatedness

Some definitions of penetrability entail that perception is only truly penetrated by affective or cognitive states when there is a semantically coherent relation between the content of these states and the content of the penetrated perceptual process (e.g., Pylyshyn, 1999). This criterion for penetrability has also been referred to as the semantic criterion (e.g., Cecchi, 2014; Stokes, 2013). One could argue that such a meaningful, or semantically coherent, relationship between the penetrating state and perception was present in the studies presented in Chapter 2. We theorized that the affective meaning of one's current state (i.e., positive or negative) shaped the content of the perceptual judgment (i.e., up or down pitch shift) in a meaningful (i.e., positive = up; negative = down) way. Such meaningful relationship however was less clearly present in Chapter 3 and 4. The aim of the studies in these chapters was to examine to what extent auditory sensitivity in general was associated with affective state or trait. Such an effect may be considered similar to a change in heart rate due to a belief that there is danger looming, which can be explained purely in biological or physical terms, and thus is not a case of cognitive or affective penetration (Pylyshyn, 1984; see Cecchi, 2014). We did not examine to what extent sensitivity to specific stimuli or features, and thereby the content of perception, was meaningfully related to the content of the affective state. That is, we did not use different stimuli to examine differential effects on sensitivity depending on the affective meaning of the state. So even if in Chapter 3 we had found unequivocal changes in auditory sensitivity due to changes in mood, according to some definitions of penetrability, this would not have demonstrated cognitive penetrability of auditory processing by affect. Thus, while the sensitivity measure in Chapter 3 and 4 offered a more "pure" measure of perception, this came at the expense of being able to measure bias in perceptual content.

Summary

Given the inconclusiveness regarding the (perceptual or decisional) locus of the effects found and the fact that there was no semantic relatedness between affect and perception in all chapters, the findings of the presented chapters do not yet permit firm conclusions regarding affective penetration of early audition. However, we did find that basic auditory perceptual judgments were dependent on affective state in a meaningful way (Chapter 2). This does suggest that auditory perceptual experience is at least to some degree penetrable by affect. This is not a trivial notion, because affective penetration of perceptual experience may have consequences for how we further appraise and respond to the stimuli in our environment and thus for our daily interaction with the world. The next section will elaborate on this point. The subsequent section, on limitations and suggestions for further research, will describe some ideas for studies that may allow more conclusive statements about affective penetrability of early auditory processing.

Implications for understanding responses to environmental sounds

Implicit in the reasoning towards formulation of the research question has been the belief that if affect were to influence basic auditory processing and perception, this would establish the pervasiveness of affect in auditory processing. This, in turn, would make a stronger case for taking affective influences seriously when studying determinants of day-to-day responses to sounds, including reactivity or annoyance. In other words, if affect influences basic perceptual processes such as those underlying pitch shift perception and sensitivity to sounds, it will likely also influence higher-level affective responses and cognitive beliefs regarding sound. At the time the research questions were formulated there was some evidence that brief affective states modulated early auditory brain potentials (Al-Abduljawad et al., 2008; Baas et al., 2006), and a limited number of behavioral studies had suggested that affect impacted visual perception (Bocanegra & Zeelenberg, 2009; Phelps et al., 2006). Given that we found some tentative indication that basic auditory perception is affectively informed, our findings fit within this body of research. For a full understanding of auditory perception, it thus seems noteworthy to take affective influences into account. Future studies may examine directly whether affect-induced changes in basic perception mediate changes in annoyance responses or attitudes towards sounds or other environmental stimuli.

The findings of Chapter 4 have additional implications for our understanding of noise annoyance or annoyance produced by other day-to-day environmental nuisances. In particular, the findings have implications for examining the temperamental and psychophysical determinants of annoyance. In Chapter 4 we found that reward reactivity suppressed the relation between (auditory and general perceptual) sensitivity and punishment reactivity. Reward reactivity will thus likely also suppress any association between perceptual sensitivity and noise sensitivity, which can be understood as a measure of punishment reactivity in the auditory domain and which is an important predictor of noise annoyance. This could lead to the conclusion that perceptual sensitivity is a negligible factor in explaining noise sensitivity or annoyance. However, based on the findings of our study we would expect that there is a relation between perceptual sensitivity and noise sensitivity, but this may only be revealed when reward reactivity is controlled for. Therefore, it is advisable to include measures of reward reactivity to strong stimuli in future studies and to control for it in order to gain a more complete picture of the determinants of noise annoyance. This is likely also the case for understanding other types of annoyance.

Finally, based on the findings of Chapter 2 it can be speculated that affective biases towards specific features of environmental stimuli contribute to the perpetuation of affective states and perhaps even symptoms of affective disorders. The argument here is as follows: If perceptual judgment is biased by current mood, and perception is taken by the individual to reflect reality, mood biased perception thereby justifies and perpetuates the individual's current mood. This is similar to the notion that the recall of mood-congruent memories facilitated by one's current mood will strengthen and prolong this mood (Bower, 1981). It also fits with findings of mood-congruent attention biases found in individuals with affective disorders (García-Blanco, Perea, & Livianos, 2013; Koster, De Raedt, Goeleven, Franck, & Crombez, 2005; F. C. Murphy et al., 1999) and the idea that such biases play an important role in the etiology and maintenance of mood disorders (Beevers & Carver, 2003). In fact, mood biases in basic perception may be particularly persistent. Why would this be the case? For one thing, in daily life, perceptual experiences are ordinarily taken to provide true knowledge of the outer world and are used to justify our beliefs about it (e.g., S. Siegel & Silins, 2014). For another, it may be difficult to become aware of such biases because they do not concern obvious or explicitly affective content. It thus seems a worthwhile endeavor to explore whether biasing effects of mood on pitch shift perception extend to more chronic affective states as found in mood-disorders and the possible role of such biases in the maintenance of these states.

Limitations and Suggestions for Further Research

Various limitations to our studies and suggestions for further research have been provided within the chapters concerned and earlier in this discussion. This section will elaborate further on some of these limitations and suggestions and where possible integrate them across chapters.

Separating bias and sensitivity

As mentioned, the effect of mood on pitch shift judgment found in Chapter 2 may be explained by an increase in sensitivity to mood congruent cues (i.e., up-going pitch shift in happy mood), by a lowered criterion for identifying mood congruent cues, or by a combination of both. Similarly, as discussed before (see Introduction chapter and Chapter 3), previous findings of increased perceived loudness in high arousal negative mood (E. H. Siegel & Stefanucci, 2011) may also be explained as increased auditory sensitivity and/or as biased judgment. It thus seems warranted to explicitly investigate the relative contributions of bias and sensitivity to mood modulation of auditory perception. The designs used in Chapter 2 and also in the other chapters did not allow for investigating this. In Chapter 3 and 4 we opted for a 2IFC adaptive method, instead of a signal detection task that allows calculation of bias and sensitivity. As explained in the Introduction chapter the reason for this choice was that task efficiency was an important consideration given the likely fleeting nature of induced moods. At the time we designed the experiments, there were no efficient (i.e., adaptive) testing methods available that yielded estimates of both sensitivity and the criterion. However, recently new methods have been developed based on signal detection theory and Bayesian adaptive inference that do exactly this (Lesmes et al., 2015). Using these new methods for investigating effects of mood on perception provides a promising avenue for further research.

A word of caution is in place here in case one aims to apply signal detection measures (adaptive or non-adaptive) to establish perceptual bias. In order to study biasing effects of mood, or other conditions, on perception of particular stimuli or features, it seems suitable to employ a discrimination task and compare the outcome on this task between conditions. A discrimination task requires participants to decide on each trial which of two different signals was presented (e.g., whether a tone pair with up-going pitch shift or a tone pair with down-going pitch shift was presented). Note that this task is different from a detection task where participants decide whether a signal was present or not. If a discrimination task is used, it is important to realize that it is ill suited to look at differences in sensitivity (d') between conditions to determine if there was a bias in perception or not (Witt et al., 2015). A bias in perception will not show up in the sensitivity measure but in the criterion calculated from these tasks. However, one can also not simply interpret a shift in the criterion as measure of perceptual bias because it can be confounded by decision or response bias. One solution to this problem is to use a detection task instead of a discrimination task. If a detection task is used, perceptual biases will be reflected in the sensitivity measure (e.g., higher detection sensitivity for up-going tones in positive compared to negative mood) and the criterion will reflect only decisional processes.[1]

It should be noted, however, that effects on perception of near threshold stimuli typically used in detection tasks do not necessarily translate to supra threshold levels because different processes may be at work (Dalton, 1996). Therefore, it is important to use evidence obtained by a variety of other techniques. This points aligns with a general recommendation that should be followed to answer the question to what extent affect influences auditory perception and/or judgment: Various methods should be used and it should be examined to what extent outcomes of these methods converge (see also, Philbeck & Witt, 2015). For example, as discussed in the Introduction chapter, a promising approach is to use behavioral and psychological measures in combination with neuroimaging and electrophysiology techniques. The latter allow measurement of the location and timing of the effects in the brain, and the former provide interpretations of these effects. In the case of pitch shift direction, first more should be learned about the process that transforms stimulus information to the decision outcomes, such as which auditory-driven responses are used as evidence to form the pitch shift decisions (see Tsunada et al., 2016). While in recent years some progress has been made in understanding how and where in the brain sensory inputs are translated into perceptual decisions, this is still a matter of ongoing research (Tsunada et al. 2016).

[1] This is an important issue because, as Witt et al. (2015) argue, several researchers using a discrimination task appear to have erroneously concluded that effects of a manipulation were not perceptual but due to response bias. These researchers arrived to this conclusion because they only found effects of a manipulation on the criterion and not on the sensitivity measure derived from a discrimination task. As mentioned in the text, this conclusion is erroneous because when a discrimination task is used a bias in perception will in fact generally show up as an effect on the criterion and not on the sensitivity measure. The perceptual bias does not show up in the sensitivity measure because the manipulation does not only shift the probability distribution (see Introduction chapter) of one of the signals but of both of the signals. In other words, the distance between the distributions, and thus the sensitivity measure, remains the same regardless of the manipulation. Instead, the shift in the two distributions will show up as a change in the criterion. However, an effect on the criterion does not guarantee that there is a perceptual bias, because the criterion reflects both perceptual and response bias. So, in the context of discrimination tasks, perceptual bias and response bias cannot be discerned. If instead of a discrimination task a detection task is used, the manipulation will only shift the S (signal) and not the SN (signal+noise) distributions and therefore perceptual biases will be reflected in the sensitivity measure and the criterion will reflect only decisional processes. For more information, examples and graphical explanations regarding this issue see Witt et al. (2015)

Semantic relation between affect and perception

As discussed above, the type of affective influence that Chapter 3 and 4 aimed to measure did not follow the semantic relatedness criterion used in some definitions of penetrability. The aim of the studies in these chapters was to examine to what extent auditory sensitivity in general was associated with affect. Future studies are needed to elucidate to what degree affect, depending on relatedness in affective meaning, selectively influences sensitivity to specific stimuli or features. To this end, the methods of Chapter 3 (with the improved adaptive methods discussed above) and Chapter 5 may be combined. In Chapter 5 we showed that EC induces long lasting changes in affective quality of short sounds. By using positively and negatively conditioned sounds as targets in (separate) adaptive masked threshold tasks, it can be investigated to what extent effects of mood on auditory sensitivity depend on the affective quality of the sound. Furthermore, a meaningful connection between the affective state and the stimuli used for the perceptual task may also elicit more clear effects of affect on perception than those found in Chapter 3, which focused on perception of a 1 kHz tone that had no clear affective connotation.

Mechanisms

Each of the first three empirical chapters have provided suggestions for plausible neural mechanisms that may underlie affective modulation of auditory perception. So far, however, we have not tested these mechanisms explicitly. Further research should be designed to specifically test which of these mechanisms indeed mediate affective modulation of auditory perception. The following discussion briefly describes the three main mechanisms we have proposed in the empirical chapters and how these mechanisms may be tested. In Chapter 2 we suggested that biased competition mechanisms may explain mood biases in perception. One of the ways to test plausibility of this mechanism is to use neural network modeling techniques to verify if psychophysical findings, and, if available, neuroimaging findings of mood biased pitch shift perception can be explained by biased competition (for a neural network modeling study of pitch shift bias by auditory context, see Huang, Englitz, Shamma, & Rinzel, 2015). Furthermore, in Chapter 3, we suggested that changes in tonic NE activity of the LC may mediate effects of arousal on auditory sensitivity. Indeed, animal studies provide some support for the hypothesis that tonic NE modulates sensory coding in the brain and it has been suggested that NE plays a role in adaptation of perceptual processing to the demands of the current context. However a causal link between NE modulation of sensory neurons and perceptual changes has not been clearly established (Devilbiss, 2019). As we have suggested in the discussion of Chapter 3, parametric manipulations of arousal are needed to further investigate the possibly curve-linear relationship between arousal and auditory perceptual sensitivity. This should be combined with monitoring NE activity, for example by the use of pupil dilation as an index of NE[2] (Aston-Jones & Cohen, 2005; P. R. Murphy, Robertson, Balsters, & O'Connell, 2011; Nieuwenhuis, De Geus, & Aston-Jones, 2011), in order to analyze to what extent this index of NE mediates the influence of affective arousal on perception (see Jepma & Nieuwenhuis, 2011 [pupil size and decision making in humans]; McGinley et al., 2015 [pupil size and auditory perception in mice]). Finally, in Chapter 4 we proposed that individual differences in the tendency to engage the salience network may explain the relationships we found between reactivity measures and perceptual sensitivity. This can be investigated in a neuroimaging study that examines how reactivity and sensitivity traits relate to functional connectivity of the salience network in rest (see e.g., Markett et al., 2013; Seeley et al., 2007) and, possibly, also during task performance (see e.g., van Tol et al., 2013).

Generalizability

A final limitation of our studies is that most of the participants involved were young-adult females. Our findings should not be too hastily generalized to males and older individuals. Some differences between men and women in terms of pitch perception discrimination abilities and auditory sensitivity have been found (Rammsayer & Troche, 2012). Age has also been associated with hearing sensitivity (D. Robinson, 1988). Whether sex and age interact with effects of emotion on these auditory abilities is a question to be further investigated.

6.3 Conclusion

The studies described in this thesis contributed towards answering the question to what extent basic auditory perception and processing is associated with affect. Based on the results from these studies the following brief answer can be provided. Overall, we found some evidence for involvement of affect

[2]It should be noted however, that while pupil size is closely coupled to NE activity, it may also reflect activity of other neuromodulators (for recent discussions, see McGinley, David, & McCormick, 2015; Totah, Logothetis, & Eschenko, 2019).

in auditory perception, although the effects and relations were subtle. We found a small, but significant effect of mood on pitch shift judgment. Pitch shift direction was more frequently judged upwards by individuals in a happy mood compared to individuals in a sad mood. We also studied the effects of mood on auditory sensitivity. The effects of the arousal dimension of mood on sensitivity to sound in noise were inconclusive and seemed conditional on the mood induction modality. No effects of the pleasure dimension of mood on auditory sensitivity were found. However, we found that auditory sensitivity as well as general perceptual sensitivity were associated with affect disposition, specifically, affective reactivity towards strong stimuli. Notably, this association was only revealed when both approach reactivity and avoidance reactivity were taken into account. Finally, our last study showed that evaluative conditioning, used as a method to create affective quality in sounds, offers promising prospects to study auditory processing of affective sounds, because it allows avoiding the pitfall of confounding by low-level stimulus features.

Although our findings indicate that seemingly straightforward auditorily determined responses such as pitch shift perception and detection of sound in noise are associated with affective state or trait, more research is still needed to draw definitive conclusions regarding penetrability of early auditory perception by affect. There are various ways to further investigate this matter, for example by combining the research methods used in the different chapters.

The associations we found between affect and auditory perception may have implications for responses to sounds in our day-to-day environment. For example, speculatively, in daily listening, seemingly purely auditory perceptual experiences of sounds may be infused with affect, which in turn could influence further appraisal of these sounds and perpetuate mood states. These are hypotheses that deserve to be further explored.

To conclude, the findings of this thesis suggest that aspects of basic auditory perception are susceptible to affective influences. This fits with the notion that our brain integrates various sources of perceptual and non-perceptual information, including affective information, in order to create auditory percepts from the often distorted, incomplete or ambiguous input that our auditory senses receive at a given instance. Furthermore, these findings underpin and stimulate research into the mechanisms through which this integration occurs and at which levels of auditory processing in the brain this happens.