

THE ROLE OF INTERINDIVIDUAL DIFFERENCES IN TASK-BASED APPROACH-AVOIDANCE BEHAVIOR

DISSERTATION

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Kim L. Fricke

aus Langenfeld (im Rhld.)

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Erstgutachter: Prof. Dr. Thomas Jacobsen

Zweitgutachterin: Prof. Dr. Susanne Vogel

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ABSTRACT

Approach and avoidance are evolutionary highly conserved mechanisms of survival, realized by approaching rewarding and avoiding punishing stimuli in one's environment. In the laboratory, approach-avoidance behaviors are often measured using experimental tasks. In this thesis, the relationship of interindividual differences with behavioral outcomes of those so-called approach-avoidance tasks was investigated. Firstly, the literature on approach-avoidance tasks and interindividual differences was systematically reviewed. Secondly, the influences of the stress mediators cortisol and noradrenaline as well as self-reported interindividual differences was investigated with a pharmacologically validated approach-avoidance conflict paradigm in a double-blind study with healthy participants. Lastly, the approach-avoidance conflict paradigm was compared to two more established approach-avoidance tasks, the joystick and manikin tasks, in their efficacy to relate to self-reported interindividual differences. Both, systematic review and the conducted research indicates that relationships between task-based approach-avoidance measures and interindividual differences are ambiguous in nature with few exceptions, e.g. in the case of specific phobias. The approach-avoidance conflict paradigm was not affected by the stress mediators, but related to self-reported behavioral inhibition, physical aggression and verbal aggression whereas the joystick and manikin tasks did not. Even those findings appear to be ambiguous, as while interactions of aggression were found in the comparison study, they were not in the pharmacological study, possibly due to a lack of power. Internal consistency measures of all three tasks indicated subpar consistencies for joystick and manikin task and robust consistencies of approach-avoidance conflict paradigm measures. Potential reasons such as differences in the level of abstraction between task and trait measures, particularities of the task designs as well as ideas to resolve or improve them, for example, by employing more ecologically valid designs, are discussed.

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ABBREVIATIONS

AACT: approach-avoidance-conflict task

aPFC: anterior prefrontal cortex

BART: Balloon Analogue Risk Task

BAS: behavioral activation system

BAT: behavioral approach task

BDI-II: Becks Depressions Inventar II

BII: blood-injection-injury type phobia

BIS: behavioral inhibition system

CW-BIS: behavioral inhibition scale by Carver and White

CW-BAS: behavioral activation scale by Carver and White

DAF: Deutscher Aggressionsfragebogen

dIPFC: dorsolateral prefrontal cortex

dmPFC: dorsomedial prefrontal cortex

FFFS: fight-flight-freeze system

HPA: hypothalamic-pituitary-adrenal axis

MDBF: Mehrdimensionaler Befindlichkeitsfragebogen

NA: noradrenaline

OFC: orbitofrontal cortex

PTSD: posttraumatic stress disorder

RQ: research question

rRST: revised Reinforcement Sensitivity Theory

SAM: sympathoadrenal medullary axis

SNS: sympathetic nervous system

SSS-V: Sensation seeking scales V

STAI-S: State-Trait-Angstinventar – State component

STAI-T: State-Trait-Angstinventar – Trait component

TICS: Trierer Inventar zum chronischen Stress

TSST: Trier Social Stress test

VAS: visual analogue scales

vIPFC: ventrolateral prefrontal cortex

1 INTRODUCTION

1.1 WHAT ARE APPROACH AND AVOIDANCE BEHAVIORS?

From the first unicellular organism billions of years ago to today's modern human, the approach and avoidance of positive and negative stimuli, respectively, has been an intrinsic aspect of life. For simple cellular lifeforms, approach and avoidance are innate behavioral responses towards the environment based on own needs. They display taxis like chemotaxis, moving along a chemical gradient towards the strongest or weakest concentration of the substance, or phototaxis, moving in response to light (Kendeigh, 1961). Even on this basic level, the potential complexity becomes apparent: What if light and a desired chemical are concentrated in opposing areas, but the cell needs both? What if a desired and a repelling chemical are concentrated in the same area and the cell needs to determine whether to approach or not? Humans, having the (mis-)fortune of being markedly more complicated than single-cell organisms, have a lot more relevant stimuli they want to navigate by approach and avoidance behaviors. This "want" may take place on an instinctual level, recoiling from a spider that has come too close for comfort without us noticing, or reciprocating a smile from someone who just smiled at us. It may also be the product of habit such as unwanted snacking and other addictive behaviors. The "want" to approach or avoid can also be more conscious and goal-directed, for example, deciding to approach a potential employer at a networking event in hopes of securing a job opportunity. As with cells, complexity

arises due to a multitude of stimuli being relevant in a situation at the same time that may invoke conflicting tendencies. Maybe there is also a group of peers at the networking event drinking beers and you need to decide whether to approach them or the potential employer at the other side of the room. Perhaps an intimidating individual is standing nearby, exuding an aggressive demeanor, which could deter you from approaching anyone at all. It is up to you to figure out if approaching the potential employer is worth the potential risk of getting into conflict with this person. Unlike for cells, even singular stimuli can evoke opposing behavioral tendencies in humans. Approaching others may result in positive interactions, but carries the risk of being rejected or criticized. After the networking event, the shortest way home may lead through a dark alley, so you have to evaluate whether the trade-off of time vs. safety is worth it. These cases are examples of approach-avoidance conflicts in which one needs to decide whether to approach or to avoid. It becomes apparent that approach and avoidance underlie essentially all of our behaviors (and that of the living beings around us) and that it is of interest to understand the basic workings of our approach-avoidance-systems, aiding understanding of the behaviors that are built from them. In the scientific community, interest in approach and avoidance has also picked up in the last decade with a drastic increase in the number of articles published on the topic as seen in Figure 1.

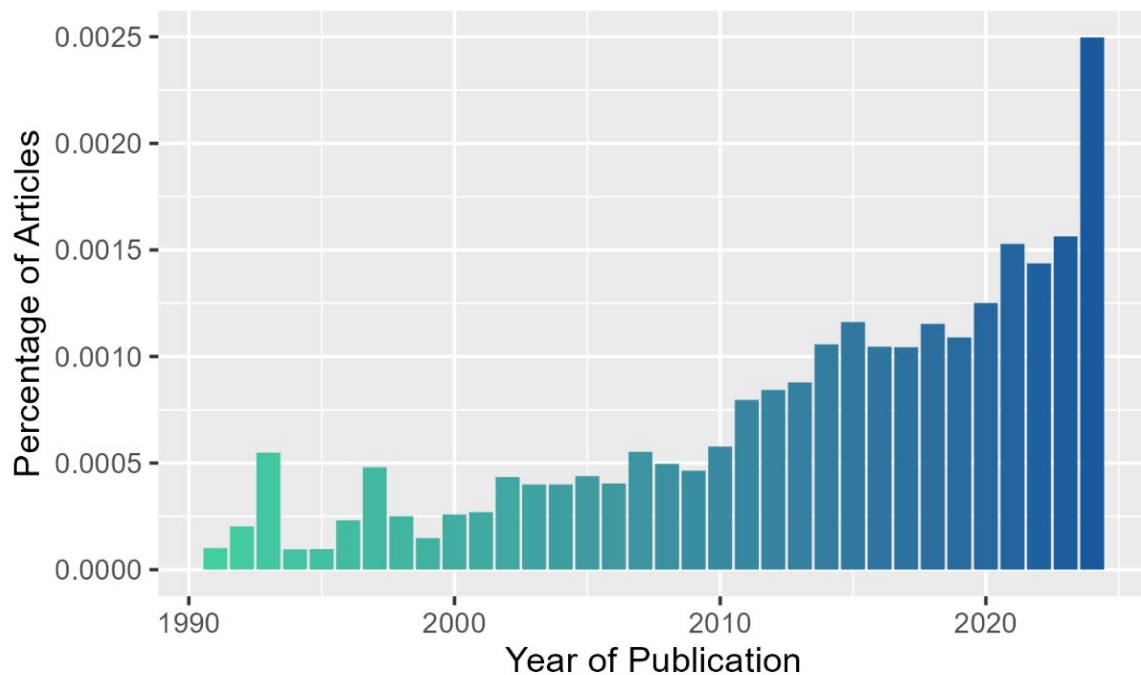


Figure 1.

PubMed search results for "Approach-Avoidance" as percentage of search results for "Psychology" carried out on the 27th of February, 2024 (<https://pubmed.ncbi.nlm.nih.gov>).

1.1.1 Approach and avoidance – A working definition

In Gray's revised version of his Reinforcement Sensitivity Theory (rRST), first published in 2000, one of the most popular theories on approach-avoidance that is still upholding today, affective stimuli can be either positive or negative. The absence of a negative stimulus is equivalent to a positive stimulus being present, while the absence of a positive stimulus is equivalent to a negative stimulus being present (Gray & McNaughton, 2003). Here, stimulus does not necessarily refer to a single item, but could be a set of items, a situation or anything in-between. Approach and avoidance

can be broadly defined as getting closer (i.e., active approach) or staying close (i.e., passive approach) to a positive stimulus and getting away from (i.e., active avoidance) or staying away from (i.e., passive avoidance) a negative stimulus, respectively. They are the most basic form of behavior underlying all other behaviors.

In contrast to the taxis described above, more complex approach-avoidance behaviors include a motivation component and a cognitive component (McNaughton et al., 2016). They are more advanced, flexible and include internal goal-representations of a desirable endpoint. This means that the organism does not execute a number of learned or genetically programmed stimulus-response reactions without knowing where following those stimulus-response pairings may ultimately lead, but rather that the organism has a goal in mind and works towards reaching it in a flexible, adaptive manner. The motivation component is dependent on the organism's current need for a stimulus and whether the stimulus is present in the environment. To decide whether to approach or avoid, the internal value of a stimulus, i.e. the internal goal-representation, needs to be determined first. To accomplish this, the drive for a given stimulus and the contingency of said stimulus need to be both taken into consideration (McNaughton et al., 2016). For example, the drive for a cold beverage is higher when thirsty and higher in the summer heat than in a snowstorm. For contingency, being in a situation that could result in getting a cold drink might be valued moderately in favor of approach, while getting a drink taken away from you might be valued strongly negative (loss aversion) and approaching a situation that helps to keep the drink strongly positive. Taken together, the drive and contingency will make up the internal value assigned to the stimulus. In motivation accounts, this internal value may also be called a goal, signifying the cognitive component involved. It follows that there can be both positive and negative goals that are behaviorally acted on with approach and avoidance, respectively. The cognitive component of approach-avoidance behaviors allows the comparison of different place, time and stimulus combinations to select the ones most in line with current motivations (McNaughton et al., 2016).

In the rRST, Gray and McNaughton (2003) posit that approach and avoidance in the goal-directed sense are not just situation-specific, but due to underlying general

systems that govern them, respectively. The behavioral activation system (BAS) is involved in reactions to both, conditioned and unconditioned positive stimuli and is responsible for approaching them. In contrast, the fight-flight-freeze system (FFFS) is the avoidance system. It mediates the reactions to both, conditioned and unconditioned negative stimuli and is responsible for eliciting avoidance responses. A third system, the behavioral inhibition system (BIS), is the conflict detection system and becomes active in situations where goal-conflicts need to be resolved. These conflicts can involve either or both of the other systems (approach-approach, avoidance-avoidance, or approach-avoidance conflict). To manage conflict resolution, the BIS is said to, among others, be able to inhibit conflicting behaviors, engage in risk assessment, scan the environment and relevant memories and feed increased negative valence of stimuli to the FFFS until either an approach or avoidance action has been elicited and the conflict resolved. All three systems have an underlying hierarchically structured neurobiology that partially overlaps (Gray & McNaughton, 2003).

Keeping this working definition in mind is important during the reading of this dissertation. In the experimental literature, approach and avoidance are often conceptualized in terms of distance (and potentially distance in time) towards the stimulus, which will also be seen in the tasks that attempt to measure approach-avoidance behaviors in Chapters 2-4. For example, a person with spider phobia would likely react to a spider at a moderate distance with avoidance behavior, i.e., keeping the distance or creating even more distance towards the spider (e.g., Rinck & Becker, 2007). In contrast, a person suffering from alcohol use disorder would likely react to alcoholic beverages with approach behavior by taking the beverage and drinking it, i.e., closing the distance to the stimulus (e.g., Field et al., 2008). Other theories, for example, the consistency theory by Grawe would posit that approach is the fulfillment of basic needs, while avoidance can be conceptualized as the avoidance of having the basic needs violated, threatened or disappointed (Grawe, 2004). Here, the reaction of the person with spider phobia would still be understood as avoidance behavior, while someone with alcohol use disorder drinking alcohol may also be understood as being avoidant as it is likely that the drinking of alcohol serves a function that aligns with avoidance goals, for example, drinking to better deal with hardships or stress.

1.2 COMMON MEASURES OF APPROACH-AVOIDANCE BEHAVIORS IN HUMANS

Approach-avoidance behaviors in human participants can be measured through many different means. They can, for example, be observed in natural or structured observations, determined in clinical assessment, or in interviews. In the experimental literature researching approach-avoidance behaviors and related constructs, however, self-report measures such as questionnaires and behavioral tasks appear to be the most commonly used types of measurements. The most prominently used self-report measure in the approach-avoidance literature are the behavioral inhibition and behavioral activation scales (CW-BIS/CW-BAS scales) by Carver and White (1994). They are based on Gray's original reinforcement sensitivity theory, which posits the BAS to respond to reward cues, the BIS to punishment, non-rewarding stimuli and uncertainty, and the FFFS to threat (Gray, 1982) and include only the BIS and BAS components. High CW-BIS scores reflect a high sensitivity to punishment and the responding to punishing stimuli with inhibition and heightened anxiety. In contrast, high CW-BAS scores are related to high reward sensitivity and the active approach of potentially rewarding stimuli. In Gray's revised theory as stated above, the CW-BIS scale from Carver and White was found to more closely reflect aspects of both, the BIS and the FFFS (e.g., Perkins & Corr, 2006).

Regarding behavioral tasks, the most commonly used ones are reaction-time tasks intended to capture action tendencies by requiring both stimulus-valence-congruent and -incongruent approach and avoidance actions. For example, a joystick can be used to either push or pull positive and negative stimuli appearing on a computer screen (Chen & Bargh, 1999). Pushing away a positive stimulus is expected to take longer than pulling it towards oneself. Similarly, pulling a negative stimulus should require more mental effort than pushing it away. Usually, a block design is used with explicit instructions of which kind of stimulus to approach or avoid varying between blocks. An example would be to instruct participants to approach happy and avoid angry faces in even blocks, while approaching angry and avoiding happy faces in uneven blocks.

Also common are implicit study designs in which participants are instructed to perform approach and avoidance movements based on an irrelevant stimulus feature with positive and negative stimuli varying across the irrelevant feature. Here, it is common to use background color or orientation, i.e. landscape or horizontal, of the image as irrelevant stimulus feature (e.g., Wiers et al., 2013). Measuring the difference in time between approach and avoidance of a stimulus can give insights into whether the person prefers to approach or avoid said stimulus. Of course, it is not necessary to use a joystick. Keyboard, mouse or other modes of input can be used. The representation is also sometimes changed to third person, resulting in tasks where the participants control the approach and avoidance behavior of a figure on screen instead of doing the approaching or avoiding themselves (De Houwer et al., 2001). While these tasks measure automatic action tendencies which may not translate into the goal-directed behavior in real life situations, it should be noted that the instruction to approach undesired stimuli, i.e. a negative goal, requires instrumental responding and may therefore involve a form of conflict detection and resolve as seen in the BIS. While paradigms akin to the ones just detailed are most commonly found in the literature, there is a variety of paradigms that attempt to capture approach-avoidance processes. While some of them show commendable attempts to measure approach-avoidance differently, they often are not represented in the literature enough to interpret whether they are reliable measures. One class of paradigms is especially interesting as they are inspired by animal research and pharmacologically validated by showing that anxiolytics have the expected effects (for example, Bach et al., 2018; Korn et al., 2017). One of these tasks, the approach-avoidance conflict task (AACT) by Bach et al. (2014), has been used in both experimental articles included in this thesis (Chapter 3 and 4). In addition, Chapter 4 also investigated two of the more common task designs, the visual approach-avoidance task (Rinck & Becker, 2007) and the manikin task (De Houwer et al., 2001). For a detailed description of how the tasks have been utilized in the experiments, please refer to the according methods sections.

1.3 APPROACH AND AVOIDANCE BEHAVIORS AND INTERINDIVIDUAL DIFFERENCES

Our behavior is shaped by our (epi-)genetics, our environment and their interplay. It is therefore not surprising that different people display vastly different approach-avoidance behaviors. Even if our basic needs may be the same, the goals people abstract from them, i.e. the values they assign, are unique. One person may love white chocolate, and hate Brussels sprouts, while another may be the exact opposite. Similarly, while one person may prefer a shortcut through a dangerous neighborhood, another person may take a longer, safer route. Gray's rRST postulates that the BIS, BAS and FFFS are the underlying biological systems that originate all interindividual differences, which can be described as differences in the sensitivity to reward, punishment and motivation. It follows that any interindividual difference in behavior can be due to changes in approach, avoidance or conflict sensitivity, or the interaction of two or all of them (Gray & McNaughton, 2003). The traits, stable differences in personality, defined in this way are most likely different from those derived from multivariate statistical techniques in personality research that have resulted in prominent trait descriptions as the Big Five model (Goldberg, 1990). In the rRST, fear and panic map onto the FFFS, optimism, reward-orientation and impulsivity map onto the BAS and worry-proneness and anxiety map onto the BIS (Corr & Perkins, 2006). This is also true for the mental disorders that are associated with imbalances in approach-avoidance behaviors. For example, excessive avoidance contributes significantly in anxiety disorder and phobias (World Health Organization, 1992). In contrast, excessive approach may result in pathological aggression or substance use disorders (Carver & Harmon-Jones, 2009; Wiers et al., 2014). Researching approach-avoidance behaviors and the implication of different individual differences for them better may therefore aid the understanding of psychological disorders, their onset and maintenance.

Despite the strong neurophysiological theoretical basis and a large body of research, studies investigating approach-avoidance behaviors and their discriminatory

power of interindividual differences in experimental human studies paint an often ambiguous picture. In Chapter 2, a systematic review of task-based approach-avoidance behavior and how well these tasks associate with further measures of interindividual differences is presented. Traits that should be clearly associated with either of the systems, for example, anxiety, are shown to either culminate in the expected behaviors or show no effects on approach-avoidance at all. Comparison is further complicated by studies displaying large variations in the studied populations, experimental and analytical methods as well as different fields preferring different tasks. A positive exception is phobia which clearly maps on avoidance behaviors of negative goals. These findings raise two important questions. Firstly, what could be potential confounds in the association of interindividual trait differences and approach-avoidance measures. One possibility would be that the current state interacts with more stable personality traits and therefore obfuscates findings. In Chapter 3, we explore how a state component, namely stress and its mediators, influences approach-avoidance behaviors in combination with trait measures. Secondly, if approach-avoidance tasks are ambiguous in their results across studies, it stands to reason to have a closer look at the different tasks used to find commonalities as well as differences in their outcome measures and see which of those map on a selection of interindividual differences, especially since only few prior comparisons exist (Kersbergen et al., 2015; Krieglmeier & Deutsch, 2010). As previously mentioned, we explore this question in Chapter 4 by comparing the approach-avoidance conflict task, the visual joystick task and the manikin task and their relations to several self-report measurements.

1.4 STATE INFLUENCES ON APPROACH-AVOIDANCE BEHAVIORS – THE ROLE OF STRESS AND ITS MEDIATORS

Next to stable personality differences, i.e., traits, the current state also plays a role in approach-avoidance decisions. In the example of the networking event above, current

mood may influence the decision of whether to approach a potential employer or to head over to have a beer with one's peers at the bar. Stress is another important factor to consider, especially so, since it is implicated in the onset and maintenance of several mental disorders (e.g., anxiety and substance use disorders; see Koob et al., 2014; Shin & Liberzon, 2010) that are likely to also relate to altered approach-avoidance behaviors.

Stress can be understood as emotionally and/or physiologically challenging experience (McEwen, 2007). To deal with these stressful experiences, our bodies release multiple mediators, which are intended to allow adaptation to the current situation and environment and ultimately return the body to homeostasis. There are many stress mediators, for example, neurotransmitters such as noradrenaline, dopamine and serotonin, steroid hormones such as cortisol, and neuropeptides such as vasopressin or corticotropin-releasing hormone. The variety in stress mediators allows us to respond appropriately to different stressors that may require different bodily responses (Joels & Baram, 2009). Two of the most researched and, often considered to be major, subsystems of the stress response are the autonomic nervous system and the hypothalamic-pituitary-adrenal (HPA) axis (Ulrich-Lai & Herman, 2009).

Immediately after detection of a stressor, the sympathoadrenal medullary (SAM) axis activates the fight-or-flight response through the sympathetic arm of the autonomic nervous system via the hypothalamus. This leads to a heightened heart rate, blood pressure and energy mobilization as well as an increase of adrenaline and noradrenaline levels, excreted, among others, by the adrenal medulla, the locus coeruleus, and sympathetic nerves respectively (Hermans et al., 2014; Ulrich-Lai & Herman, 2009). The release of these monoamines is fast and promotes behavior that helps to face and survive the stressor, for example increased attention and instinctive behaviors, in tradeoff against higher-order cognitive functions, pleasure-seeking and other processes not immediately necessary for survival of the situation (Habib et al., 2001). While important in the first phase of the stress response, the release of both adrenaline and noradrenaline usually stops when the stressor is not present anymore and therefore does not need to be dealt with (Joels & Baram, 2009). This is achieved via the

parasympathetic nervous system, which acts counter-regulatorily to the sympathetic nervous system.

The response of the HPA axis, made up of the paraventricular nucleus of the hypothalamus, the pituitary gland, and the adrenal cortex, is slower than the autonomic nervous system, with glucocorticoid levels (prominently cortisol) starting to gradually increase within a few minutes and reaching peak levels about 20 to 30 minutes after the appearance of the stressor and staying elevated for a considerable time (Dickerson & Kemeny, 2004). This is achieved via a cascade that ultimately initiates the synthesis of glucocorticoids and releases them into the systemic circulation. Here, the glucocorticoids promote mobilization of stored energy via glucose metabolism and potentiate the above-mentioned effects of the SAM. The HPA axis regulates itself via inhibitory feedback and allows the return to homeostasis after the stress response (de Kloet et al., 2005; Joels & Baram, 2009; Ulrich-Lai & Herman, 2009)

Taken together, both the autonomous nervous system, especially the SAM, and the HPA axis are major stress systems playing important roles in the stress response. While the SAM is mostly involved in fast responding and the HPA axis more involved in a slower stress response, the systems interact and form a feedback loop as cortisol targets the limbic system, which is responsible for innervating the hypothalamus in the face of a stressor (Chrousos, 2009). Similarly, noradrenaline has been shown to mediate effects of cortisol, for example, in the hippocampus and prefrontal cortex (e.g., Barsegyan et al., 2010; Schwabe et al., 2010, 2012). To understand the stress response better, especially its influences on behavioral processes, it is paramount to investigate how the different stress systems and mediators (e.g., noradrenaline and cortisol) interact and in how far they are sufficient to invoke changes in our behavior individually.

In the context of approach-avoidance behavior, the authors Vogel and Schwabe (2019), for example, investigated the influences of a psychosocial stress induction before performing the approach-avoidance conflict task, the foraging under predatory threat paradigm that was also used in Chapters 3 and 4 of this thesis. In the study,

stress led the healthy participants to avoid faster, when threat was initially close (i.e., active avoidance) in comparison to when the threat was initially far away (i.e., passive avoidance). Interestingly, approach-avoidance behavior was modulated differently depending on the personality traits of anxiety and aggression. Stress led to higher approach in participants with higher trait aggression, while it seemingly abolished the avoidance behaviors correlated with trait anxiety in the non-stressed control group. In short, the study showed differential effects of stress based on traits, suggesting that both state components such as stress as well as trait components such as aggression and anxiety played a role in the participants' behaviors and were interacting. It is possible, that the effects of stress on the balance of approach-avoidance behaviors are due to the shift of goal-oriented towards habitual behavior. Habitual behaviors are an important part of the stress response as they are cognitively less demanding, allowing more resources to be allocated to increased situational awareness and survival. Evidence for this shift under stress comes mostly from the fields of learning and memory research (e.g., Schwabe et al., 2010; Vogel et al., 2017). Personality traits may therefore have a stronger (or altered) influence on approach-avoidance behaviors under stress as they can be understood as longer-term stabilities in patterns of states, reflecting the likelihood of being in a specific state depending on the current goals, which could also be interpreted as the "habitual" state (McNaughton et al., 2016). This would in part explain the reported interaction effects of stress with personality traits from Vogel and Schwabe (2019) and make stress a modulator of approach-avoidance behavior that has to be studied in more detail to have its role fully understood. One way to achieve this could be the pharmacological manipulation of stress subsystems during approach-avoidance behavior to understand their role in the modulation as detailed above.

1.5 RESEARCH OBJECTIVES

Based on the previous chapters, I am able to formulate several research questions (RQs) for this thesis that can be assigned to two overarching aims. The systematic

review and original research articles that are presented in Chapters 2-4 can be assigned to these research goals as indicated in Table 1. at the end of this section.

Aim 1. Critical evaluation of current behavioral tasks that assess approach-avoidance behavior and their relationship with interindividual differences.

RQ 1.1 *Which interindividual differences impact task-based approach-avoidance behavior?*

There are many articles addressing task-based approach-avoidance behavior and their relationship with interindividual differences. However, a systematic literature search reviewing the existing literature and finding the underlying commonalities is yet missing. Here, together with my colleagues, I set out to group together studies regarding the same or comparable interindividual differences to arrive at conclusions about their influence on approach-avoidance behavior. In addition, my colleagues and I conducted two studies that addressed trait anxiety, trait aggression, trait approach and avoidance, and further traits in behavioral approach-avoidance tasks, which are theoretically related to approach-avoidance, to contribute to the existing literature.

RQ 1.2 *Which tasks are specifically sensitive to interindividual differences?*

One problem in detecting the influences of interindividual differences on approach-avoidance behaviors may be that prominently used tasks may not be sensitive enough to track all interindividual variation well enough to differentiate behaviors related to it. While Chapter 2 suggests that this is the case for most interindividual differences (see phobia section for a counterexample), more research is necessary to arrive at definite conclusions. Therefore, I present a study in Chapter 4 that investigates two established tasks as well as a novel paradigm that was inspired by preclinical tasks and has proven to be sensitive to anxiolytics. I compared the tasks in their ability to explain the variance in interindividual differences as well as their reliability.

RQ 1.3 *How do approach-avoidance tasks differ? Which best practices should be adopted as scientific standards?*

To further understand differences and commonalities of the three behavioral tasks that were investigated in the context of this thesis, it would be interesting to see how their outcome measures may or may not relate to one another or map onto common factors (see Chapter 4). Best practices of task design and approach-avoidance research are also relevant to investigate as they may allow more standardization as well as potentially a higher to measure approach-avoidance behavior at the level of the individual (see Chapter 2 and 4).

Aim 2. Critical evaluation of the role of acute stress in approach-avoidance related behaviors.

RQ 2.1 *What is the specific role of the central stress mediators cortisol and noradrenaline in the balance of approach-avoidance behavior?*

The role of acute stress in approach-avoidance related behaviors is not entirely clear with seemingly opposite results in the few studies investigating stress and cortisol as well as studies missing the opportunity to research the influences of noradrenaline (see Chapter 2). To elucidate how cortisol and noradrenaline contribute to the balance of approach and avoidance behavior, my colleagues and I employed a double-blind study in which either hydrocortisone (the hormone cortisol as medication), yohimbine (to increase the release of noradrenaline), both combined, or a placebo were administered (Chapter 3). This allowed us to see whether one of the two stress mediators is sufficient to change approach—avoidance behavior, whether both mediators need to work together or whether the pharmacological interventions are not sufficient to show changes in approach-avoidance behavior compared to a control condition. Healthy participants completed the approach-avoidance conflict task, which is known to introduce ambiguous approach-avoidance conflicts, after intake of the pharmacological manipulation or placebo.

RQ 2.2 *How do the acute stress mediators cortisol and noradrenaline moderate personality or sex-based differences of approach-avoidance behavior?*

In Chapter 3, self-report questionnaires were utilized to see whether the administered stress mediators and personality traits result in altered responses of approach-avoidance behavior. The effects of gender and how those may interact with stress were also investigated.

Table 1. Contribution of articles to the research questions. Full coverage can be understood as in-depth attempts to answer a research question, while partial coverage may include addressing the research ideas in more or less detail. RQ = research question.

PAPER TITLE	RQ	RQ	RQ	RQ	RQ
	1.1	1.2	1.3	2.1	2.2
How interindividual differences shape approach-avoidance behavior: Relating self-report and diagnostic measures of interindividual differences to behavioral measurements of approach and avoidance (Chapter 2)	●	◐	◐	◐	○
The effects of hydrocortisone and yohimbine on human behavior in approach-avoidance conflicts (Chapter 3)	●	○	○	●	●
Comparison of two reaction-time-based and one foraging-based behavioral approach-avoidance tasks in relation to interindividual differences and their reliability (Chapter 4)	●	●	◐	○	○

Legend: no coverage of RQ ○ partial coverage of RQ ◐ full coverage of RQ ●

RQ 1.1 Which interindividual differences impact task-based approach-avoidance behavior?
RQ 1.2 Which tasks are specifically sensitive to interindividual differences?
RQ 1.3 How do approach-avoidance tasks differ? Which best practices should be adopted as scientific standards?
RQ 2.1 What is the specific role of the central stress mediators cortisol and noradrenaline in the balance of approach-avoidance behavior?
RQ 2.2 How do the acute stress mediators cortisol and noradrenaline moderate personality or sex-based differences of approach-avoidance behavior?

2

HOW INTERINDIVIDUAL DIFFERENCES SHAPE APPROACH-AVOIDANCE BEHAVIOR: RELATING SELF-REPORT AND DIAGNOSTIC MEASURES OF INTERINDIVIDUAL DIFFERENCES TO BEHAVIORAL MEASUREMENTS OF APPROACH AND AVOIDANCE

2.1 ABSTRACT

Responding to stimuli in ambiguous environments is partially governed by approach-avoidance tendencies. Imbalances in these approach-avoidance behaviors are implicated in many mental disorders including anxiety disorders, phobias and substance use disorders. While factors biasing human behavior in approach-avoidance conflicts have been researched in numerous experiments, a much-needed comprehensive overview integrating those findings is missing. Here, we systematically searched the existing literature on individual differences in task-based approach-avoidance behavior and aggregated the current evidence for the effect of self-reported approach/avoidance traits, anxiety and anxiety disorders, specific phobias, depression, aggression, anger and psychopathy, substance use and related disorders, eating

disorders and habits, trauma, acute stress and, finally, hormone levels (mainly testosterone, oxytocin). We highlight consistent findings, underrepresented research areas and unexpected results, and detail the amount of controversy between studies. We discuss potential reasons for ambiguous results in some research areas, offer practical advice for future studies and highlight potential variables such as task-related researcher decisions that may influence how interindividual differences and disorders drive automatic approach-avoidance biases in behavioral experiments.

2.2 INTRODUCTION

One of the essential principles of life is adaptability, i.e., the ability of an organism to respond to the external environment. Behavioral approach and avoidance can be seen as fundamental building blocks allowing us to adapt to an ever-changing environment (Koshland, 2002). For example, we tend to approach stimuli of positive valence such as food when we are hungry and tend to avoid stimuli of negative valence such as pain or predatory threat. Approach and avoidance are complex reactions, shaped by underlying genetics and prior experience, and guided by both reflex and cognitive control (McNaughton et al., 2016). As the stimuli in our environment are often ambiguous, they frequently result in so-called approach-avoidance conflicts. Should one enter a dark alley on the way home or take a detour? Should one take the last piece of cake despite the dietary implications and angry looks of the remaining party guests? Different people display strikingly divergent behaviors when faced with these types of conflicts. However, the reasons for these individual differences remain largely unclear and are the focus of this review.

Previous research has shown the striking interindividual variation in approach-avoidance tendencies to the point that aberrant approach-avoidance behaviors have been interpreted as an integral part or even cause of many pathologies such as excessive approach of addiction-related stimuli in addiction and unreasonable avoidance of social stimuli in social anxiety disorder (e.g., McNaughton et al., 2016). In a more general sense, recent findings highlighted possible associations between personality

traits and some psychiatric diagnoses. For instance, individual differences in the fight-flight-freeze system assessed by self-report were found to mediate the relationship of psychopathy and externalizing behaviors (Johnson et al., 2014) and interactions between neuroticism, extraversion and conscientiousness were predictive of depression (Allen et al., 2018). Theoretical work is also done to extend current nosologies with novel models in which personality traits play larger roles in defining psychopathologies (e.g., Allen et al., 2018; Kotov et al., 2017). However, the underlying mechanisms of how interindividual differences related to approach and avoidance map onto psychopathology are not fully understood as of yet. Understanding these mechanisms is urgent, considering that despite the unknown background, approach-avoidance trainings are used in clinical research and practice. For example, approach-avoidance tasks have been utilized to train participants to avoid stimuli that are detrimental to their health such as alcohol in problematic drinkers (Eberl et al., 2013) or food-stimuli in bulimia nervosa patients (Brockmeyer et al., 2019). Likewise, other studies trained participants to approach stimuli that they avoid to an unhealthy extent such as contamination-related stimuli in obsessive compulsive disorder (Weil et al., 2017) or social stimuli in social anxiety disorder (Asnaani et al., 2014). While there are reports that training may be effective in reducing alcohol use, cigarette smoking, and unhealthy eating (Kakoschke et al., 2017a), evidence is certainly not found in all studies (e.g., Aulbach et al., 2019; Dickson et al., 2016; Ferentzi et al., 2018; Lester et al., 2015; Sharbanee, Hu, et al., 2014) and the reasons for this inconsistency are currently unclear.

2.2.1 Systems involved in approach-avoidance behaviors and sources of interindividual variance

Approach-avoidance behavior is theorized to be controlled by multiple motivational systems activated by appetitive and aversive stimuli. One well-established idea, Gray's revised reinforcement sensitivity theory, postulates that individual differences in sensitivity to reward, punishment and motivation originate from three distinct but interacting brain-behavioral systems (Gray & McNaughton, 2003). According to this

theory, the behavioral activation system (BAS) is involved in basic control of approach towards positive stimuli, while the fight-flight-freeze system (FFFS) is activated in case of aversive stimuli to elicit avoidance. The third system is the behavioral inhibition system (BIS), which becomes active in situations of conflict. Thus, the BIS serves as conflict detection system and mediator for conflicts within and between the other two motivational systems. The control of basic approach and avoidance is therefore believed to be handled by separate systems (BAS and FFFS), while the simultaneous activation of both approach and avoidance tendencies will lead to the activation of all three systems. It follows that interindividual differences in behavior can be the result of changes in approach, avoidance or conflict sensitivity, or a combination of these (Gray & McNaughton, 2003).

These different systems involved in approach-avoidance can be affected by individual differences at various levels. For instance, the initial evaluation of a stimulus will depend on the internal value an individual assigns to it and this value varies based on the current level of drive the stimulus elicits and the type of contingency in a given situation (McNaughton et al., 2016). For example, the elicited approach-avoidance reactions of two individuals towards a piece of cake will vary, for instance based on their personality traits, current level of drive (e.g. hunger) and the contingency (e.g. potential gain of a piece of cake or potential loss of a piece of cake warrant different reactions).

Furthermore, rodent experiments have shown that approach and avoidance gradients appear to generally differ in their steepness with approach gradients being shallower and avoidance gradients being steeper. This means that positive stimuli may be approached from a relatively longer distance, while negative stimuli elicit a strong avoidance response in close proximity to the stimulus, which can ‘override’ the shallower approach gradient (McNaughton et al., 2016). The so-called reversal point is located where steep avoidance gradients become comparatively stronger than the shallower approach gradients leading to shifts in the involved approach-avoidance responses.

This phenomenon makes distance a crucial factor in approach-avoidance conflicts. Indeed, manipulating gradients by changing task parameters such as threat level or distance has been shown to affect the approach-avoidance responses of participants on both behavioral and neuronal level (e.g., Fung et al., 2019). Importantly, this study demonstrated that personality traits affect how threat level and distance can influence behavior. The same might hold true for states or other traits. In general, different experimental procedures may lead to different results in terms of approach-avoidance behavior due to being perceived on opposite sides of the reversal point.

The distance at which approach-avoidance conflicts take place will further shift based on individual differences of approach-avoidance gradients' steepness, i.e. an individuals' sensitivity to approach and avoidance. In addition, conflict enhances avoidance motivations, which further impacts observed behaviors. Thus, mixed motivations will lead to different approach-avoidance behaviors in human experiments based on where the given stimulus is perceived in space (or time), and this cognitive distance can vary based on experimental procedures and interindividual differences.

Mixed motivations in human experiments can arise not only from the approach-avoidance conflicts introduced by the task, but also by the experimental situation itself. Experimental situations may affect approach-avoidance behavior even prior to the start of the experiment as individual sensitivity for approach and avoidance differs and motivational forces are already at play, for example, in participants sensitive to conflict or anxiety. It is therefore conceivable that tasks which target approach or avoidance tendencies distinctly, still elicit the activation of the BIS due to cognitive conflict introduced by the experimental situation or instructions (e.g. it could be possible that the instruction to approach aversive stimuli leads to activation of the BIS as conflict detector). In summary, individual differences may affect one or several motivational systems of approach-avoidance. Which systems are involved in approach-avoidance tasks may be influenced by researcher choices in task design and various other factors, e.g., individual cognitive distance and the experimental situation itself.

2.2.2 Neural structures involved in approach-avoidance responses

There seems to be some consensus about the neural structures involved in approach-avoidance responses measured in approach-avoidance tendency tasks in humans, particularly in social situations (for a recent review, see Kaldewaij et al., 2017). An important brain region controlling approach-avoidance behaviors in these tasks is the anterior prefrontal cortex (aPFC), where activity increases in cases of approach-avoidance conflict due to incongruity of instructions and action tendencies (Volman, Roelofs, et al., 2011; Volman, Toni, et al., 2011). In addition, the amygdala and its functional coupling with the aPFC has been implicated in the control of approach-avoidance decisions as the aPFC suppresses automatic action tendencies incompatible with current goals (Volman et al., 2013; Volman et al., 2016). In more translational approach-avoidance conflict tasks, the anterior hippocampus seems to play a causal role especially in avoidance behaviors (Bach et al., 2014; Korn & Bach, 2019; O'Neil et al., 2015) and may serve as control region, particularly tracking the current level of threat (Bach et al., 2014). For instance, patients with hippocampal lesions demonstrated reduced inhibition and passive avoidance behavior in a foraging task under threat of predation (Bach et al., 2014; O'Neil et al., 2015). Additionally, the amygdala is of key importance for anxiety-like behaviors in these approach-avoidance conflict tasks as well (Korn, 2017). However, no increase in amygdala activity was reported in response to conflict in several affective/pain punishment-induced conflict tasks, indicating that different types of approach-avoidance conflicts may activate different brain regions (Kirlic et al., 2017). Moreover, a recent study nicely illustrated that slow threat may involve higher cognitive areas, i.e. hippocampus and PFC, while the response to fast threat may rely on different areas such as the periaqueductal grey (Qi et al., 2018). Further regions that have been implicated in the control of approach-avoidance conflicts and making optimized decisions are the dorsomedial, dorsolateral and ventrolateral prefrontal cortex regions (dmPFC, dlPFC, vlPFC) and the orbitofrontal cortex (OFC; Aupperle et al., 2015; Korn & Bach, 2019; Roelofs, Minelli, et al., 2009; Volman, Toni, et al., 2011). To summarize, PFC areas and anterior

hippocampus are implicated in the control of approach-avoidance behaviors, albeit in different types of tasks and not in all reported studies. Interestingly, these brain areas have been implicated in various psychiatric disorders that present with altered approach-avoidance behavior. Approach-avoidance research thus possibly opens a way to better understand how these disorders develop and persist.

2.2.3 A review on individual differences in approach-avoidance conflicts

Despite the multitude of studies employing approach-avoidance tasks in a variety of research fields such as anxiety or substance use and recent advances in the investigation of neuronal underpinnings, a comprehensive review of the literature addressing interindividual differences in approach-avoidance behaviors is missing. Integrating results from previously conducted studies is important, however, to ensure better, more reliable interpretation of findings and assess implications for, among others, the disorders that have been strongly associated with aberrant approach-avoidance behavior and therapeutic practices. Here, we set out to summarize the current level of knowledge about those interindividual differences that drive disparities in approach-avoidance behavior.

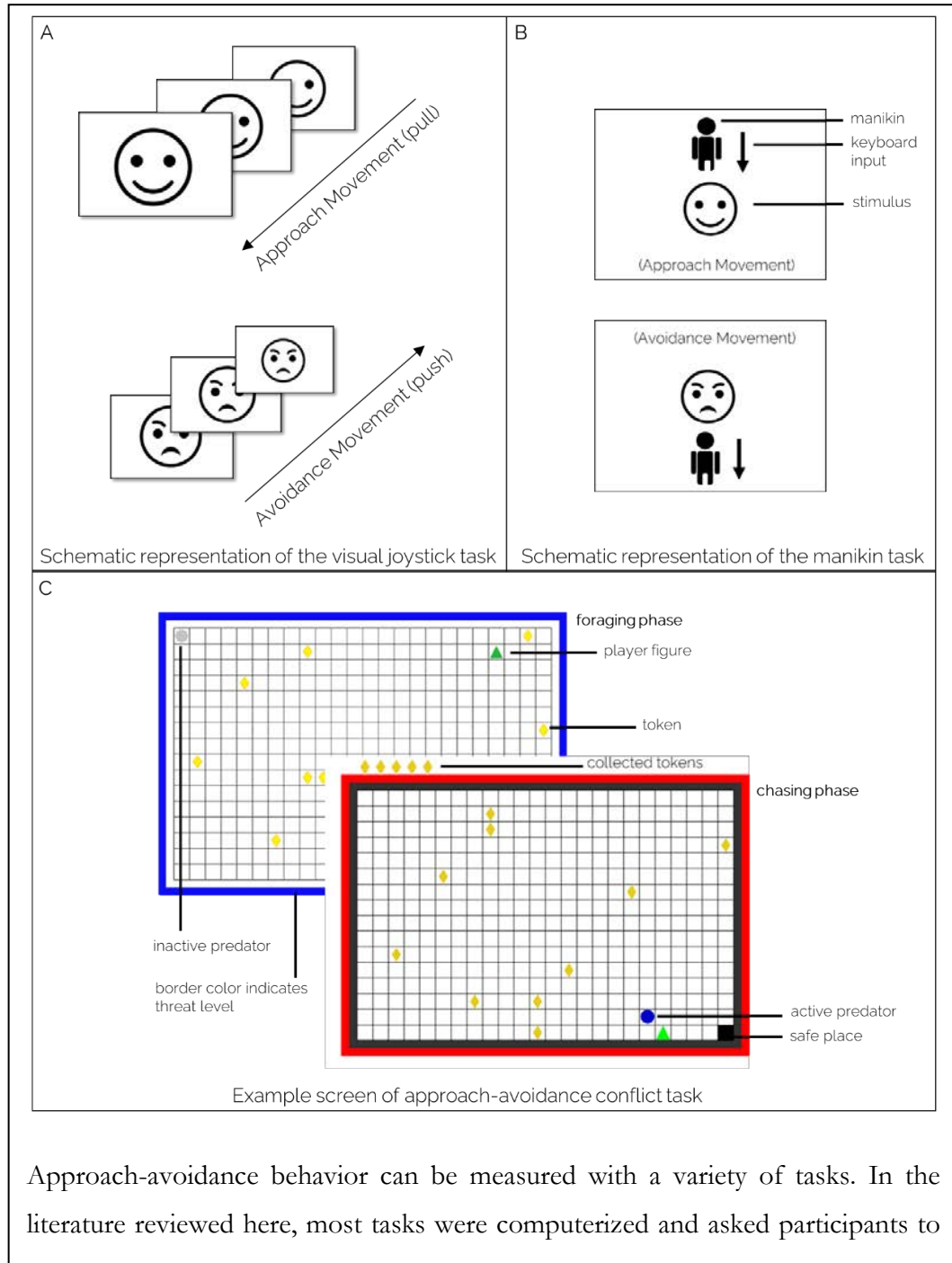
To this end, we focused on behavioral experimental human studies that addressed interindividual differences and examined a distinct approach-avoidance conflict (see methods for inclusion and exclusion criteria). We combined findings pertaining interindividual differences of a certain research field (e.g., anxiety disorders) where possible, i.e., if enough articles were present to allow for an integration of findings. Therefore, research in relation to the following concepts is presented: self-reported approach/avoidance traits, anxiety and anxiety disorders, specific phobias, depression, aggression, anger and psychopathy, substance use and related disorders, eating disorders and habits, trauma and acute stress and, finally, hormone levels (mainly testosterone, oxytocin). Articles that were initially included, but could not be grouped to accumulate evidence are detailed in the supplementary material (section 7.1).

Approach-avoidance decisions have been investigated employing a variety of tasks and populations differing in various states or traits resulting in a large body of research. The majority of the articles investigated here utilizes tasks falling in the broad category of approach-avoidance tendency tasks. These are intended to capture action tendencies, for example by instructing to approach stimuli of positive valence and avoid stimuli of negative valence or the other way around. These tasks thus create an environment where either congruent or incongruent approach-avoidance behaviors are required, and the differences in behavior between those instructions are then analyzed (for detailed descriptions see Box 2). Approach-avoidance tendency tasks target automatic tendencies, but require goal-directed instrumental responding to overcome these tendencies in case of incongruencies and may involve one or more of Gray's postulated approach-avoidance systems. Other tasks create approach-avoidance conflict within the task by creating ambiguous environments with stimuli that represent positive and negative potential outcomes simultaneously. These tasks clearly target all three approach-avoidance systems (BIS, BAS, FFFS). While we employ a definition of conflict that includes conflict introduced by instruction as seen in approach-avoidance tendency tasks, the tasks are very differently set up and likely activate different neural systems (see section 2.2.2). To appreciate the different types of tasks used, the result sub-sections include tables detailing characteristics of the tasks, stimulus types etc.

We hope that this review provides valuable information for fundamental and clinical research by shedding more light on approach-avoidance behaviors in health and disease and discussing their theoretical implications. We identify interindividual differences that reliably drive divergent approach-avoidance responses in commonly used approach-avoidance paradigms but also highlight current inconsistencies. This is of interest in the design of new studies since lacking replicability may warrant higher numbers of participants, clearer separation of participant groups or the use of other tasks or task versions. The review further helps to gain insight into psychiatric disorders in which approach-avoidance behavior is aberrant such as substance use or anxiety disorders and the role the distorted approach-avoidance behavior may play in disease manifestation or treatment. Moreover, we will highlight research areas in which

current findings are inconclusive or lacking and more research is required to understand the sources and actions of interindividual differences. Finally, we will discuss translational research that may contribute relevant knowledge to determine the causal factors driving variation of approach-avoidance tendencies.

Box 2 – Approach-Avoidance Tasks.



Approach-avoidance behavior can be measured with a variety of tasks. In the literature reviewed here, most tasks were computerized and asked participants to

decide to approach or to avoid stimuli, one by one, according to instructed rules (tendency tasks). Mostly, so-called joystick (top left) and manikin tasks (top right) were used. Approach-avoidance behavior was further investigated in translational versions of tasks inspired by preclinical rodent research (bottom), whole-body movement tasks and card selection tasks among others and included both tendency and conflict tasks.

Joystick Task

Joystick tasks are by far most frequently used in automatic approach-avoidance tendency research. They are so common indeed that they are usually referred to as Approach Avoidance Task (AAT). Joystick tasks make use of the finding that when instructed to push or pull stimuli, participants are generally faster in pulling pleasant stimuli towards themselves and pushing aversive stimuli away from themselves than the respective opposite. This has been reliably shown since 1960 (Solarz, 1960) and can be extended to any stimulus that is expected to elicit an approach or avoidance response. Participants are instructed to act affect-congruently (approach happy faces and avoid angry faces) or affect-incongruently (avoid happy faces and approach angry faces) with instruction-reversal between blocks. The differences in reaction times of affect-congruent and affect-incongruent conditions are used to estimate whether participants are biased towards approach or avoidance. The stimuli can also be task-irrelevant in implicit versions of the task where participants make approach or avoidance movements according to, for example, the color of the picture border or the orientation of the picture. As foreshadowed by the task name, most research uses a joystick, which is first held in a neutral position and flexion or tension of the arm is required to perform approach-avoidance movements (Chen & Bargh, 1999). However, also the use of response buttons requiring comparable arm movements has been successful. In recent years, a visual joystick task version has been popularized with a zooming effect based on the joystick movements to reduce influences of differently interpreting the movements (removing your arm from the presented stimulus instead of pulling the stimulus towards oneself; Rinck & Becker, 2007). The non-zooming version is still sometimes used, especially in neuroimaging

studies to prevent visual motion effects potentially confounding the effects of the task.

Manikin Task

Another way to test automatic approach and avoidance is the manikin task (De Houwer et al., 2001), which can be found in the literature under the names of Symbolic Approach-Avoidance, or sometimes under the broad umbrella terms Stimulus Response Compatibility Task (SRC) or Affective Simon Task. The idea of the manikin task is similar to the joystick task with the important difference that approach-avoidance movements are performed for a manikin present on the screen and not for oneself, hence it being called a symbolic approach-avoidance task. On screen, a stimulus is presented with the manikin appearing either above or below it. The participant has to move the manikin toward or away from the stimulus via button presses. The necessity of arm flexion and extension is therefore omitted and button presses can represent an approach or avoidance action depending on manikin location. Otherwise, the task is similar in design and instructions to the joystick task and is used with both explicit and implicit instructions.

Other

To exemplify the variety of other tasks used in approach-avoidance research, we describe one translational conflict task, which was inspired by anxiety research in rodents (see discussion sections 2.5.4. and 2.5.5.) This computerized task includes a player figure on a 24x16 field on which coins are randomly spawned that often translate to monetary outcome. An initially inactive predator is placed in one corner and can wake up and chase the player with fast speed at any given time resulting in the loss of all coins collected in that particular trial. Participants start either in the same corner as the predator or in the safe place in the opposite corner, which cannot be invaded by the predator. Participants are instructed to collect as many coins as possible without being caught. Different predators can be used that

correspond to varying levels of threat, for instance by varying wake up probabilities (Bach et al., 2014). The approach-avoidance conflict arises by having to approach the coins, but also avoid the predator which is several folds faster than the player. Possible outcome measures are the number of collected coins over trials, the time spent in threat quadrant or safety quadrant, whether the participant has been caught and the latency to start foraging. This foraging latency is interesting as, for example moving away from the predator after trial initiation has been found to be faster than approaching the field starting from the opposite site when under stress, suggesting a freeze response (Vogel & Schwabe, 2019). Further, movements within trials can be tracked in detail (e.g. walking speed, distance to predator, wall or safe place).

2.3 METHODS

2.3.1 Literature Search Strategy

To identify articles that addressed individual variation in approach-avoidance conflict behavior, a literature search for articles in the databases PubMed and EBSCOhost (including for instance PsycINFO, SocINDEX, and Medline) was conducted on 25-01-2019. In our main search strategy, we selected English papers on the inclusion of the following search terms: approach-avoidance behavior OR approach-avoidance conflict OR approach-avoidance task (hits in PubMed: 741; EBSCO: 802). As we noticed that several studies utilizing Stimulus Response Compatibility Tasks (see Box 2) were missing after the main search, a secondary search including articles in the databases up to 25-01-2019 was added using the following terms: (stimulus response compatibility task OR src task OR manikin task OR affective simon task OR ast task) AND (approach OR avoidance); hits in PubMed: 164; EBSCO: 102.

We identified 1809 articles of which 1174 remained after duplicate removal in Endnote X7. Title, abstract and, in case of uncertainty, full text were screened based

on the following inclusion criteria: Articles had to be primary studies conducted in humans in an experimental setting with an approach-avoidance task measuring an approach-avoidance conflict. These criteria were chosen to focus on articles allowing for behaviorally-based conclusions, which is important as some of the measures investigated here have been interpreted in approach-avoidance contexts without using behavioral anchors. This is especially interesting as direct behavioral implications are often hypothesized or even assumed. On this basis, studies using questionnaires only, hypothetical conflicts such as rating the willingness to approach specific stimuli or classification tasks such as the implicit association task were excluded (for details, see section 7.1). One inclusion criterion we state here is the need for approach-avoidance conflicts within the task. For this review, we employ a rather soft definition of conflict, which may either occur directly within the task or due to incongruence of approach-avoidance tendency and instruction, to guarantee a comprehensive examination of the approach-avoidance field. Individual differences in response to these conflicts may be due to any or several of the aforementioned distinct approach-avoidance systems regulating basic approach and avoidance as well as conflict sensitivity. Articles were first classified by the first author and articles containing approach-avoidance or closely related concepts were revisited by the second author. After screening, 329 articles remained and were examined in full text. In the thorough full text examination, papers were included when investigating an interindividual difference component that was related to an approach-avoidance task. Both stable and acute influences were considered. Examples for stable influences are traits, pathologies, hormone levels, or habitual behaviors, while acute influences could be current states or manipulations prior to the approach-avoidance task, e.g. medication or stress induction. Studies utilizing approach-avoidance task trainings akin to cognitive bias modification that were then compared to a different training regimen or a placebo condition were included if they reported further measures of interindividual differences in association with an approach-avoidance task. We incorporated studies regardless of whether they investigated group differences, employed correlative approaches or administered drugs in a pre-post design. In total, 209 articles fulfilled all inclusion criteria (see Figure 2.1). For each article, we recorded the following information: main findings, number of participants, type of task (see Box 2), stimuli used, stable or acute influences reported

and type of study design (group, correlation, pre-post design). A brief overview of the studies including task design, individual differences and participant information is provided in tables in the result sections (Tables 2.1-2.11). 137 articles were included in the result section. The remaining 72 papers and included articles with individual differences not addressed in the results section are listed in section 7.1. In general, the articles not included in the review utilized similar tasks as the ones reviewed here and cover a variety of topics ranging from disorders (e.g., borderline personality disorder, schizophrenia, autism spectrum disorder) over genetic variation and drug administration to less frequently researched traits, e.g. religiousness.

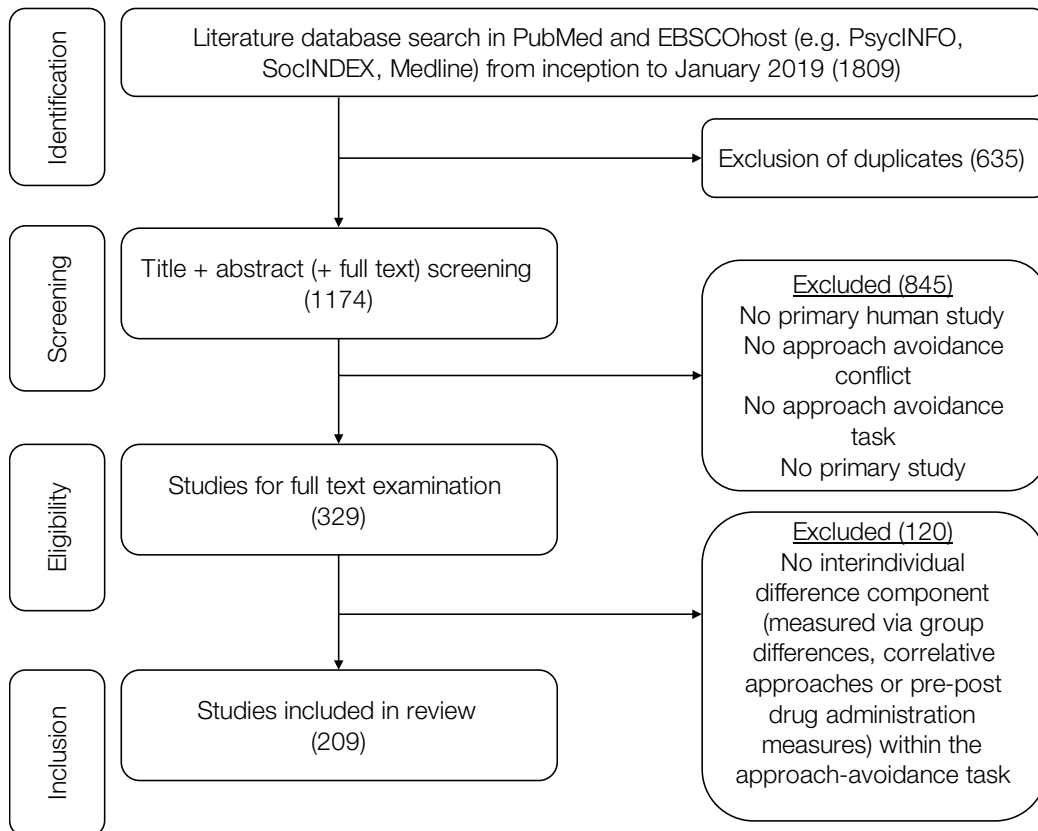


Figure 2.1. Schematic of the literature search strategy.

2.4 RESULTS

2.4.1 Self-reported trait approach and trait avoidance are not consistently associated with behavior in experimental tasks

Trait approach and avoidance are frequently assessed as self-reported measures in the approach-avoidance literature, most prominently using the behavioral inhibition and activation scales (CW-BIS/CW-BAS) by Carver and White (1994). Intuitively, behavior in approach-avoidance conflicts should be reflective of those self-reported traits. However, associating approach-avoidance tendencies measured by behavioral tasks with trait approach-avoidance questionnaires led to largely inconclusive results.

For instance, self-reported behavioral approach was associated with more approach bias for both social (Ernst et al., 2012; Radke et al., 2016) and non-social stimuli (Aupperle et al., 2011; Gonen et al., 2016; May et al., 2016). Additionally, one study successfully related self-reported behavioral inhibition to avoidant behavior and approach to more approaching behavior in a risky gambling task (Rollwage et al., 2017). However, several other studies were unable to find any correlation between approach-avoidance tendencies in behavioral tasks and questionnaires in healthy or psychiatric participants confronted with different types of social and non-social stimuli (Ferrari et al., 2018; Kotynski & Demaree, 2017; Radke et al., 2018; Sleuwaegen et al., 2018; Struijs et al., 2017; Turner et al., 2019; van Peer et al., 2007). Of note, Struijs et al. did not find evidence for correlative effects in an impressive sample of anxious and depressed participants, remitted patients and healthy controls exceeding other sample sizes by far ($n > 1700$). Similarly, impulsivity, a concept closely related to behavioral approach, was not correlated with approach-avoidance biases in two independent studies (Christiansen et al., 2012; Kakoschke et al., 2017c). Thus, we are unable to unequivocally confirm the hypothesis that behavioral measures of approach-avoidance conflicts reflect self-reported approach-avoidance.

The revised reinforcement sensitivity theory by Gray further postulates that the behavioral activation system is sensitive to conditioned incentives, i.e. responsive to instrumental rewards, whereas the behavioral inhibition system primarily serves conflict detection (Gray & McNaughton, 2003). To test this, a task creating an approach-avoidance conflict by mixing hedonic and instrumental incentives was developed (Berkman et al., 2009). Partially supporting the theory, a higher behavioral approach score related to overall faster responding, while a higher behavioral inhibition score correlated with faster responding in incongruent trials only. However, also these findings were not replicated in two smaller studies (Berkman & Lieberman, 2010; Roelofs et al., 2005).

In short, studies that found significant effects related trait approach to behavioral approach and trait inhibition to behavioral avoidance. However, other studies failed to replicate these links, leaving the question whether tasks and questionnaires indeed examine the same underlying systems unanswered. It should be mentioned that the CW-BIS/CW-BAS-scales, which have been utilized in most of these papers, have been derived using lexical methods without behavioral validation, i.e. not showing a relationship to behavior but merely to self-report trait or state questionnaires (Carver & White, 1994). The CW-BIS scale has further not been validated based on anxiolytic drugs, which had been initially used to fundamentally define the BIS as separate of the basic control of avoidance (Gray, 1977). These might be reasons why tasks and questionnaires did not necessarily correlate in the articles examined here (for details of task designs and sample characteristics see Table 2.1).

Table 2.1

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2.4.2 Trait anxiety and social anxiety often lead to avoidance behavior

Papers investigating the relationship of anxiety and approach-avoidance behavior usually hypothesized that highly anxious individuals display avoidance or inhibition in response to anxiety-related stimuli. This hypothesis was long supported in the literature, but challenged by recent studies.

Initially, several studies found that self-reported trait social anxiety led to more pronounced avoidance behavior towards angry and happy, but not neutral faces (Heuer et al., 2007; Lange et al., 2008; Roelofs et al., 2010). Another study showed that anxiety disorder patients' stronger avoidance tendencies correlated with more severe self-reported social anxiety (Enter et al., 2016). Beyond social anxiety, studies found that social stimuli (Pittig et al., 2014; Roelofs, van Peer, et al., 2009; Voncken et al., 2012) and non-social stimuli (Harari-Dahan & Bernstein, 2017) elicited avoidance in highly trait anxious individuals. Somewhat in contrast with these studies, slowed approach of neutral, but not of disgusted faces was present in a sample of social anxiety disorder patients, which the authors interpreted as an avoidant reaction towards ambiguity, since neutral faces are less clearly interpretable than faces displaying disgust (Kuckertz et al., 2017). Concerning potential gender differences, findings were inconclusive. While one study suggested that trait anxiety had more pronounced effects in men (Aupperle et al., 2011), another study showed no effects of gender (Harari-Dahan & Bernstein, 2017). Notably however, most studies did not test gender differences or were conducted in unisexual samples.

Some recent articles were unable to report differences in approach-avoidance behavior based on interindividual differences in anxiety (Ferrari et al., 2018; Kampmann et al., 2018b; Radke et al., 2013). Importantly, a large longitudinal study ($n > 1700$, 65.8% female, including healthy controls, patients currently suffering from anxiety, depression or both and remitted patients) found no link between anxiety and task behavior (Struijs et al., 2017). Further, the approach-avoidance task behavior could not predict onset or chronicity of anxiety disorders in this sample (Struijs et al., 2018).

In conclusion, several studies associated higher anxiety with more avoidance behavior, especially when angry faces were used as stimuli. These results, however, were not supported by all articles and particularly recent findings from one very large sample raise questions about the reproducibility of the findings reported earlier.

In contrast to anxious traits, state anxiety was assessed in only three studies, for example, in a virtual elevated plus maze, a novel translational task commonly performed in rodent anxiety research, in which stronger avoidance was found in highly state anxious individuals (Biedermann et al., 2017; see supplementary material for others). These studies suggest that state anxiety may lead to similar behavioral patterns as suggested for trait anxiety, i.e. the avoidance of unpleasant stimuli, but more research is clearly needed (for details of task designs and sample characteristics see Table 2.2).

Table 2.2

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2.4.3 Specific Phobias: Spider phobia is consistently associated with excessive avoidance

Specific phobias are anxiety disorders defined, according to DSM-5, by an unreasonable and excessive fear of a specific object or situation. As strong avoidance patterns are a defining feature of specific phobias, it is not surprising that phobias have been investigated with approach-avoidance tasks. Interesting to note is that all but one article investigated spider phobia, possible due to its prevalence making it easier to find participants or the relative ease of creating appropriate stimuli. As predicted, fear of spiders was consistently associated with heightened avoidance of spider stimuli in approach-avoidance tasks (Bartoszek & Winer, 2015; Nicholson & Barnes-Holmes, 2012; Pittig et al., 2018; Reinecke et al., 2010; Rinck & Becker, 2007), which could however be reduced by both monetary and social instrumental incentives (Pittig et al., 2018). In children, one study reported general avoidant behavior towards spider stimuli and this avoidance bias was linked to self-reported fear of spiders in girls (note the overall higher scores on self-reported fear of spiders in girls in this study; Klein et al., 2011). Concerning potential differences related to the task used, Krieglmeier and Deutsch (2010) tested the efficacy of different approach-avoidance tasks (explicit manikin task and visual joystick task, see Box 2) and found a correlation of spider fear and avoidant behavior only in the explicit manikin task. One single study was unable to find a correlation between approach-avoidance behavior and spider fear (Effting et al., 2016), which was interestingly the only study using an implicit version of the manikin task.

This pattern of fear stimuli eliciting stronger avoidance in participants with more phobic symptoms was confirmed by studies using the behavioral approach task (BAT) in which participants had to perform increasingly approaching behavior towards the feared object, e.g., a large living spider (Reinecke et al., 2010; Rinck & Becker, 2007). A BAT was also performed in participants with blood-injection-injury type phobia (BII) utilizing blood and insect stimuli. Patients with BII phobia were less willing to

perform the BAT involving blood stimuli and interestingly also the later stages of a second BAT involving insect stimuli compared to non-phobic controls, thus displaying both domain-specific and generalized effects (Koch et al., 2002).

In conclusion, all but one study showed that stimuli relating to specific phobias reliably elicit strong avoidance behavior in approach-avoidance tasks with some evidence favoring explicit manikin tasks. However, it should be highlighted that research was almost exclusively focused on spider phobia. One reason that may have led to the high consistency across studies could be that images of spiders may act as real reinforcers at close distance for participants with spider phobia and therefore elicit stronger avoidance responses (for details of task designs and sample characteristics see Table 2.3).

Table 3

2.4.4 Depression: No consistent evidence for generally lowered behavioral activation

According to diagnostic criteria, major depression is associated with lowered behavioral activation and decreased approach behavior. In the same vein, anhedonia, which is often associated with major depression would be expected to lead to a comparatively reduced tendency to approach positive stimuli. It should be noted, however, that while depression can lead to lowered behavioral activation or anhedonia, they are not a necessary consequence (American Psychiatric Association, 2013). Supporting lowered behavioral activation, one study demonstrated that healthy controls approached happy and avoided angry faces, while depressed participants had significantly lower reaction times in general and showed no approach or avoidance tendencies (Radke et al., 2014). Regarding decreased approach behavior, depressed participants indeed showed slower approach towards positive over neutral stimuli (Bartoszek & Winer, 2015). Other studies were less interpretable in terms of the above diagnostic criteria. Rumination was associated with stronger avoidance of loss stimuli (Eisma et al., 2015). On the contrary, one study showed that depressed patients displayed greater approach and less avoidance towards ‘disliked’ over ‘liked’ activity words (Szczeapanik et al., 2017), suggesting no general approach deficit and no excessive avoidance. Similarly, bereaved participants with prolonged grief pulled grief-related pictures faster towards themselves than that they pushed them away, which again counters the idea of generally lowered approach (Maccallum et al., 2015). Moreover, the effects of depression may depend on symptom severity and current mood. For instance, a sad compared with a happy mood induction led to stronger avoidance of happy faces in participants with more severe symptoms of depression, while no general pattern of approach-avoidance was observed in participants with fewer depressive symptoms (Vrijnsen et al., 2013).

Despite this first evidence of depressive symptoms influencing approach-avoidance tendencies, the field was recently challenged by the same large sample-sized study ($n > 1700$) that has been described in the context of trait approach/avoidance (2.4.1) and anxiety (2.4.2). This study showed no difference in approach-avoidance

behavior based on depressive symptomatology and task behavior had no predictive value for onset or chronicity of the disorder (Struijs et al., 2018; Struijs et al., 2017).

While results may thus be somewhat mixed, it appears that symptoms of depression may lead to decreased approach behavior of positive stimuli. In contrast, negative stimuli, such as “disliked” words or grief-related pictures may be approached more. Generally lowered behavioral activation, reflected in significantly slower reaction times overall, has been stated in only one article in the present literature to our knowledge (for details of task designs and sample characteristics see Table 2.4).

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Table 4

2.4.5 Aggression, Anger and Psychopathy: Aggression stimuli elicit approach responses in aggressive individuals

Moyer (1968) classified seven forms of aggression, which are ethologically and neurally distinct, e.g. predatory, maternal or territorial aggression. These different forms of aggression are differently motivated and can lead to distinct approach-avoidance behaviors depending on the situation or stimulus. Despite this conceptual complexity, the studies presented here all focused on variation in approach-avoidance tendencies related to aggressive traits, for instance trait anger or psychopathy. In these instances, higher trait aggression or anger were expected to lead to behavioral approach tendencies. In line with the expectation, higher trait anger correlated with stronger approach after provocation (Robinson et al., 2016) and was linked to approach towards facial, particularly angry, stimuli (Veenstra et al., 2017). One study painted a more intricate picture, showing that patients with self-reported reactive aggression approached attack related scenes, while patients with proactive aggression displayed avoidance of attack related scenes (Lobbestael et al., 2016). Overall, although there were surprisingly few studies investigating trait aggression, it seems to elicit consistent approach behavior, especially towards stimuli that depict forms of aggression. Interestingly, two studies in children showed that aggression can go hand in hand with avoidance. For instance, an avoidance bias towards names of class mates in an approach-avoidance task was correlated with more relational aggression and bullying (Lansu et al., 2013), and more aggression when allowed to allocate punishment (Lansu, 2018), at least in girls.

Pathological forms of aggression as in psychopathy were investigated both in violent offenders and as continuous trait in more diverse samples. In violent offenders, avoidance behaviors towards angry faces seem to be diminished (Ly et al., 2016). This absence of avoidance behavior was related to self-reported instrumental aggression and the inability to feel personal distress when observing another's negative experiences (von Borries et al., 2012). However, an fMRI study found no behavioral

approach-avoidance effects of psychopathy in a smaller sample of violent offenders (Volman et al., 2016).

In other studies in which trait psychopathy was assessed as a continuum, higher cold-heartedness was trend-level correlated with keeping a shorter distance to fearful faces (Vieira et al., 2017) and a shorter interpersonal distance (Vieira & Marsh, 2014). However, in contrast to the Vieira 2017 study, one study found that individuals with stronger psychopathic traits showed less approach toward fearful faces (Hammer & Marsh, 2015). Overall, the majority of studies showed that approach towards angry faces is stronger in highly psychopathic participants, even though the evidence is not unequivocal. Behavior towards other emotional stimuli, however, is less clear (for details of task designs and sample characteristics see Table 2.5).

Table 5

2.4.6 Substance use

When testing approach-avoidance tendencies of people suffering from substance use problems, the prevailing hypothesis is that they would approach stimuli relating to their desired substance. Most articles by far related to alcohol use.

2.4.6.1 Alcohol: No consistent association between alcohol (ab-)use and heightened approach bias

An approach bias was indeed found in alcohol dependent patients (Ernst et al., 2014; Wiers et al., 2014) and the quantity of alcohol consumed by alcohol dependent patients was correlated with stronger approach tendencies towards alcohol images (Barkby et al., 2012). Two studies, however, found no general approach bias in alcohol dependent patients (Barkby et al., 2012; Wiers et al., 2017). Interestingly, abstinent alcohol dependent patients were more avoidant of alcohol stimuli than controls (Spruyt et al., 2013). Approach bias in heavy drinkers without dependency was supported by several articles (Christiansen et al., 2012; Field et al., 2011; Field et al., 2008; Kim & Lee, 2015; Peeters et al., 2012; Van Duijvenbode et al., 2016; Willem et al., 2013). However, almost as many articles did not replicate this finding (Cousijn et al., 2014; Ernst, Plichta, et al., 2013; Groefsema et al., 2016; Janssen, Larsen, et al., 2015; Junger et al., 2017; van Hemel-Ruiter et al., 2011). Healthy adults at risk for alcohol use disorder due to low sensitivity towards alcohol did show approach behavior in one study (Fleming & Bartholow, 2014), but approach was diminished after depressive mood induction in drinkers with enhancement motives (Ralston et al., 2013). Finally, there were no overall effects of alcohol use on approach behavior in healthy adolescents, and approach tendencies were not consistently predictive for alcohol use over time (Janssen, Wood, et al., 2015; Pieters et al., 2014).

To investigate task differences potentially accounting for these highly inconclusive findings, one study used both manikin and joystick task in explicit and implicit form in hazardous drinkers and found approach bias only in explicit tasks (Kersbergen et

al., 2015; see also Field et al., 2011 for similar results). It should be noted though, that this claim is not unequivocal as several implicit studies reported approach biases, too (Fleming & Bartholow, 2014; Korucuoglu et al., 2016; Peeters et al., 2012), while some explicit tasks resulted in no effects (Groefsema et al., 2016; Janssen, Wood, et al., 2015). Other studies suggested that the effect of alcohol on approach-avoidance behaviors may be moderated by cognitive abilities. For instance, problem drinkers show greater alcohol approach bias when they have low working memory capacity in general (Sharbanee et al., 2013) or a low current memory load, i.e. less interference (Sharbanee, Stritzke, et al., 2014). However, light drinkers did not significantly differ in their approach-avoidance behavior from heavy drinkers in a sample including both participants with average IQ and patients with mild to borderline intellectual disability (Van Duijvenbode et al., 2016; van Duijvenbode et al., 2012) and patients with alcohol-related major neurocognitive disorder (Korsakoff syndrome) even displayed alcohol avoidance (Loijen et al., 2018). To summarize, results concerning alcohol use and approach-avoidance behavior seem mixed with some articles reporting an approach bias while others could not replicate this finding.

In studies using alcohol administration, general approach motivations may be amplified by alcohol consumption itself as alcohol consumption could reduce the inhibition of drinking behavior due to anxiolytic effects (Gilman et al., 2008). However, alcohol administration induced no approach bias for several stimulus types (Field et al., 2005; Junger et al., 2017; Korucuoglu et al., 2014; Schoenmakers et al., 2008). The exception is one study showing that drinking alcohol led to faster approach of sexual imagery and faster avoidance of contraception images (Simons et al., 2016). In another study, reported results were mixed depending on whether bias scores or reaction times were analyzed (Korucuoglu et al., 2016). Furthermore, administering alcohol seems to necessitate careful selection of the control condition due to potential placebo effects (Christiansen et al., 2013). These authors showed that consuming alcohol elicited the same approach bias in participants as did the belief that they had consumed alcohol compared to a control drink condition in which it was made clear that the beverage would contain no alcohol.

Summarizing these findings, it can be noted that in both alcohol dependent patients and heavy drinkers, approach biases towards alcohol were sometimes present. However, the similarly numerous accounts of null findings warrant closer examination and do not allow definite statements. In alcohol administration studies, usually no approach bias was found, but studies are few and results may be impacted by the control condition and the stimulus type used. Findings might further be complicated by the fact that alcohol and other drugs affect many neurotransmitter and hormone systems in a complex and time-dependent manner, possibly preventing simple conclusions (Chastain, 2006; Rachdaoui & Sarkar, 2013). Moreover, alcohol approach is often driven by incentive motivation. Therefore, the stimuli used in a given task may be of particular importance as alcohol itself may have very different effects compared to alcohol-related visual stimuli. Finally, in some cases where individuals suffer from substance use disorder comorbid with depressive or anxiety disorders, approach might be driven by self-medication and affect behavioral approach differently than would be the case with other approach motifs (Ralston et al., 2013; Robinson et al., 2009; for details of task designs and sample characteristics see Table 2.6).

2.4.6.2 Smoking: Smoking-related stimuli do not elicit approach behavior in smokers

Besides alcohol, we found surprisingly few substances being addressed in studies with approach-avoidance tasks concerning interindividual differences. In contrast to the mixed results from studies investigating the effects of alcohol, most studies in smokers found no approach bias towards smoking-related stimuli (Larsen et al., 2014; Machulska et al., 2015; Weckler et al., 2017; Woud et al., 2016) with only one exception (Wiers et al., 2013). Cigarette craving was correlated with approach bias, but this approach bias increased rather than decreased after reducing craving by smoking a cigarette (Watson et al., 2013). Another seemingly counterintuitive study found increased approach bias towards smoking stimuli in smokers with lower levels of nicotine dependence as compared to smokers with higher levels of dependence (Mogg et al., 2005). This finding might suggest that approach tendencies change with the

development of dependency. Reasons could be a shift in the steepness of approach-avoidance gradients or reduced incentive motivation towards the stimuli as substance use shifts from substance ‘liking’ to ‘wanting’ during prolonged substance consumption (Berridge, 2004). Similarly, a shift of behavioral control towards ‘wanting’ could also explain the results of a study implying that the pleasantness of the smoking stimuli might play a role. Here, stronger approach bias towards unpleasant smoking-related stimuli was found in smokers compared to non-smokers, while no group difference in behavior towards pleasant smoking cues was observed (Bradley et al., 2008). Overall, smoking-related stimuli did not elicit approach behavior in smokers. Aspects of smoking such as craving, dependence and cue pleasantness might modulate approach-avoidance tendencies, but should be investigated in more detail for definite conclusions.

2.4.6.3 Further substance use

Approach bias towards cannabis was reported in heavy users compared with controls (Cousijn et al., 2011; Field et al., 2006; Wolf et al., 2016), but not replicated in one study (Cousijn et al., 2012). Only one study investigated heroin use, indicating potentially enhanced approach towards addiction-related stimuli in former heroin users (see supplementary materials; for details of task designs and sample characteristics see Table 2.6).

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2.4.7 Food-related pathologies and habits may be associated with approach-avoidance alterations, but evidence is often equivocal

Many types of disordered eating behavior were investigated utilizing approach-avoidance tasks, usually with food-related stimuli. As expected, female patients with anorexia nervosa exhibited less approach bias towards food than healthy controls (Paslakis et al., 2016; Veenstra & de Jong, 2011). However, one study investigating anorexia nervosa patients showed no correlation of self-reported symptomatology and behavior in an approach-avoidance task (Neimeijer et al., 2015). In contrast, evidence in restrained eaters with normal weight is more equivocal as one study showed enhanced approach behavior towards food images compared to non-restrained eaters (Veenstra & de Jong, 2010) whereas another study could not replicate this finding (Ahern et al., 2010). Finally, a third study showed avoidance toward food pictures in restrained eaters when food was task-relevant, but the implicit, task-irrelevant presentation of food stimuli elicited strong behavioral approach after positive mood induction and avoidance after sad mood induction (Neimeijer et al., 2017). To summarize, patients with anorexia nervosa tend to show reduced approach towards food stimuli whereas the evidence for restrained eating in healthy individuals is, as of yet, inconclusive.

In obese or overweight patients, results were also ambiguous. While one study found stronger approach towards food compared to normal-weight controls (Mehl et al., 2018), this finding could not be replicated and some studies even reported avoidance of food-stimuli in obese participants (Havermans et al., 2011; Kakoschke et al., 2017b; Paslakis et al., 2017; Schmidt et al., 2018). Other types of disordered eating behavior as established by eating disorder questionnaires (e.g. external eating, emotional eating) did not consistently relate to behavioral differences in two studies using food stimuli as one study found heightened approach (Brignell et al., 2009) and one study found no effect (Khan & Petroczi, 2015). Likewise, two studies using body

type stimuli showed no consistent effects of BMI or eating habits (Leins et al., 2018; Woud et al., 2011) .

To summarize, evidence from the presented articles remains largely equivocal. Overall, participants that have pathologies related to overeating might approach food stimuli more, while participants that heavily control their food intake (mainly anorexia nervosa patients) showed less approach behavior in experimental tasks. However, restrained eating may also indicate strong automatic approach tendencies towards food as seen in two restrained eating behavior studies presented above in which food was a task-irrelevant stimulus. This effect might suggest an ambivalence present in restrained eating where explicit behavioral avoidance is accompanied by strong approach when stimuli are displayed as task-irrelevant distractors. Of note is that the majority of studies was conducted in female-only samples or samples with mostly women (for details of task designs and sample characteristics see Table 2.7).

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2.4.8 Trauma might strengthen avoidance behavior, but the effects differ by stimulus type and study

Avoidance is a defining feature of trauma-related disorders like posttraumatic stress disorder (PTSD). Accordingly, several studies investigated avoidance of stimuli both related and unrelated to traumatic events. In line with the idea of trauma-related avoidance, women exposed to sexual trauma showed greater avoidance of high-threat sexual pictures compared to healthy controls (Fleurkens et al., 2014). In a sample of adult participants that had been exposed to childhood trauma, a similar avoidance pattern could be observed. Participants who had received more negative caregiving as a child displayed greater bias to avoid sad, but not other expressions in infant faces (De Carli et al., 2017). Somewhat in contrast, however, in combat-exposed PTSD patients, worse symptomatology was related to greater avoidance of happy faces, but not faces showing negative affect (Clausen et al., 2016). Moreover, other studies did not show any group differences, for instance after childhood maternal love withdrawal (Riem et al., 2017) or between participants suffering from displacement-related PTSD, traumatized healthy control participants and non-traumatized controls (Wittekind et al., 2015). It should be noted, though, that this study investigated elderly participants (> 70 years) who experienced childhood trauma decades ago. In contrast to the findings in this study using the parent generation, the offspring of these traumatized participants without PTSD showed increased avoidance of displacement-related stimuli in comparison to non-trauma exposed participants' offspring, whereas offspring of parents with PTSD unexpectedly did not differ from either group (Wittekind et al., 2017). To conclude, some studies suggested enhanced avoidance in traumatized participants, but the stimulus type that is excessively avoided varies enormously between studies, ranging from negative to positive. Thus, trauma appears to be a complex phenomenon with a lot more research needed to establish how traumatized participants with and without PTSD diagnosis, and potentially their offspring, interact with trauma-related and non-trauma-related stimuli (for details of task designs and sample characteristics see Table 2.8).

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Table 8

2.4.9 Equivocal effects of laboratory stress induction on approach and avoidance

Stress is a potent risk factor for many disorders with altered approach-avoidance behavior, e.g., anxiety disorders or substance use disorders (Koob et al., 2014; Shin & Liberzon, 2010). However, relatively few studies investigated the effects of (non-traumatic) stress in a laboratory setting and especially studies addressing stress-related differences in healthy participants are largely missing. While some studies showed effects of acute stress on approach-avoidance behaviors, the direction of the effect differed strongly between studies and appeared to be dependent on sample characteristics. For instance, acute stress induction via a cold pressor test did not affect behavior in healthy controls, but accelerated approach of angry faces in psychogenic non-epileptic seizure patients (Bakvis et al., 2011). In contrast, stress increased avoidance of social threat stimuli in social anxiety disorder patients, which was related to stronger cortisol responses to the Trier Social Stress test (TSST). This stress-induced avoidance enhancement was not present, however, in PTSD patients or healthy controls (Roelofs, van Peer, et al., 2009), defying general conclusions and possibly hinting towards inverted-U-shape effects of acute stress depending on baseline levels of anxiety or arousal. Another study supported the hypothesis that stress effects may vary depending on participant characteristics. In this study, approach toward attachment figures was increased in a distressing context, but this effect was moderated by individual differences in attachment anxiety and avoidance, which led to approach or avoidance of attachment respectively (Dewitte et al., 2008).

In another small sample of healthy participants with a high cortisol response to the TSST, diminished congruency effects were found after stress, resulting mainly from increased reaction times for congruent actions, thus resembling both reduced avoidance and approach of congruent actions (Roelofs et al., 2005). A potential role for the stress hormone cortisol in changing approach-avoidance behavior in healthy individuals was further suggested by one study reporting that lower baseline cortisol levels were associated with increased congruency effects in the explicit joystick task, mainly for angry facial stimuli (Roelofs, Minelli, et al., 2009). In contrast, however,

when cortisol was administered, it enhanced congruency effects for angry faces in highly avoidant individuals, with no effect in low avoidant individuals (van Peer et al., 2007).

Stress is also believed to play an important role in the development and maintenance of addiction (Koob et al., 2014). One group investigated how generally heightened approach behavior in approach-avoidance tasks may be one potential link between stress and enhanced approach of addictive substances. In this study, approach behavior was positively correlated with substance use at high levels of stress and also correlated with substance use when combined with blunted sympathetic reactivity (Hinnant et al., 2017; Hinnant et al., 2016), which might be driven by attempts of self-medication to cope with acute stress. However, more research is needed to investigate the possibility of stress-induced substance approach in vulnerable individuals.

In conclusion, the few studies investigating the influence of stress on approach-avoidance behavior showed both approach and avoidance tendencies elicited by stress, but also null-findings, the latter mainly in healthy participants. The influence of cortisol is equally inconclusive with administered cortisol and endogenous cortisol release under stress displaying opposing effects depending on the population investigated. More research is needed to elucidate the effects of the stress-response, but also more chronic stressors on approach-avoidance behavior and how it may be interconnected with personality traits and other interindividual differences (for details of task designs and sample characteristics see Table 2.9).

Table 9

2.4.10 Testosterone: Endogenous testosterone levels are not associated with approach-avoidance behavior

In contrast to the original hypothesis of approach-enhancing effects of testosterone (Zuckerman, 2012), endogenous testosterone levels had no effect on approach-avoidance task behavior towards faces differing in dominance and trustworthiness (Radke et al., 2018). Likewise, no behavioral effects of endogenous testosterone were detected in two fMRI studies on healthy male adults (Volman, Toni, et al., 2011) and psychopathic offenders (Volman et al., 2016), irrespective of whether happy, neutral or angry facial stimuli were used. The exception is one study in 14-year old adolescents, in which lower levels of endogenous testosterone were associated with increased approach of happy faces and avoidance of angry faces (Tyborowska et al., 2016).

However, when testosterone was administered to female participants in a within-subject design, testosterone diminished avoidance of angry faces or even resulted in significant approach towards angry faces compared to happy and neutral faces (Enter et al., 2014, 2016). Nevertheless, an fMRI study with between-subject design reported no behavioral differences due to testosterone administration of the same dosage (Radke, Volman, et al., 2015).

In summary, the presented studies indicate that endogenous testosterone levels are not associated with task-related approach-avoidance differences in adult participants. When given extraneously, however, testosterone might reduce avoidance and increase approach. Prior evidence for effects of testosterone levels on behavior has largely been in relation to risk-taking (e.g. Mehta et al., 2015; Stanton et al., 2011), mostly by measures of endogenous testosterone. The results of the studies here may therefore be influenced by level of conflict and amount of risk-taking the task affords, which are both variables that could be advantageous to control for in future studies (for details of task designs and sample characteristics see Table 2.10).

Table 10

2.4.11 Oxytocin: Exogenous oxytocin may increase approach and reduce avoidance depending on stimulus and participant characteristics

Surprisingly, the effects of endogenous oxytocin concentrations on approach and avoidance behavior were investigated in only one study, which showed that oxytocin levels correlated with enhanced avoidance of angry faces in schizophrenic patients (Brown et al., 2014). No studies were available for other sample populations, thus severely limiting the ability to draw conclusions. In comparison, more studies addressed the effects of administering oxytocin. For instance, oxytocin increased approach towards angry faces in low anxious individuals (Radke et al., 2013) and alleviated exaggerated avoidance towards negative stimuli in highly anxious individuals (Harari-Dahan & Bernstein, 2017). Additionally, oxytocin administration enhanced monogamous bonds formed earlier in men in a monogamous relationship, as suggested by greater distances put between themselves and an attractive female (but not male) experimenter and stronger avoidance in the joystick task towards attractive females (Scheele et al., 2012). Women, in contrast, displayed decreased social distance towards attractive and friendly male but not female experimenters after oxytocin administration independent of relationship status, and approached pleasant social scenes in the joystick task faster (Preckel et al., 2014).

Other studies, however, showed only minor behavioral effects such as selective changes in error rate (Yao et al., 2018), increases in reaction times and error rates in men, for which the authors reported that they did not survive multiple comparison corrections (Radke et al., 2017) or faster reaction times in women but not men (Theodoridou et al., 2013). Likewise, oxytocin administration did not consistently affect behavioral approach in response to alcohol-related and other stimuli in alcohol abusers (Mitchell et al., 2016).

In summary, the influence of endogenous oxytocin concentrations on approach avoidance behavior is unfortunately hardly investigated. The few studies that utilized exogenous oxytocin indicate that oxytocin can enhance approach and reduce

avoidance, but the effects differ depending on the stimuli used and both the individual's gender and anxiety level. As with testosterone, oxytocin may influence approach-avoidance behaviors in a variety of ways, hampering the comparison of studies. Oxytocin may, for example, change behaviors based on the level of trust, conflict, or risk-taking involved in a given task (Baumgartner et al., 2008; Bozorgmehr et al., 2019; Kosfeld et al., 2005; for details of task designs and sample characteristics see Table 2.11) .

2 | HOW INTERINDIVIDUAL DIFFERENCES SHAPE APPROACH-AVOIDANCE
BEHAVIOR: RELATING SELF-REPORT AND DIAGNOSTIC MEASURES OF
INTERINDIVIDUAL DIFFERENCES TO BEHAVIORAL MEASUREMENTS OF APPROACH
AND AVOIDANCE

Table 11

2.5 DISCUSSION

Approach-avoidance behavior plays a major role in the development, persistence, and recovery of several psychiatric disorders. Despite a large body of research, the precise influences of interindividual differences on automatic approach-avoidance tendencies assessed in behavioral tasks are largely unknown and a concatenation of prior research urgently needed to make informed decisions about future studies, directions of research and potentially new mental health interventions. Here, we investigated 137 experimental human studies sorted in categories of individual variation that emerged based on a systematic literature screening. Our results show that the investigated interindividual differences may be linked to altered approach-avoidance behavior in experimental tasks with findings rarely being directly opposing (with the exception of stress). Rather, the studies either show the expected direction of effect (approach or avoidance tendency) or, surprisingly often, null-findings, i.e., no clear links between the investigated interindividual variation and directionality of the approach-avoidance response.

Overall, the number of studies varied strongly by field with substance abuse and eating disorders being investigated more frequently, while much needed research on endocrine differences, other disorders (e.g. autism spectrum disorders) or personality traits is often missing. For instance, only one study investigated endogenous oxytocin levels and few studies addressed stress, aggression, or depression.

2.5.1 Individual differences in task-based approach-avoidance behavior are more ambiguous than thought

Oversimplified, the studies that found effects suggest that increased approach behavior was associated with trait approach assessed with the CW-BAS scale, anger, aggression, psychopathy and substance use. Trauma might also increase approach, but the interpretation is more difficult as some studies reported approach towards positive and

others towards negative trauma-relevant stimuli. In contrast, increased avoidance was associated with trait inhibition as assessed with the CW-BIS scale, trait anxiety and spider phobia. The latter was the overall most consistently described effect whereas the interpretation for the other categories is more complicated due to many null-findings. While not necessarily affecting avoidance, stronger symptoms of depression were correlated with less approach behavior. Endogenous testosterone levels seem to have reliably no effect on approach-avoidance behavior as assessed in the tasks used. In the other categories, findings were much more inconsistent with both approach and avoidance behaviors being found. For instance, eating habits and disorders include a variety of underlying symptoms making overall conclusions and interpretations difficult (e.g. avoidance of food stimuli in anorexia nervosa; approach of food stimuli in restrained but healthy eaters). Similarly, laboratory stress induced both approach and avoidance behavior, which might depend on interaction effects with personality traits or explained by the differences in study populations. Studies administering testosterone or oxytocin also did not cater to any overarching interpretation.

Thus, areas of research in which approach-avoidance behavior is assumed to correlate strongly with symptom severity or traits appear to be a lot more ambiguous than, or not as investigated as, initially thought. This is true even for self-reported approach-avoidance tendencies, which show low consistency in their correlation with behavioral approach-avoidance. Thus, the most striking finding of our literature search may be the unexpected number of null-findings that can be seen across fields with the exception of specific phobias. The inconsistency in some fields is especially relevant as approach-avoidance tasks are trialed as clinical interventions, for example, in patients with substance use disorder. If it turns out that these tasks do not reflect interindividual differences as well as initially thought, therapeutic success should be evaluated carefully.

2.5.2 Possible explanations for heterogeneous findings: Heterogeneity of interindividual differences

A possible answer to why investigating interindividual differences with approach-avoidance tasks often led to inconclusive results could be that the individual differences were sometimes loosely defined and the homogeneity of traits not guaranteed. For instance, the broad categorization of complex pathologies such as major depression, which include a multitude of possible symptom combinations, may result in heterogeneous populations that hamper clear-cut associations with behavioral measures. While depression can sometimes produce anhedonia, which would be expected to decrease behavioral approach, especially of positive stimuli, this is not necessarily the case. Another example would be the inclusion of participants with different levels of (hyper- and hypo-)arousal. This might add considerable variance in patient studies. Here, symptom level or subtype-based studies, for instance using Research Domain Criteria (RDoCs), may offer advantages and could lead to more consistent findings. Supporting this interpretation is the fact that articles on spider phobia with arguably less variability in symptom combinations strongly overlap in their findings. The heterogeneity of symptoms may also lead to subgroups of patients employing opposite approach-avoidance strategies and thus hampering overarching conclusions.

Studies also investigated traits in diverse healthy and patient populations with varying inclusion criteria, potentially hampering reproducibility of findings. A good example for the variety in populations are trauma studies that investigated participants differing strongly in trauma type and recency. Nevertheless, interaction effects could still present themselves even over heterogeneous studies if differences in the assessed trait impact basic approach-avoidance behavior in a consistent manner and further individual variation is controlled for by study design. However, the sample sizes needed to assess this variation might be larger than previously thought, particularly for correlations. For example, to achieve stable and significant estimates for small to medium-sized correlations (as typical in psychology), the required n would be 150 to 250 individuals (Schönbrodt & Perugini, 2013). Critically, this number is much higher than what most studies employed in this review.

Another way in which heterogeneity of individual differences adds to inconsistent findings is that human experimental situations themselves contain approach-avoidance dynamics prior to the beginning of the experiment. Individuals sensitive to factors affecting those dynamics, e.g. conflict or anxiety, may differ from other participants in how they accomplish the task due to differences in motivational forces. The establishment of procedures to measure baseline approach-avoidance variation prior to the experimental task may therefore be a good step to partially explain variance between participants, for example with state questionnaires targeting interindividual differences in motivation or approach-avoidance behavior (e.g. conflict sensitivity, anxiety).

2.5.3 Possible explanations for heterogeneous findings: Heterogeneity of stimuli and task designs

Across studies, one might argue that the articles we integrated here were very heterogeneous, making summarizing statements perhaps less convincing than the effects actually are. Indeed, articles differed strongly in tasks, stimuli and design (group, correlation or repeated measures). The variation in the stimulus-types used is additionally dependent on the research area of interest with high consistency across studies in specific phobia of spiders (spider and butterfly stimuli) and also many studies investigating trait anxiety, aggression or depression employing facial stimuli (often angry and happy faces). In contrast, studies on trauma, substance use or eating disorders were much more varied in their stimulus presentation (e.g., studies displaying either food items with different caloric value or food and non-food items, which cannot be easily compared). While this flexibility in stimulus choice is a tremendous advantage of classical approach-avoidance tasks as virtually any stimulus set can be used, it may also contribute to the effects being less comparable. A stringent

investigation of the effects of different stimulus sets or a better standardization of stimuli would therefore be desired to increase comparability of studies.

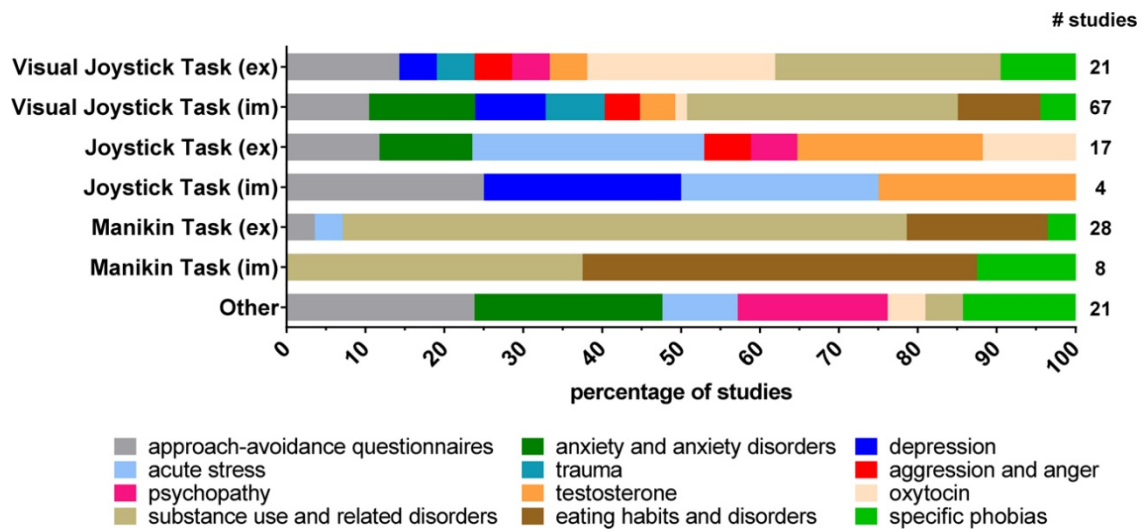


Figure 2.2. Percentage scores of approach-avoidance studies per research area sorted by task-type. Tasks using stimuli relevant to task instructions are indicated as explicit (ex), while tasks using task-irrelevant stimuli are marked implicit (im). The approach-avoidance task most often employed was the implicit visual joystick task. However, depending on the research area, different types of tasks seem to be favored. Studies investigating more than one interindividual difference or employing more than one task appear in the graph separately for all differences and tasks used. Figure for illustrative purposes only.

Further, a standardization of task designs beyond mere stimulus selection might similarly increase the consistency of findings. Different tasks are commonly employed in approach-avoidance research, but task choices seem to differ by research area (see Figure 2.2). For some of the categories we reported, it has been suggested that task type matters. For instance, some articles have discussed the importance of task types (e.g., joystick task or manikin task) and stimulus-presentation (e.g., explicit or implicit; Kersbergen et al., 2015; Krieglmeyer & Deutsch, 2010; Neimeijer et al., 2017; Phaf et al., 2014; Woud et al., 2016), arguing for instance that implicit instructions result in null-findings as relevant stimulus features are not consciously processed (Phaf et al., 2014). Based on the literature reviewed here, we are, however, unable to support these claims in their entirety (Figure 2.3). The number of null-findings does not seem to be strongly linked to the type of task used. For the type of instruction, it appears that implicit tasks descriptively slightly favor null-findings in comparison to explicit

instructions. For lack of comparability between categories, we cannot make general claims and would like to point out that also explicit tasks have a considerable amount of null-findings. Future studies would certainly benefit from following previous study designs as closely as possible to allow not only qualitative but also quantitative means of comparison. Direct replications would allow meta-analytic integration of findings and much needed quality control. For instance, a systematic assessment of publication bias would be desirable as null-findings with measures which can be obtained with relative ease (e.g. questionnaires) are potentially underreported. Inconsistencies due to small n, particular study samples, or operational specifics would also be more clearly separable from inconsistencies due to underlying differences within the data.

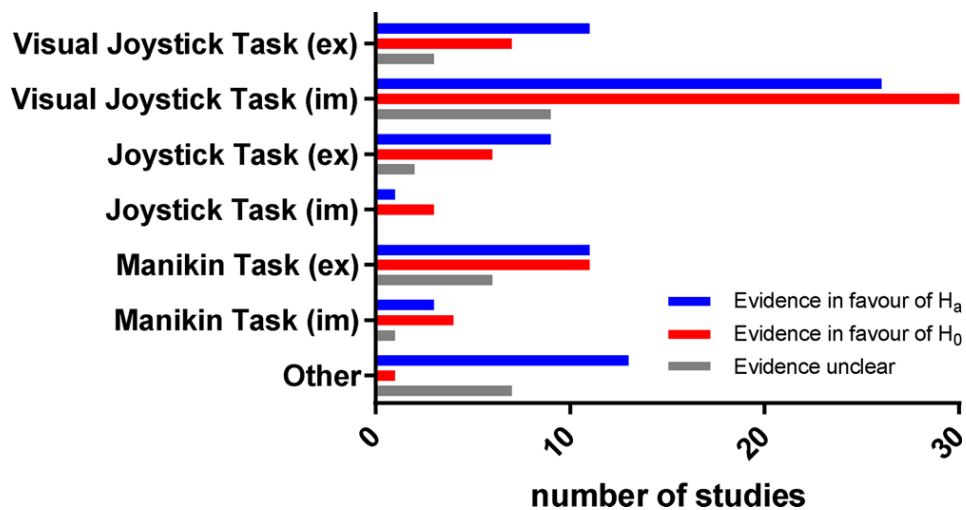


Figure 2.3. Explorative illustration of approach-avoidance studies sorted by task-type and significance of results. Tasks using stimuli relevant to task instructions are indicated as explicit (ex), while tasks using task-irrelevant stimuli are marked implicit (im). Studies are categorized based on the statistical significance of the correlation between main outcome of the approach-avoidance task and the reported interindividual difference. Studies were labelled as “evidence unclear” if the alternative hypothesis could neither be clearly accepted or rejected. Studies investigating more than one interindividual difference or employing more than one task appear in the graph for all differences and tasks used. Figure for illustrative purposes only.

2.5.4 Possible explanations for heterogeneous findings: Differences to real life approach-avoidance conflicts

It might be that some approach-avoidance tasks measure aspects of approach-avoidance behavior that are less strongly influenced by individual variation than previously thought. In disorders associated with e.g. increased trait anxiety, trait depression, or trait aggression, the situations in which divergent approach-avoidance would be triggered are rather well-defined (e.g. avoidance of angry social stimuli with higher trait anxiety, approach of these stimuli with higher trait aggression). As this behavior is not consistently found across research experiments, the tasks might not mimic these situations enough or might test aspects of approach-avoidance that are rather robust towards interindividual variation. One study that might support this claim showed no predictive value of an implicit visual joystick task and the BAT on everyday social anxiety, while questionnaires were able to capture this anxiety better (Kampmann et al., 2018b). More generally, approach-avoidance tasks are often much less ambiguous than the approach-avoidance decisions made in everyday life. This may in turn lead to different interpretations dependent on whether a person is in a clearly instructed experiment or makes real-world decisions.

Interestingly, other approach-avoidance tasks have been used with much more consistent results in rodents to investigate fear and anxiety among others (Campos et al., 2013; Kirlic et al., 2017; for a review of paradigms; Toth & Neumann, 2013). Of course, rodent studies offer highly controlled environments and allow the comparison of clearly and more invasively separated groups through methods of breeding, knock-out mutations and drug application, for example. Animal studies can therefore investigate causal relationships that might be much harder to tackle in humans. However, we argue that translational paradigms may have additional potential to model individual variation in experimental approach-avoidance conflicts as they are grounded in preclinical work. For instance, a promising study that involved a virtual reality elevated plus maze (Biedermann et al., 2017) showed that humans, similar to rodents,

avoid the open arms of the elevated plus maze and feel distress, which was influenced by their state anxiety, acrophobia and sensation seeking. An anxiolytic agent decreased the avoidance of open arms, while noradrenergic stimulation increased avoidance, further validating this paradigm. Likewise, a novel translational paradigm investigating complex foraging decisions under threat was sensitive to variations in trait anxiety, displayed by prolonged time in an area safe from threat in addition to less and slower foraging (for task description see Box 2; Bach et al., 2018; Korn et al., 2017). This translational paradigm, too, was sensitive to several anxiolytics, strongly supporting the validity of these novel tasks. One challenge in designing and using translational tasks to assess human approach-avoidance behaviors will be the careful consideration of advantages and disadvantages specific non-human animal tasks have to offer. The elevated plus maze used by Biedermann et al., for example, has been criticized in rodent experiments for its ‘one-trial-tolerance’, meaning that successive trials are very different from being first exposed to the maze. Adaptations of an elevated T-maze might therefore be better suited for researchers interested in measuring performance over several trials (File & Zangrossi, 1993; Graeff et al., 1998). Translational efforts are further complicated due to fundamental differences in training, motivation and reward between rodent and human paradigms. For instance, rodents are typically highly trained and thus display more habitual behavior, rendering them less sensitive to manipulations of the supposed underlying motivation, whereas human paradigms rely on direct instructions with typically rather weak reinforcers (e.g., Dickinson, 1980; McNaughton, 1985). This might make direct translation attempts cumbersome as approach-avoidance tasks may not involve motivational systems relevant to the investigated interindividual differences when requiring habitual or low-drive behavior only. Additionally, it remains to be seen whether these paradigms for anxiety can be adapted and uphold their sensitivity to individual variation in other trait domains or whether translational paradigms can be developed for other fields in which the role of approach-avoidance behavior is currently less clear.

2.5.5 New paradigms employ increased ambiguity of conflict

Translational and other newly developed paradigms may also contribute to approach-avoidance research by creating more ambiguous approach-avoidance conflicts than traditional tasks. The stimuli in our environment are often ambiguous and such are approach-avoidance decisions when dealing with them. In both joystick and manikin tasks, however, participants are clearly instructed to make approach or avoidance movements depending on the stimulus displayed. If instructed to push away all angry faces, it is undoubtedly clear that push-movements are correct and pull-movements are incorrect. The tasks rely on reaction time measurements that indicate automatic tendencies by comparing congruent (e.g., push angry face away) and incongruent (e.g., push happy face away) trials. A clear advantage of this task is that approach and avoidance can be differentiated on a trial-by-trial basis, possibly allowing for more clearly interpretable results. However, it is thinkable that participants in those tasks display habitual or low-drive behavior over time, thus activating simple action systems rather than motivational systems that are meant to be captured by questionnaires or traits (e.g. diagnoses of psychiatric disorders). While this explanation could explain some inconsistencies in tasks measuring automatic tendencies, a meta-analysis suggested the involvement of motivational systems, at least in tasks with explicit instructions (Phaf et al., 2014). Another downside may be that the tasks do not reflect typical everyday approach-avoidance decisions where the optimal response is unclear and interindividual differences in responding may be easier to observe. Tasks that create ambiguous approach-avoidance conflicts without an immediately clear correct response might therefore be better suited to investigate interindividual differences. Examples could again be the aforementioned elevated plus maze in which natural movements are observed (Biedermann et al., 2017) or an open field test that was employed using real life GPS-tracking (Walz et al., 2016). Similarly, whole body movements to position oneself in relation to given stimuli could be used (Ly et al., 2016). Other tasks that need a less complicated experimental setup create approach-avoidance conflicts through risk-reward paradigms. Foraging for money under probabilistic threat of getting chased by a predator taking all reward requires constant deciding of whether to continue foraging or not without a clearly correct way to solve the task (Bach et al., 2018). Importantly, these novel tasks allow researchers to manipulate predatory behavior (e.g. speed or closeness) and the time participants have

to decide whether to avoid or not (Fung et al., 2019). The relative ease of changing task parameters such as predatory threat level or threat distance has additional advantages such as the creation of neural maps based on participants' reaction to different task variants during neuroimaging (McNaughton, 2019). One more potential benefit of these virtual predator paradigms lies in the ability of a manifested threat to act as more potent reinforcer at a well-defined distance, which might enhance comparability with real world scenarios.

Fung et al.'s study is especially interesting as it offers another potential explanation for some null-findings we encountered. While fast predatory threat did not lead to behavioral differences between individuals low and high in trait anxiety, a slower predator increased avoidance in participants with higher trait anxiety. It could be hypothesized that very fast, automatic approach-avoidance tendencies are less affected by more complex cognitive interindividual differences than approach-avoidance behavior in slower situations. This could explain why tasks with constantly required fast actions such as the joystick and manikin task are especially suited to capture interindividual differences in specific phobia where fast, automatic responses to stimuli also occur in real life, while they struggle with modeling behaviors influenced by other traits that are perhaps less automatically entrained. To test this hypothesis, it would be interesting to systematically investigate individual differences using various task types and to compare the results for traits of varying cognitive complexity in a specific task and between tasks. To conclude, studies with ambiguous approach-avoidance conflicts may be better suited to investigate some types of individual variation. However, depending on the research question, the missing discernibility of approach and avoidance in these tasks might be of concern and would have to be addressed during study design. Since the paradigms we mentioned mostly come from the anxiety and fear literature, investigating different interindividual differences might furthermore require the development of other tasks.

2.5.6 Investigating moderating factors in approach-avoidance differences

One finding that was unexpected to us was that stress had strikingly opposing effects on approach-avoidance behaviors in different studies. Notably, several articles reported interaction effects of stress or cortisol levels with other moderating traits leading to either increased approach or avoidance behavior under stress. Given that stress is a potent risk factor for a large variety of psychiatric disorders that come about with different alterations of approach-avoidance behavior, it is not farfetched to assume that personality traits may modulate how stress affects participants' behavior. In a recent study, participants were stressed via the TSST before foraging for monetary rewards under predatory threat. Stress did not have strong main effects on behavior, but increased the importance of threat distance and modulated approach-avoidance behavior differently based on participants' individual differences in anxiety and aggression (Vogel & Schwabe, 2019). More generally, the effects of experimental conditions on approach-avoidance behavior may depend on current states of participants or moderating biological or personality traits. It is thinkable that these interaction effects of acute influences, personality traits, and task characteristics are common and that future studies also beyond stress research could benefit from assessing multiple psychological and biological traits.

One possible moderator that is so far underrepresented is gender. This is particularly striking as many psychological disorders for which there are strong hypotheses on altered approach-avoidance behavior display a gender disparity in prevalence. Considering and controlling gender of participants or investigating the impact of sex hormones is therefore increasingly relevant. This has also been acknowledged recently by funding agencies such as the NIH favoring research with sex as biological variable in their funding schemes (The National Institutes of Health, 2015). While most articles we investigated included descriptive data on participants' gender, they rarely analyzed effects of gender or its interaction with other variables on approach-avoidance behavior. This is especially important in the field of eating habits and disorders, where studies often include very few or no male participants or in anxiety research where many studies were conducted in unisex samples. To better understand the underlying mechanisms of approach-avoidance conflicts and the role they play in diseases with gender differences in prevalence, research on gender

differences may be a promising route to take. It would be remiss not to mention that analysis of multiple interactions could have been underpowered in many approach-avoidance studies due to the sample size. Analyses of gender effects may therefore not have been feasible but could be included in future studies.

2.6 CONCLUSION

In summary, we investigated how interindividual differences drive action tendencies in experimental approach-avoidance conflicts by conducting a large literature review encompassing 137 studies organized in distinct research areas. While many studies reported findings supporting their hypotheses, we found surprisingly many null-findings or ambiguous results, even in research areas in which approach-avoidance behavior is assumed to correlate strongly with certain disorders or traits. This lack of consistency in some research fields is especially noteworthy as approach-avoidance tasks are being tested as clinical interventions. Here, we described possible explanations for these findings and argued that some approach-avoidance tasks might not be as sensitive to individual differences as initially thought. While inconsistencies in findings may be owed to the large variability of stimuli, tasks and populations investigated, sometimes even quite comparable studies did not show the same effect patterns. We highlighted recent promising developments of alternative tasks, for instance with a translational approach, that have been mainly used in anxiety research and will be a challenge to implement for other traits of interest. We further emphasized the potential of interaction effects between different states and traits and the importance of potential moderators such as gender or stress, which might partially cover or blur differences related to traits or disorders. Our review indicates that the mechanisms underlying individual variation in approach-avoidance conflicts are still poorly understood and urgently warrant further research. Overcoming these challenges will be important as understanding the dynamics of approach-avoidance behavior will further our understanding of human behavior and open-up new paths for clinical prevention and intervention to better regulate behavior in omnipresent and ambiguous approach-avoidance conflicts.

3 THE EFFECTS OF HYDROCORTISONE AND YOHIMBINE ON HUMAN BEHAVIOR IN APPROACH-AVOIDANCE CONFLICTS

3.1 ABSTRACT

Rationale: Balancing approach of positive and avoidance of negative stimuli is essential when faced with approach-avoidance conflicts, e.g., situations with both positive and negative outcomes. This balance is disturbed in several mental disorders, e.g., excessive avoidance in anxiety disorders, and heightened approach in substance use disorders. Since stress is assumed to impact these disorders' etiology and maintenance, it seems crucial to understand how stress influences behavior in approach-avoidance conflicts. Indeed, some studies suggested altered approach-avoidance behavior under acute stress, but the mechanism underlying these effects is unknown.

Objectives: Investigate how the pharmacological manipulation of major stress mediators (cortisol and noradrenaline) influences task-based approach-avoidance conflict behavior in healthy individuals.

Methods: Ninety-six participants (48 women, 48 men) received either 20mg hydrocortisone, 20mg yohimbine, both, or placebo before performing a task targeting foraging under predation in a fully crossed double-blind between-subject design.

Moreover, we investigated effects of gender and endogenous testosterone and estradiol levels on approach-avoidance behavior.

Results: While biological stress markers (cortisol concentration, alpha amylase activity) indicated successful pharmacological manipulation, behavior in approach-avoidance conflicts was not affected as expected. Although yohimbine administration affected risky foraging latency under predation, we found no main effect of hydrocortisone or their interaction on behavior. In contrast, we found gender differences for almost all behavioral outcome measures, which might be explained by differences in endogenous testosterone levels.

Conclusions: The investigated major stress mediators were not sufficient to imitate previously shown stress effects on approach-avoidance conflict behavior. We discuss potential reasons for our findings and implications for future research.

3.2 INTRODUCTION

Approach and avoidance are highly conserved behaviors across both, species and time. Stimuli of positive valence are approached, while negative stimuli are avoided via generalized goal-oriented systems sensitive to reward and punishment (Gray, 1975). These systems also mediate conflict-resolution in situations in which conflicting stimuli (or features) are present, for example, both reward and punishment. Importantly, these systems are sensitive to the perceived distance between oneself and either reward or punishment. Rewards elicit approach even at long distances, while avoidance of punishment outweighs approach motivations when close to the punishing stimulus. Distance also influences the behavioral response itself, for example, when faced with threat (fight, flight, or freeze response; Blanchard & Blanchard, 1988; McNaughton et al., 2016).

Approach-avoidance behaviors are imbalanced in many mental disorders, e.g., excessive avoidance in anxiety disorders or disproportionate approach in pathological

aggression and substance use disorders (Carver & Harmon-Jones, 2009; Wiers et al., 2014; World Health Organization, 1992). Since stress is implied in both onset and maintenance of mental disorders (e.g., Koob et al., 2014; Shin & Liberzon, 2010), some studies have investigated the impact of acute stress on approach-avoidance behaviors, utilizing different paradigms and resulting in equivocal effects (see Fricke & Vogel, 2020 for a recent overview). These equivocal effects could be due to a more nuanced effect of stress on approach-avoidance behavior as a recent study suggested (Vogel & Schwabe, 2019). There, healthy participants underwent a psychosocial stressor before performing the approach-avoidance conflict task (AACT; Bach et al., 2014). In the AACT, foraging for monetary rewards under threat is encouraged, creating an ambiguous situation with conflicting approach and avoidance motivations. While stress did not have strong general effects on risky foraging, it increased the importance of threat distance: Stressed participants displayed faster escape responses when threat was close (active avoidance) compared to further away (passive avoidance, i.e., inhibition of behavior when faced with distant threats). Additionally, stress further led to differences in approach-avoidance behavior based on the participants' individual trait anxiety and aggression, seemingly abolishing differences in trait anxiety, while amplifying approach behaviors in more physically aggressive individuals. Stress was therefore shown to override or exacerbate the effects of personality traits for trait anxiety and aggression, respectively, suggesting that differences in approach-avoidance behavior may be closely linked to both acute levels of stress and more stable personality traits. However, the mechanism of *how* stress affects approach-avoidance behavior is unclear.

Although stress comes with a multitude of physiological changes, often two major subsystems of the stress response are investigated with regard to cognitive effects, namely the hypothalamic-pituitary-adrenal (HPA) axis and the sympathetic nervous system (SNS; Ulrich-Lai & Herman, 2009). While the combined roles of cortisol as major end product of the HPA axis and noradrenaline (NA) as main neurotransmitter of the SNS in balancing approach and avoidance have not been investigated as of yet, their interaction has been clearly demonstrated as the mechanism underlying acute stress effects in other cognitive domains such as memory consolidation (Barsegyan et

al., 2010; Barsegyan et al., 2019; Quirarte et al., 1997; Roozendaal, Okuda, et al., 2006), instrumental learning (Schwabe et al., 2010, 2012) and fear conditioning (Roozendaal, Hui, et al., 2006). In the case of approach-avoidance behavior, few studies have investigated either of the systems, but no study investigated their interaction. Endogenous and pharmacologically administered cortisol has been investigated in a few task-based approach-avoidance studies, which were highly varied in their designs, participants and results and suggested interactions of cortisol effects with interindividual differences (Dapprich et al., 2021; Roelofs, Minelli, et al., 2009; van Peer et al., 2007). For NA, we found only one study, which indicated no effect of noradrenergic stimulation on approach-avoidance behavior (Deuter et al., 2021). Importantly, these studies did not include a manipulation of threat distance which has a critical impact on approach-avoidance behavior.

To investigate the effects of cortisol, NA, and their interaction on the balance of approach-avoidance conflict behavior, 96 healthy participants received a double-blinded pharmacological intervention to increase their cortisol concentration (20mg hydrocortisone), activity of NA (20mg yohimbine), both or neither. Afterwards, participants performed the AACT in which they foraged for tokens (approach motivation) under probabilistic threat of virtual predators (avoidance motivation). Importantly, this task included a manipulation of initial threat distance.

We hypothesized that, in line with research from other cognitive domains, the combination of both cortisol and NA would mimic previously shown stress effects on approach-avoidance behavior (Vogel & Schwabe, 2019). Therefore, the combined administration of cortisol and NA should amplify the importance of threat distance for avoidance behaviors. As the study by Vogel and Schwabe (2019) suggested more nuanced stress effects based on interindividual differences, we hypothesized our intervention to increase approach behavior in more trait aggressive individuals and abolish effects of trait anxiety differences. We further expected more approach behavior in trait aggressive and sensation-seeking individuals and more avoidance behavior in trait anxious participants, independent of drug condition. Finally, we expected men to perform better than women based on previous AACT studies (Bach

et al., 2020; Vogel & Schwabe, 2019). Due to striking gender differences, we exploratively investigated effects of basal testosterone and estradiol levels on task-based approach-avoidance behavior as they have not been extensively investigated (Fricke & Vogel, 2020).

3.3 EXPERIMENTAL PROCEDURES

3.3.1 Participants

Our recruitment strategy as well as detailed exclusion and inclusion criteria, also in respect to factors affecting the HPA axis or the noradrenergic nervous system, can be found in section 7.2.1. Ninety-six healthy individuals (48 self-identified men, 48 self-identified women, age: 18-35 years, mean: 24.69, SD: 4.47) completed the experiment. Two noncompliant participants were excluded, leading to a total sample size of 94 participants. The target sample size of 96 was supported by an a-priori power analysis, allowing the discovery of medium-sized effects at an alpha error probability of .05 and a power of 80% for repeated measures ANOVAs with between participant variables resulting in four groups (G*Power 3.1.9.7; Faul et al., 2007). Participants provided written informed consent and received monetary compensation (30 Euro; or 5 Euro and partial course credit) for participation. The study was approved by the local ethics committee (Ethik-Kommission der Ärztekammer Hamburg; PV 5310).

To determine how cortisol, NA, and their interaction affect the balance of approach- and avoidance-behavior, we employed a fully crossed double-blind between-subject design. Participants were pseudo-randomly assigned to four groups, while balancing for gender, and received 1) 20 mg hydrocortisone and placebo (n=23), 2) 20 mg yohimbine and placebo (n=23), 3) 20 mg hydrocortisone and 20 mg yohimbine (n=24), or 4) placebo (n=24) via three identical-looking pills containing 20 mg hydrocortisone, 10 mg yohimbine, or placebo.

3.3.2 Experimental Procedures

Participants were tested between 12:20 and 18:45 to control for the diurnal rhythm of cortisol. They were instructed to arrive well-rested, limit themselves to light physical exercise on the day of the experiment and avoid the use of alcohol and other psychoactive substances starting the day prior to the experiment. Participants were asked to have a light meal roughly two hours before the experiment and avoid food and drink intake (except water) in the 30 minutes leading up to the experiment.

After arrival, participants answered questionnaires assessing current mood (MDBF; Steyer et al., 1994, and three visual analogue scales (VAS; anxious, upset, stressed)), trait anxiety (STAI-T; Laux et al., 1981), chronic stress (TICS; Schulz et al., 2004; not reported here), trait aggression (DAF; Werner & von Collani, 2014) and sensation seeking (SSS-V; Beauducel et al., 2003). This was followed by a baseline measurement (T1) of vital signs (heart rate, diastolic and systolic blood pressure) and saliva sampling (cortisol concentration, alpha amylase activity as marker of noradrenergic activity, testosterone and estradiol concentrations). Detailed descriptions of vital sign and saliva sampling methods can be found in section 7.2.2.

After baseline measurements, participants performed a risk-taking task, the Balloon Analogue Risk Task (BART; Lejuez et al., 2002; not reported here), and received the assigned pharmacological intervention orally. Afterwards, saliva and vital signs were taken every 15 minutes for a total of three times (T2-4), during which participants were allowed to read. Another assessment of current mood and a slightly altered BART followed. This protocol was in line with previous studies for both, the dosages and the 45-minute waiting period before the onset of the first task (Schwabe et al., 2010, 2012; Schwabe & Wolf, 2013).

Approximately 65 minutes after medication intake, participants began the AACT (average duration: 42 minutes), followed by final saliva sample, vital signs and mood assessments (T5). Finally, participants indicated which pharmacological intervention

they believed to have received and were debriefed about study procedures. The experiment lasted about 2 hours and 40 minutes.

3.3.3 Approach-Avoidance conflict task and outcome parameters

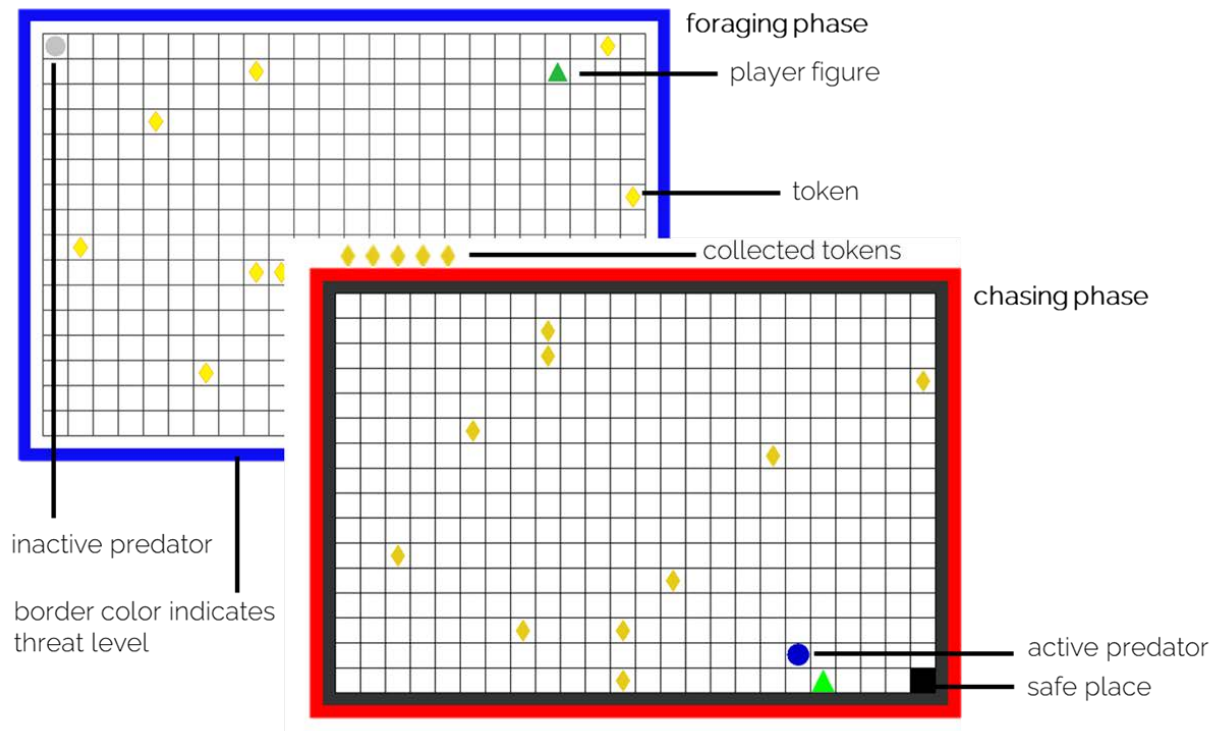


Figure 3.1. Approach-avoidance conflict task, adapted from Bach, et al. (2014).

Participants were tasked to collect as many of the tokens placed at random as they could, while avoiding capture by a predator. Trials (160 in 4 blocks) varied in time between 6 and 15 seconds after which the predator woke up in 20% (low threat; 50% of trials) or 60% of trials (high threat) and chased the participant for 3.5 seconds, if not caught. The predator is at minimum 2.5 times faster than the player. At trial start, the player figure is placed next to the predator or in the safe place (where the predator could not catch them) in 50% of trials each. In the foraging phase, the border color indicates which threat level is present in the current trial, while on predator wake-up, the color changes to red. For more details, see section 7.2.3. The figure has been re-used with permission from Fricke and Vogel (2020)

To assess approach-avoidance behavior, we employed an adapted version of the AACT (programmed in Python 3.2.5 using Pygame 1.9.2 and made available under osf.io/d69pr; see Vogel & Schwabe, 2019), originally developed by Bach et al. (2014; see Figure 3.1). In each of the 160 trials (evenly divided into four blocks), participants foraged for tokens under threat of predation (high vs. low threat condition based on the probability of predator waking up) and started either close to the predator or far away in a predator-safe space to manipulate threat distance. After the AACT, participants were asked to estimate the wake-up probabilities for both predators. For a detailed description of the AACT, see section 7.2.3.

Due to the nature of the task, e.g., the ability to move freely and the intertwined goals of approach and avoidance, many variables can be considered as outcome variables (Bach et al., 2020). Here, we focused on three previously established summary measures (Bach et al., 2018; Korn et al., 2017; Vogel & Schwabe, 2019): Foraging latency (initial time to first button press) can be informative for the initial decision process within each trial, the sum of retained tokens (sum of tokens collected in all trials unless the participants were caught) as overall performance measure, and failed avoidance of threat (the rate at which participants were caught) as an additional performance measure, especially regarding risk proneness during the AACT.

3.3.4 Statistical analysis

To assess potential group differences in control variables (age, BMI) and personality traits, ANOVAs with the between-subject factor group were employed. Potential biases in sample composition over time due to the onset and development of the Covid 19-pandemic were explored in section 7.2.4. Successful blinding was assessed by testing participants' ability to correctly identify whether they had received an active treatment and if so, which treatment in particular, with Chi-Square and Fischer's exact test. To test whether the administration of hydrocortisone and yohimbine had the

expected effects on physiological measures (heart rate, blood pressure, cortisol concentration, alpha amylase activity) and affected subjective mood (MDBF, VAS), we conducted mixed-design ANOVAs with the within-subject factor time and the between-subject factors hydrocortisone (vs. placebo) and yohimbine (vs. placebo). We report main and interaction effects involving either or both drugs. Due to strong variability of data for both cortisol concentration and alpha amylase activity, a 10% winsorizing of the data was employed as outlier correction. To correct for multiple comparisons, we applied Bonferroni-Holm corrections based on outcome variables for five physiological and six subjective measures, respectively.

Regarding the AACT, we first assessed whether drug administration affected explicit task knowledge (i.e., estimated wake-up probabilities of predators) via a mixed-design ANOVA with the within-subject factor threat level (high vs. low) and the between-subject factors hydrocortisone, yohimbine and gender. Then, three previously established summary measures over all trials, i.e., foraging latency, sum of retained tokens and failed avoidance of threat, were investigated. We conducted mixed-design ANOVAs with the within-subject factors initial threat distance (long vs. short), threat level and block (1 to 4) and the between-subject factors hydrocortisone, yohimbine and gender (Bonferroni-Holm corrected for three outcome variables). For analyses on failed avoidance of threat, participants were excluded if their data contained empty cells (remaining $n=59$; placebo: $n=16$, hydrocortisone: $n=14$, yohimbine: $n=15$, hydrocortisone and yohimbine: $n=14$) due to a programming error (task blocks missing combinations of threat level x threat distance x threat wake-up for individual participants). An exploratory analysis omitting block as within-subject factor (thus including all participants) was conducted to assure that potential drug effects would not be lost due to fewer participants in the initial analysis.

To investigate the influence of personality traits (trait anxiety by STAI-T total score (Laux et al., 1981), sensation seeking by SSSV total score (Beauducel et al., 2003) and aspects of trait aggression by four subscales of the DAF, namely physical aggression, verbal aggression, anger and mistrust (Werner & von Collani, 2014)) on AACT performance, we focused on the sum of tokens retained. This decision allows

for comparability with prior work (Vogel & Schwabe, 2019) which assessed the relationship of STAI-T and DAF subscales with AACT performance under stressful and non-stressful conditions. In addition, a recent study revealed token retention as one of the most reliable task parameters, supporting our decision for this variable (Bach et al., 2020). First, we correlated each personality trait with the sum of tokens retained (Bonferroni-Holm corrected for six comparisons). To understand the influences of the pharmacological interventions, we conducted hierarchical linear regressions with introduction of the following mean-centered variables in blockwise fashion: 1) The control variables gender, age and average movement speed during the AACT, followed by 2) the interventions (hydrocortisone, yohimbine) as well as their interaction, 3) the personality trait measures detailed above, and 4) the interactions of personality trait measures with the interventions.

To explore whether basal endogenous testosterone or estradiol affected approach-avoidance behavior, we conducted exploratory correlations between sex hormone concentrations and our summary outcome measures, and hierarchical regressions for these outcome measures with blockwise introduction of 1) the control variable age and 2) either testosterone or estradiol once for all participants and additionally separated by gender. ANOVAs were used to assess whether the full model explained variance significantly better than the respective control model. Participants were excluded for the respective analyses, if their testosterone/estradiol levels differed three or more standard deviations from the mean.

To enhance comparability with previous findings (e.g., Bach et al., 2014; Bach et al., 2018; Bach et al., 2020; Korn et al., 2017), we also reanalyzed our primary hypotheses with ANOVAs for six previously described outcome variables over time-in-trial (e.g., time spent in safe space; token collection rate) as well as for outcome parameters identified as test-retest reliable over 11-32 months. For the outcome parameters chosen for their test-retest reliability, we included personality trait analyses similar to the one above regarding the sum of tokens (see section 7.2.5). As suggested by a reviewer, we also investigated in how far threat overestimation related to different AACT outcome measures (see section 7.2.6).

For significant findings in the ANOVAs detailed above, the appropriate follow-up tests, including ANOVAs and t-tests, were conducted. When sphericity was violated, we employed Greenhouse-Geisser correction. Post-hoc Bonferroni-Holm corrections for multiple testing were based on the number of separate post-hoc ANOVAs or t-tests per analysis. All reported p-values are two-tailed. All analyses were conducted in R (Version 4.2.2) and can be found at osf.io/d69pr.

3.4 RESULTS

The four experimental groups did not differ in age ($p=.517$), BMI ($p=.423$), trait anxiety ($p=.584$), trait aggression (all scales $p\geq.411$), or sensation seeking ($p=.221$, Table 7.2.3). Participants were successfully blinded to their treatment as they could not differentiate active medication from placebo intake ($X^2_{3,N=94}=2.312$, $p=.510$), or guess the exact combination of medication they had been given ($p=.227$).

3.4.1 Hydrocortisone and yohimbine administrations affect biological stress markers, but not self-reported mood

As expected, hydrocortisone and yohimbine intake led to pronounced increases in cortisol concentration and activation of the noradrenergic system, respectively. Salivary cortisol concentration changed over time dependent on hydrocortisone administration ($F_{1.78,149.67}=18.832$, $p<.001$, $\eta^2G=.126$; see Figure 3.2a). Post-hoc ANOVAs showed significant increases after taking hydrocortisone compared to not taking hydrocortisone (T3: 36.32 vs. 2.69 nmol/l, $F_{1,84}=11.231$, $p=.003$, $\eta^2G=.118$; T4: 53.73 vs. 2.69 nmol/l, $F_{1,84}=36.390$, $p<.001$, $\eta^2G=.302$; T5: 44.68 vs. 2.62 nmol/l, $F_{1,84}=158.749$, $p<.001$, $\eta^2G=.654$). After winsorization, a time dependent hydrocortisone-yohimbine interaction ($F_{1.86,156.04}=5.181$, $p=.040$, $\eta^2G=.039$) suggested that yohimbine intake further increased salivary cortisol concentration in hydrocortisone-taking participants. However, post-hoc ANOVAs did not indicate

additional significant differences at any time point. Salivary alpha amylase activity did not differ between treatment groups (see Figure 3.2b). After winsorization, we found the expected interaction of yohimbine and time ($F_{2,79,229,19}=3.238$, $p=.026$, $\eta^2G=.012$), resulting from higher alpha amylase activity in groups with yohimbine intake at T3 (raw values: 155.60 vs. 120.04 U/ml; $F_{1,82}=7.146$, $p=.036$, $\eta^2G=.080$) and T5 (204.61 vs. 128.99 U/ml; $F_{1,82}=10.700$, $p=.010$, $\eta^2G=.115$) compared to the other groups.

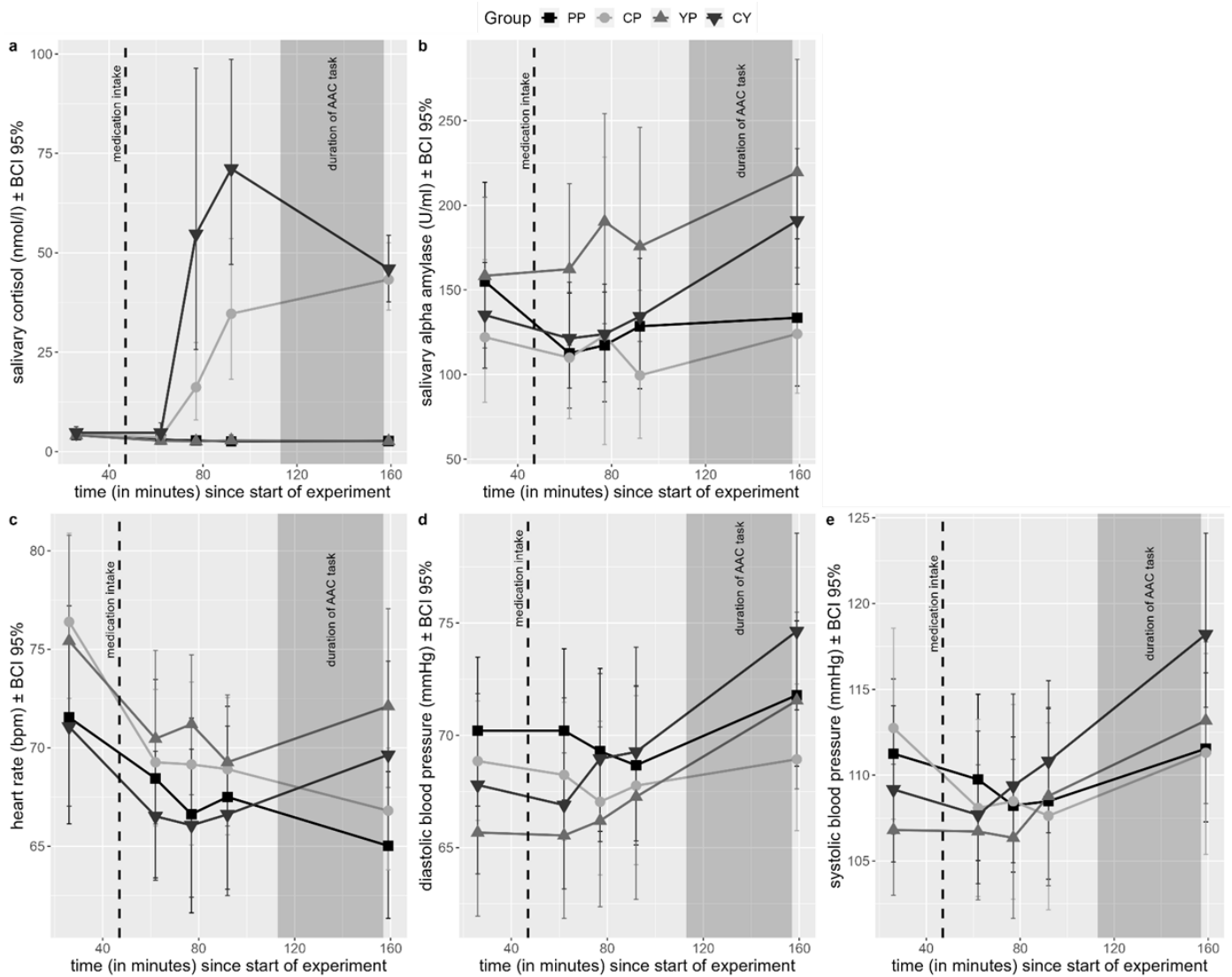


Figure 3.2. Measures of (a) salivary cortisol concentration, (b) salivary alpha amylase activity, (c) heart rate, (d) diastolic blood pressure, and (e) systolic blood pressure over time. Dotted line indicates time of medication intake. Grey overlay indicates duration of the approach-avoidance conflict task. Error bars represent bootstrapped 95% confidence intervals (BCI). Groups: placebo (PP), hydrocortisone (CP), yohimbine (YP), hydrocortisone and yohimbine (CY)

Vital signs changed over time dependent on the intake of yohimbine (heart rate: $F_{3,03,272.68}=7.889$, $p<.001$, $\eta^2G=.010$; diastolic blood pressure: $F_{3,35,301.47}=6.583$, $p<.001$, $\eta^2G=.013$); systolic: $F_{3,18,286.11}=9.387$, $p<.001$, $\eta^2G=.014$; see Figure 3.2c-e), but not hydrocortisone. However, post-hoc ANOVAs indicated no specific time point for those significant differences. Subjective mood was not affected by hydrocortisone or yohimbine intake, supporting successful blinding of our pharmacological intervention (see Table 7.2.4).

3.4.2 Participants overestimate low threat condition in the approach-avoidance conflict task

Participants differentiated between high- and low-threat predators (mean estimated wake-up probability 38.2% vs. 61.6%, $F_{1,86}=34.882$, $p<.001$, $\eta^2G=.218$), but overestimated the low-threat predator by around 20%. Threat level ratings were further affected by hydrocortisone administration ($F_{1,86}=4.734$, $p=.032$, $\eta^2G=.036$), but post-hoc tests revealed no significant effects. In general, women overestimated threat more than men (mean overestimation of wake-up probability 12.0% vs. 7.7%, $F_{1,86}=5.454$, $p=.022$, $\eta^2G=.019$, see Figure 7.2.3). For additional analyses regarding influences of threat overestimation on summary outcome variables see section 7.2.6). No other effects of gender, drug treatment or their interaction reached significance.

3.4.3 No hypothesized effects of hydrocortisone and yohimbine on behavior

In general, participants improved their performance over time. They were caught less frequently after the first block ($F_{3,153}=8.973$, $p<.001$, $\eta^2G=.025$, block 1 53.1% vs. block 2 40.4%, $t_{235}=5.03$, $p<.001$, Cohen's $d=.328$) and retained more tokens over blocks ($F_{2,61,224.82}=115.242$, $p<.001$, $\eta^2G=.071$), which interacted with threat level ($F_{3,258}=4.549$, $p=.012$, $\eta^2G=.003$, see Figure 3.3a). Post hoc tests showed that

participants retained more tokens in the second compared to the first block for both threat levels (low threat: $t_{187}=-4.88$, $p<.001$, Cohen's $d=-.356$; high threat: $t_{187}=-7.14$, $p<.001$, Cohen's $d=-.521$). In addition, participants retained more tokens when threat level was low ($F_{1,86}=246.457$, $p<.001$, $\eta^2G=.102$), but were also caught more often if the predator awoke (mean catch rate 47.4% vs. 41.7%, $F_{1,51}=7.737$, $p=.016$, $\eta^2G=.010$). When initial threat distance was long (compared to short), participants retained less tokens (sum of retained tokens 59 vs. 64, $F_{1,86}=75.760$, $p<.001$, $\eta^2G=.024$) suggestive of behavioral inhibition.

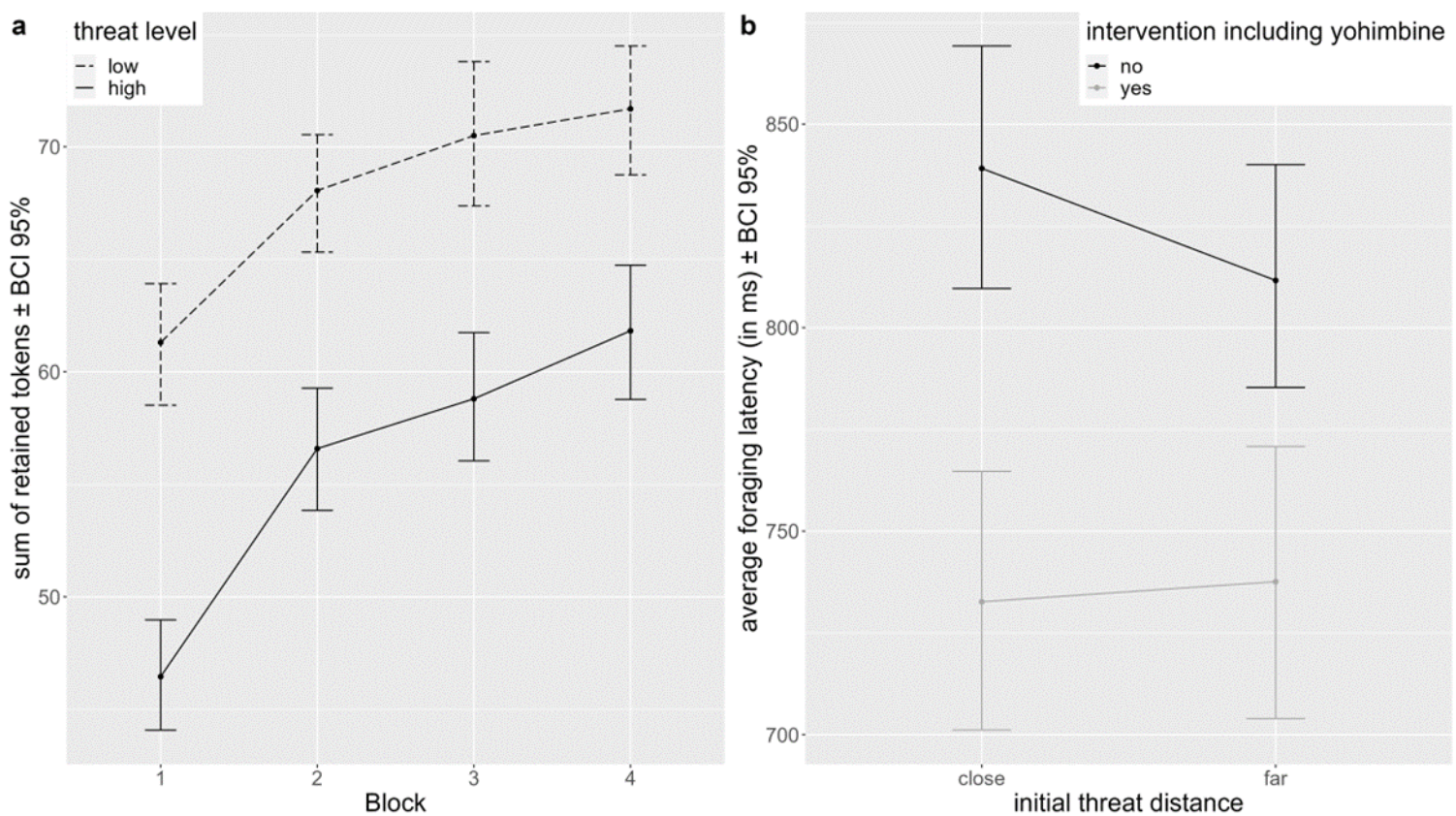


Figure 3.3. (a) Differences in initial latency to avoid/approach based on the initial threat distance and yohimbine administration (independent of whether hydrocortisone was administered). (b) Averaged retained tokens over blocks for the low and high threat level conditions. Error bars represent bootstrapped 95% confidence intervals (BCI)

Against our hypothesis, we did not find any hydrocortisone-yohimbine interaction or hydrocortisone main effect on overall task performance (see Figure 3.4a-f). For yohimbine, an interaction with threat distance was found for foraging latency

($F_{1,86}=6.494$, $p=.039$, $\eta^2G=.001$), indicating that solely participants without yohimbine administration approached foraging faster when initial threat distance was long as compared to short (mean latency 812 vs. 839 ms, $F_{1,43}=13.902$, $p=.001$, $\eta^2G=.003$, see Figure 3.3b). Analyses of pharmacological effects on further AACT outcome variables (section 7.2.5) likewise did not reveal the hypothesized effects of hydrocortisone, yohimbine or their interaction on approach-avoidance conflict behavior. Our hypotheses regarding the pharmacological intervention were thus not confirmed.

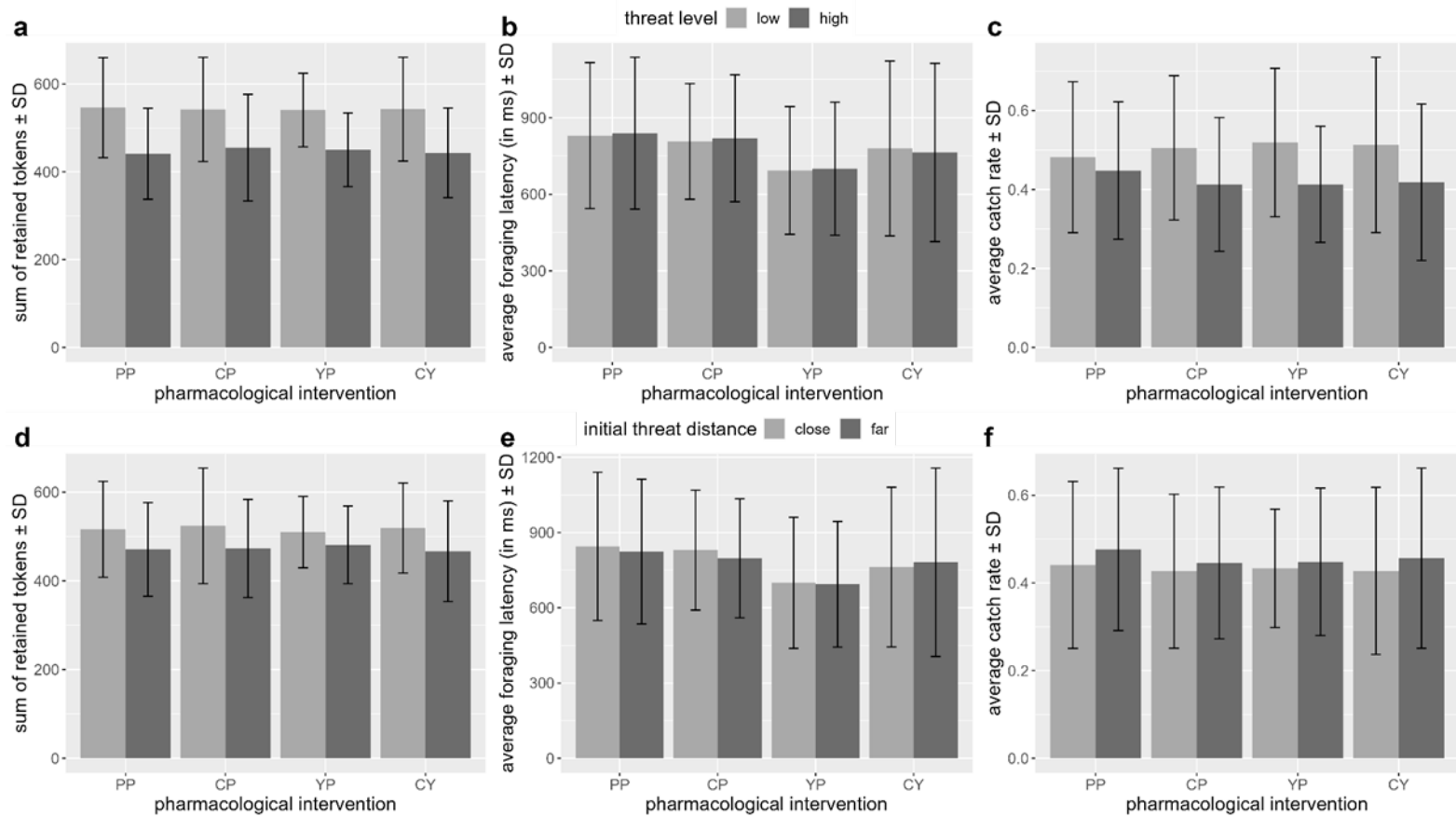


Figure 3.4. Averaged main outcome measures (left: sum of retained tokens, middle: average foraging latency, and right: average catch rate) per experimental group displayed either per threat level (top panel) or initial threat distance (bottom panel). Error bars represent one standard deviation. Groups: placebo (PP), hydrocortisone (CP), yohimbine (YP), hydrocortisone and yohimbine (CY)

3.4.4 Correlations and hierarchical regressions show no significant relationships between AACT performance and personality traits, pharmacological interventions or their interactions

Contrary to our expectations, we found no significant associations between the sum of tokens retained and any personality trait investigated here (see Figure 3.5a-f). Nonetheless, the final model of the conducted hierarchical linear regression was a significant predictor of retained tokens ($\text{adj. } R^2 = 0.691$, $F(24,69) = 9.678$, $p < .001$) and included the significant predictors speed when on grid ($\text{beta} = 350.811$, $p < .001$), physical aggression ($\text{beta} = 19.393$, $p = .022$) and the interaction of yohimbine with anger ($\text{beta} = 18.806$, $p = .032$). However, the model held no advantage over the control model, which included gender, age and the average speed on the grid, suggesting that the contributions of the factors physical aggression, and yohimbine in interaction with anger were not substantial ($F(21,69) = 0.99$, $p = .477$).

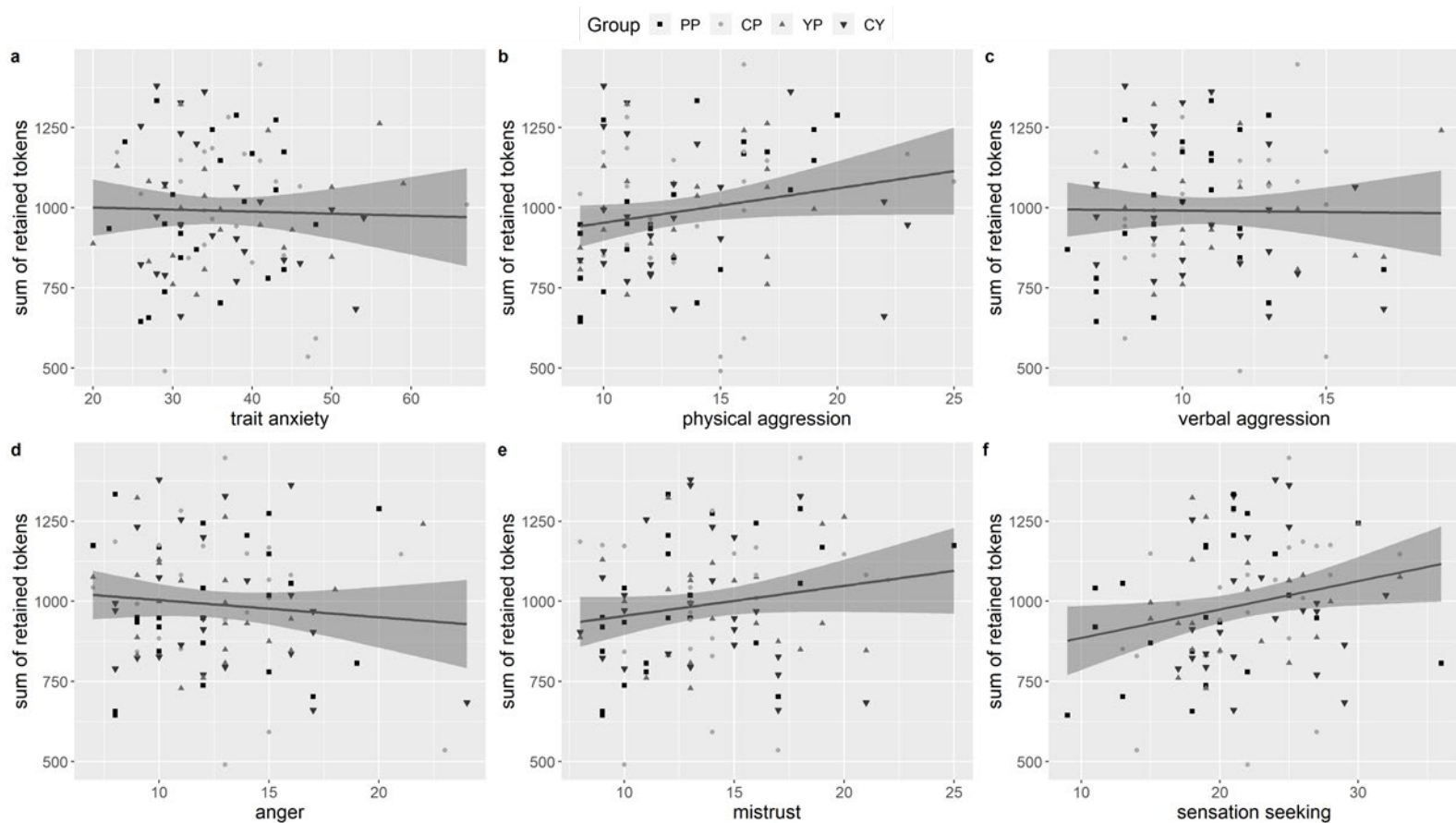


Figure 3.5. Correlations of (a) trait anxiety ($r(92) = -.028$, $p = 1$), trait aggression subscales (b) physical aggression ($r(92) = .194$, $p = .304$), (c) verbal aggression ($r(92) = -.012$, $p = 1$), (d) anger ($r(92) = -.096$, $p = 1$), (e) mistrust ($r(92) = .168$, $p = .420$), and (f) sensation seeking ($r(92) = .230$, $p = .153$) with the amount of retained tokens over all experimental trials. Line indicates linear regression over all data points with 95% confidence interval. Data points are labeled by intervention group: placebo (PP), hydrocortisone (CP), yohimbine (YP), hydrocortisone and yohimbine (CY). P-values are Bonferroni-Holm corrected for six comparisons

3.4.5 Gender and explorative sex hormone effects

As expected, men showed overall better task performance. They were caught less often (mean catch rate 38.9% vs. 49.7%, $F_{1,51}=5.980$, $p=.018$, $\eta^2G=.030$), faster to initiate foraging (662 vs. 894 ms, $F_{1,86}=18.310$, $p<.001$, $\eta^2G=.153$) and retained more tokens than women (69 vs. 55 per block, $F_{1,86}=39.878$, $p<.001$, $\eta^2G=.135$). Testosterone

levels also correlated significantly with foraging latency and token-retention (see Figures 3.6a-f) and predicted behavior better than respective control models including only age (latency and token-retention: $p < .001$). However, this was not true for the separate-gender-models. No significant effects of estradiol were found.

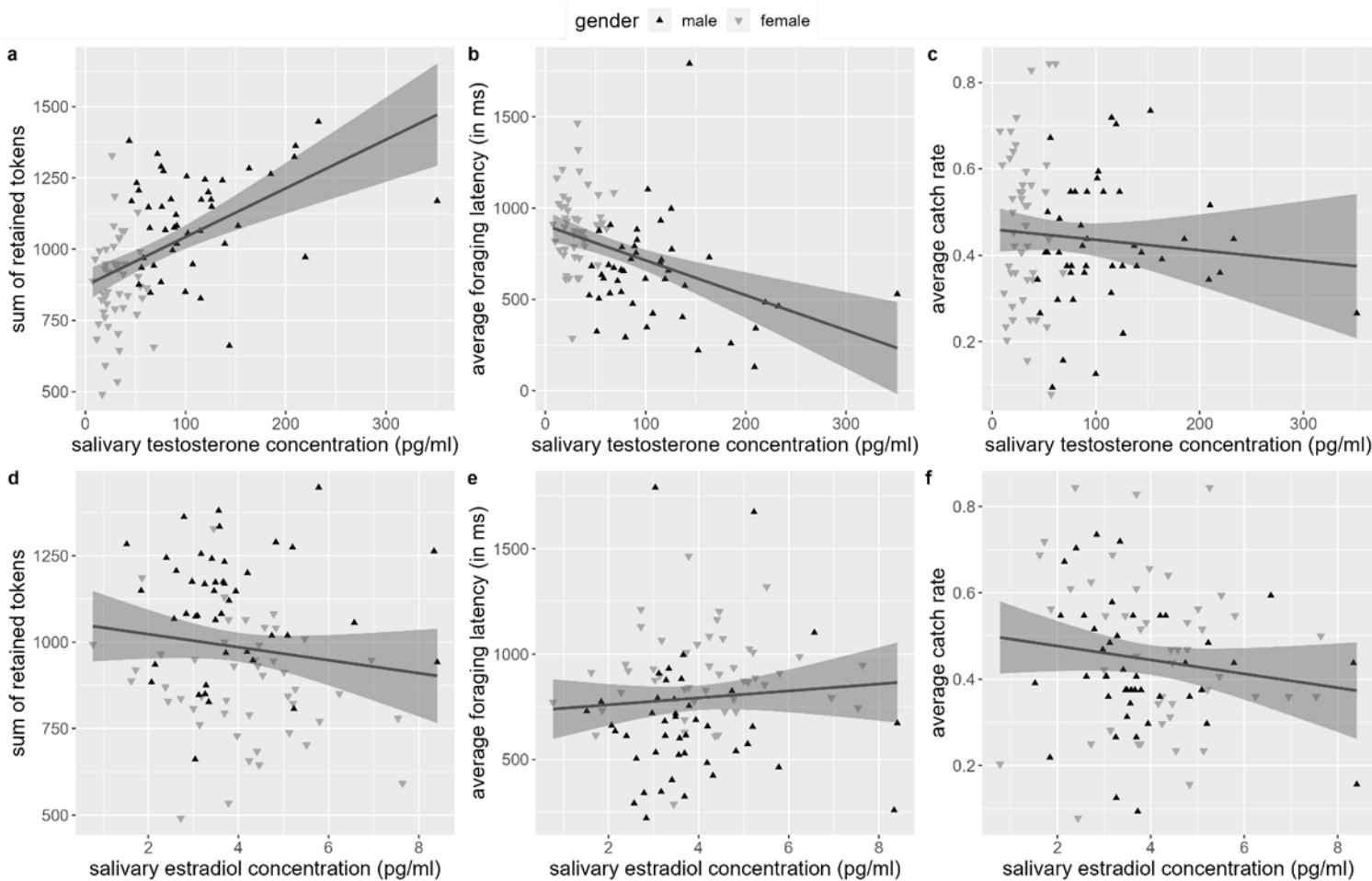


Figure 3. 6 Correlations of the salivary testosterone concentration (pg/ml) with (a) the sum of retained tokens over all trials ($r(90) = .497$, $p < .001$), (b) the average foraging latency ($r(90) = -.414$, $p < .001$), and (c) the average catch rate ($r(90) = -.087$, $p = .410$) as well as the salivary estradiol concentration (pg/ml) with (d) retained tokens ($r(89) = -.134$, $p = .204$), (e) foraging latency ($r(89) = .085$, $p = .422$), and (f) catch rate ($r(89) = -.141$, $p = .184$). Line indicates linear regression over all data points with 95% confidence interval

3.5 DISCUSSION

Stress contributes to the onset and maintenance of several mental disorders in which imbalances in approach-avoidance behaviors play a central role. Investigating how two stress subsystems, e.g., the HPA axis and the SNS, influence approach-avoidance behavior in healthy participants could therefore have important implications for understanding the etiology of stress-related mental disorders. To understand these complex interactions, we investigated the role of cortisol, NA, gender, sex hormones and personality traits on approach-avoidance behaviors in a foraging-under-threat task, namely the AACT.

3.5.1 No expected effects of hydrocortisone and yohimbine on approach-avoidance conflict behavior

Despite our successful pharmacological intervention, demonstrated by increased cortisol concentration and alpha amylase activity during task performance, hydrocortisone and yohimbine had very limited effects on approach-avoidance behavior in the AACT. Since the AACT and its manipulations (e.g., threat level and distance) had the expected effects on behavior as demonstrated, for example, by participants' improved token retention over blocks and ability to distinguish the two predators, it appears that hydrocortisone, yohimbine, and their interaction are not the underlying mechanisms of previously shown stress effects on approach-avoidance behavior (Vogel & Schwabe, 2019). While the administration of hydrocortisone and yohimbine cannot imitate something as complex as the stress response with its intricate dynamics of many biological mediators, the associated cognitive appraisal process and subjective impact (Joels & Baram, 2009), we expected stress effects to be at least partially replicated based on previous findings in other cognitive domains.

As the stress network and the receptors for cortisol and NA are present widely across the brain (Joels & Baram, 2009; Ulrich-Lai & Herman, 2009), an approximation of stress effects by a pharmacological intervention targeting HPA axis and SNS seemed plausible. However, studies with sample sizes similar to ours utilizing combined

hydrocortisone and yohimbine administration in investigation of (other aspects of) human cognition, have shown influences of hydrocortisone and yohimbine (e.g.; Margittai et al., 2018; Schwabe et al., 2010, 2012; Woodcock et al., 2019; Zerbtes et al., 2019), only hydrocortisone (e.g.; Klueen, Agorastos, et al., 2017; Klueen, Nixon, et al., 2017; Metz et al., 2021; Metz et al., 2020), or only yohimbine (e.g.; Kausche et al., 2021; Klueen, Nixon, et al., 2017). The interaction of both is therefore not always at the root of stress-like effects on human cognition in intervention studies. It is further possible that stress-related effects on approach-avoidance behavior in particular are mediated (in part) by different effectors or pathways of the stress response than the ones expected based on the promising memory effects detailed in the introduction, for example, CRH or dopamine (Joels & Baram, 2009). Inverted-U-shape effects of dosage may also play a role (Arnsten, 2009) and could be tested in the future by systematically varying the applied dosage. Taken together, it is conceivable that the pharmacological interventions were not effective or specific enough to result in stress-like effects on behavior in approach-avoidance conflicts.

The only significant interaction including one of the pharmacological interventions on our main task measures showed that participants who had not taken yohimbine approached foraging faster when further away from threat than when starting close to the predator. However, faster foraging when away from threat seems counterintuitive as escape from immediate threat (active avoidance; flight) should be faster than approaching the foraging field from the safe place due to response inhibition (passive avoidance; freezing; McNaughton & Corr, 2004; Qi et al., 2018). One explanation for the missing, but hypothesized threat distance effect in the hydrocortisone/yohimbine group could be that the subjective experience of feeling stressed prior to the AACT is necessary to emphasize the importance of threat at the beginning of each trial. Since our pharmacological intervention did not subjectively affect participants' mood, the importance of immediate threat may have been underestimated. However, this reasoning would be in contrast to previous studies using comparable pharmacological interventions which likewise reported no mood changes overall while still reporting cognitive effects of the interventions (e.g., Klueen, Agorastos, et al., 2017; Margittai et al., 2016; Putman & Roelofs, 2011; Schwabe et al.,

2012; please note that we corrected for multiple comparisons, which may have hidden otherwise observable effects). Still, the possibility remains that our results are false-negative, both in the sense that key subjective correlates of harm-avoidance cognition important for anxiety here have not been tapped by our psychometric measures, and in the sense that these measures may have been too noisy. If replicated, effect specificity to yohimbine as noradrenergic drug might be supported by the fact that the systems responsible for avoidance decisions and conflict resolution in approach-avoidance conflicts are innervated by noradrenergic cells of the raphe and locus coeruleus (Gray & McNaughton, 2003), potentially opening an avenue for pharmacological manipulation of avoidance behavior.

3.5.2 No associations between approach-avoidance conflict behavior and personality traits

In contrast to our expectations, we found no associations between the investigated personality traits, i.e., aggression, anxiety, or sensation seeking, and approach-avoidance behavior in the AACT. This is surprising as, e.g., anxiety has been shown to play a central role in approach-avoidance conflicts (Gray & McNaughton, 2003). Similarly, there were no differential influences of these personality traits on behavior depending on pharmacological treatment (see also section 7.2.5). This is striking, since underlying differences in observed approach-avoidance behaviors are part of the diagnostic criteria of several anxiety disorders (World Health Organization, 1992), strongly indicating that anxious traits should be reflected in task-based approach-avoidance behaviors. Establishing an association between personality traits and approach-avoidance behavior assessed with task-based measures, however, has proven to be difficult (Fricke & Vogel, 2020). The AACT has been pharmacologically validated using anxiolytics, e.g., reduced anxiety behavior following lorazepam, valproate and pregabalin administration (Bach et al., 2018; Korn et al., 2017), suggesting that the task might be sensitive to different levels of anxiety. It has been argued before, that the questionnaire employed here (STAI-T) is not specific for anxiety as it also correlates

strongly with depressive symptoms (Knowles & Olatunji, 2020). However, Bach et al. (2020) also found no correlations of self-reported anxiety (using a different questionnaire) and AACT outcome measures, which was interpreted as the AACT eliciting caution, but not distinguishing stable anxiety levels. Self-reported daringness on the other hand was predictive of approach-avoidance behavior, while sensation seeking in our study was not, which could be interpreted as participants acting daringly, but not recklessly in the AACT. One other reason for our null findings may be that the AACT has been initially constructed to differentiate between groups, which may make it more difficult to draw correlational results by design (Hedge et al., 2018). It may therefore have been more difficult to extract associations of trait anxiety, aggression and sensation seeking with our behavioral outcome measures.

3.5.3 Better performance of male participants

Consistent throughout our outcome parameters is the AACT's sensitivity to gender. Male participants collected more tokens, better avoided getting caught and started foraging more rapidly. This is in line with Bach et al. (2020) who suggested that preference for economic risk in men (e.g., Lewis et al., 2022), differences in video game experiences and in perception and experience of threat might explain better performance in men. The larger overestimation of threat in woman may be due to general gender differences in threat estimation (Harris & Miller, 2000) or specific to the task, could be modifiable by learning or reflecting life experience, all of which could be investigated in future designs with better, and more frequent, threat estimation checks. Differences in approach-avoidance behaviors based on gender highlight the need to take participant gender into account as large parts of the variance may be explained by those gender differences. However, approach-avoidance literature to this day often omits gender as potential moderating variable. Nonetheless, our results are not fully representative as women participated based on (non-)use of contraceptives and luteal menstrual cycle phase which limits generalizability. Regarding endogenous testosterone and estradiol, correlative and regression analyses indicate influences of testosterone across gender leading to increased and faster approach behavior. As

effects were not present in gender-separated analyses, the effects were likely driven by the general gender performance difference (however, splitting the sample by gender may have resulted in underpowered samples and a large correlation between testosterone levels and gender renders interpretation difficult).

3.5.4 Limitations and future considerations

The AACT could be an important asset to task-based approach-avoidance research due to the ambiguous conflict it creates compared with other approach-avoidance tasks with clearly instructed correct responses (e.g., Chen & Bargh, 1999; De Houwer et al., 2001). The caveat of this ambiguity is the impossibility to determine whether approach or avoidance is the driving force of behavior. A future distinction of approach and avoidance may be helpful since the underlying biological systems of approach, avoidance and conflict sensitivity are theorized to be distinct, but interacting (Gray & McNaughton, 2003). Future research on behavior in approach-avoidance conflicts should therefore consider how the systems can be measured (and experimentally manipulated) separately, while still keeping the decision space within the task broader than classical approach-avoidance tasks.

A major advantage of the AACT is that threat level and initial threat distance can be easily manipulated. However, we were unable to confirm our assumption that a short (vs. long) initial threat distance would lead to faster initial responding. Perhaps perceived threat distance was amplified by the temporal distance to threat as there was at least a 6-second window before predator wake-up and therefore enough time to escape. Moreover, the experience of threat level can also be based on the speed with which a predator becomes active (Fung et al., 2019). The differential effects of threat distance under stress may thus be partially attributed to changes in temporal processing. While stress is usually associated with the feeling of “time slowing down” (van Hedger et al., 2017), anxiety towards unpredictable events such as threat wake-up was also reported to accelerate time perception (Sarigiannidis et al., 2020), which could lead to a greater feeling of imminent threat under stress. It should thus be considered

to implement shorter latencies of predator wake-up in the future to make the unpredictable, imminent nature of the threat more present. On a final note, since another risk-taking task (BART) had been performed twice before the AACT, participants may have habituated to risk-taking in general and therefore been less sensitive to the AACT manipulations. As the tasks are very different in nature, this might not be likely, but nonetheless task-order-randomization in future studies would be advisable.

In conclusion, our hypotheses that the combined effects of cortisol and NA would resemble previously reported stress effects on approach-avoidance behavior did not hold true. We believe the most natural explanation would be that cortisol and NA are either not the (sole) relevant mediators for changes in approach-avoidance behaviors under stress, requiring further aspects of the stress response to be active, or that dosage of the interventions needed to be more fine-tuned. Gender, however, affects almost all outcome parameters investigated here. This stresses the importance of properly controlling for or specifically investigating gender in approach-avoidance research in the future.

4

COMPARISON OF TWO REACTION-TIME-BASED AND ONE FORAGING-BASED BEHAVIORAL APPROACH-AVOIDANCE TASKS IN RELATION TO INTERINDIVIDUAL DIFFERENCES AND THEIR RELIABILITY

4.1 ABSTRACT

Approaching rewards and avoiding punishments is a fundamental aspect of behavior, yet individuals differ in the extent of these behavioral tendencies. One popular method to assess differences in approach-avoidance tendencies and even modify them, is using behavioral tasks in which spontaneous responses to differently valenced stimuli are assessed (e.g., the visual joystick and the manikin task). Understanding whether these reaction-time-based tasks map onto the same underlying constructs, how they predict interindividual differences in theoretically related constructs and how reliable they are, seems vital to make informed judgements about current findings and future studies. In this preregistered study, 168 participants (81 self-identified men, 87 women) completed emotional face versions of these tasks as well as an alternative, foraging-based paradigm, the approach-avoidance-conflict task, and answered self-report

questionnaires regarding anxiety, aggression, depressive symptoms, behavioral inhibition and activation. Importantly, approach-avoidance outcome measures of the two reaction-time-based tasks were unrelated with each other, showed little relation to self-reported interindividual differences and had subpar internal consistencies. In contrast, the approach-avoidance-conflict task was related to behavioral inhibition and aggression, and had good internal consistencies. Our study highlights the need for more research into optimizing behavioral approach-avoidance measures when using task-based approach-avoidance measures to assess interindividual differences.

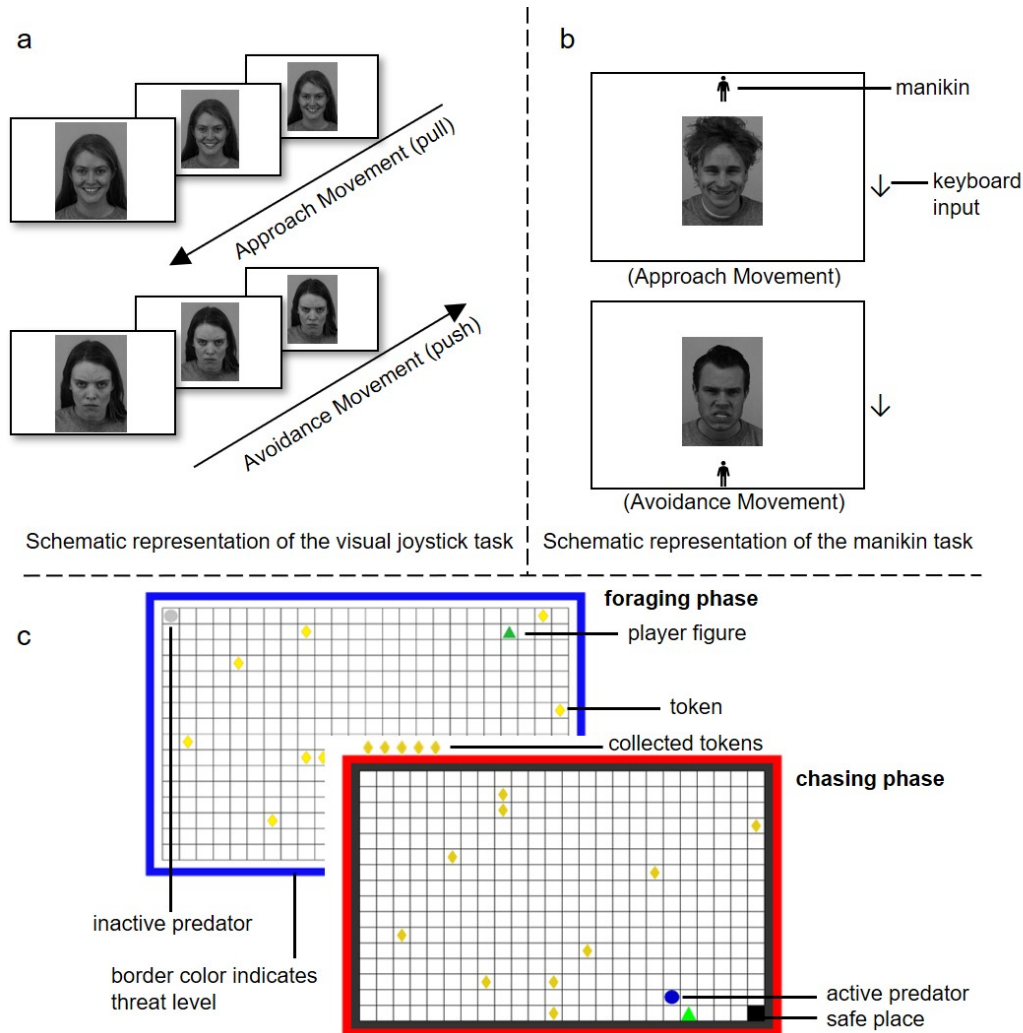
4.2 INTRODUCTION

Approach and avoidance of external stimuli are fundamental principles that shape an organism's interaction with its environment (Gray, 1975). At their core, these principles reflect the adaptive nature of behavior, as organisms strive to pursue rewards and positive consequences while simultaneously avoiding punishments and negative consequences. Gray and McNaughton (2003) proposed that three independent, but interacting, motivational systems are responsible for approach (behavioral activation system; BAS), avoidance (fight-flight-freeze system; FFFS), and conflict resolution within and between the former two systems (behavioral inhibition system; BIS). In line with this theory, interindividual variability in approach-avoidance behaviors could then be explained by differences in any and all of these systems. Investigating those individual differences in approach-avoidance is important, as understanding approach-avoidance mechanisms better can, for example, provide insights into topics such as motivation, goal pursuit, risk-taking, or emotion regulation. Furthermore, many mental disorders are characterized by dysregulated approach-avoidance patterns. For example, individuals with anxiety disorders often exhibit excessive avoidance tendencies, where they actively avoid situations or stimuli they perceive as threatening or anxiety-provoking (Barlow et al., 2004; World Health Organization, 1992). On the other hand, individuals with substance use disorders or pathological aggression may demonstrate excessive approach tendencies, while disregarding potential negative consequences (Carver & Harmon-Jones, 2009; Wiers et al., 2014). Studying approach-avoidance

tendencies could therefore aid in understanding the underlying mechanisms contributing to the development and maintenance of mental disorders.

To investigate approach-avoidance tendencies in humans, there are several options including, for example, clinical assessment or interviews, natural or structured observations. Furthermore, self-report measures like questionnaires can be used to measure constructs related to approach and avoidance, for example, the behavioral inhibition (CW-BIS) and activation (CW-BAS) scales by Carver and White (1994), which aim to assess the sensitivities of Gray's originally postulated general motivational systems (1975). Individuals with high CW-BIS-scores are believed to be highly sensitive to punishment and respond to potentially punishing stimuli with behavioral inhibition and increased anxiety, while participants with high CW-BAS-scores are highly sensitive to reward and actively approach potentially rewarding stimuli. To complement and extend these operationalizations of approach-avoidance constructs, reaction-time-based tasks have gained popularity as implicit measures of approach-avoidance tendencies, thus enabling the assessment of spontaneous responses to rewarding/punishing stimuli. Notably, the visual joystick task (Rinck & Becker, 2007; adopted from Chen & Bargh, 1999; see Figure 4.1a) and the manikin task (De Houwer et al., 2001; see Figure 4.1b) have emerged as prominent tasks for assessing approach-avoidance tendencies. In the visual joystick task, participants are instructed to push (avoid) or pull (approach) stimuli, resulting in a zoom effect, i.e., the shrinking or expanding of the respective stimuli. In the manikin task, instead, participants are instructed to direct a manikin towards or away from the stimulus. Instructions can either be directed at relevant (e.g., valence of the stimulus) or irrelevant (e.g., landscape vs. portrait presentation) stimulus features. In both tasks, approach-avoidance tendencies are quantified by the difference in response time for approaching and avoiding each stimulus, with faster avoidance indicating an avoidance bias and faster approach indicating an approach bias. To illustrate how the tasks are commonly structured, happy and angry faces, for example, are expected to elicit approach and avoidance biases, respectively. They are displayed in a congruent condition, where participants are instructed to approach happy and avoid angry faces, and subsequently in an incongruent condition with the instruction to avoid happy and approach angry

faces. The reaction time differences between the congruent and incongruent condition within each stimulus category (happy, angry) would then represent the biases that are interpreted in terms of approach-avoidance tendencies.



Example screen of approach-avoidance conflict task

Figure 4.1. Examples of the three tasks, the (a) visual joystick, (b) manikin, and (c) AACT, utilized in this study. The representations of the visual joystick and manikin task are schematic and deviate in size and background color from the tasks performed by the participants. Greyscaled versions of the images with the codes AF21ANS, AF22HAS, AM28ANS and BM32HAS from Lundqvist et al. (1998) are shown in the schematic representations of the visual joystick and manikin tasks and can be requested from kdef.se for non-commercial scientific research purposes. The figure has been adapted with permission from Fricke and Vogel (2020).

While the visual joystick and manikin tasks are most commonly used, other attempts have been made to measure task-based approach-avoidance tendencies, for example, the approach-avoidance conflict task (AACT, see Figure 4.1c) developed by Bach et al. (2014), in which participants forage for tokens under threat. The AACT offers the advantage of being pharmacologically validated by demonstrating sensitivity to anxiolytics and comes with several outcome measures inspired by preclinical research, such as tracking the distance to the nearest wall or the predator. Importantly, the AACT differs from the visual joystick and manikin tasks in several ways. The visual joystick and manikin tasks introduce conflict implicitly by necessitating the over-riding of automatic tendencies in favor of goal-directed instrumental behavior, when instruction and stimulus content are incongruent, i.e., approaching negative and avoiding positive stimuli. This way, automatic biases are measured under time pressure (reaction-time-based tasks) with a clearly defined correct response. In contrast, the AACT can be understood as a more explicit measure that introduces direct goal conflicts in an ambiguous foraging scenario, i.e., the conflict between approaching tokens and avoiding predatory threat. In the AACT, there is no correct response, but rather different strategies to solve the goal conflict optimally based on individual preferences. Participants aim to maximize success, while being presented with potential positive and negative outcomes based on their decisions simultaneously. Inherent to all three tasks is that they induce some form of conflict and therefore are expected to activate Gray's postulated approach-avoidance systems.

To facilitate understanding of approach and avoidance behavior, it is vital to investigate whether approach-avoidance measures of different tasks are comparable and map onto the same underlying constructs. Despite the widespread use of visual joystick and manikin tasks in research and clinical studies, we found only one study attempting to assess and compare their validity, showing no correlation between approach-avoidance biases of both tasks using spider and butterfly images with stimulus-relevant instructions, i.e., approaching or avoiding based on stimulus category, and thus indicating that they did not operationalize the same construct (Krieglmeyer & Deutsch, 2010). To the best of our knowledge, no studies to date have conducted direct task comparisons using emotional faces as stimuli. However, these

comparisons appear relevant as emotional faces are widely used stimuli in research on, among others, aggression, anxiety, depression, trauma and stress within the approach-avoidance literature (Fricke & Vogel, 2020). Thus, Aim 1 in this preregistered study was to investigate whether the outcome measures of emotional face versions of the visual joystick and manikin tasks are comparable operationalizations of the same underlying construct of approach-avoidance tendencies.

Next, as people observably differ in their approach-avoidance behaviors in real life, it seems further relevant to identify how well task-based measures can reproduce this interindividual variability. Based on the review by Fricke and Vogel (2020), criterion validity of approach-avoidance tasks seems not as consistent as anticipated, i.e., several interindividual differences did not reliably relate to task-based approach-avoidance measures. For instance, while several studies found links between anxiety and approach-avoidance behavior (Enter et al., 2016; Harari-Dahan & Bernstein, 2017; Heuer et al., 2007; Lange et al., 2008; Pittig et al., 2014; Roelofs et al., 2010; all joystick task studies had stimulus-irrelevant instructions), other studies did not (Ferrari et al., 2018; Kampmann et al., 2018b; Radke et al., 2013; two stimulus-irrelevant and one stimulus-relevant joystick task studies). Even in a large longitudinal study, Struijs et al. (2017) found no association between task-based approach-avoidance tendencies of face stimuli (with stimulus-irrelevant instructions, i.e., to approach or avoid based on the color of the picture filter) and clinical anxiety or depression. These ambiguous findings were mirrored for several other interindividual differences (Fricke & Vogel, 2020). For aggression, physical aggression has been linked to self-reports of the BAS (Harmon-Jones, 2003), while trait anger and psychopathy have been shown to elicit approach towards angry faces in approach-avoidance tasks (Dapprich et al., 2021), but also not without some level of ambiguity (Fricke & Vogel, 2020). We therefore aimed not only to compare the tasks, but also to assess their relationships with self-reported interindividual differences in behavioral inhibition and activation as well as trait anxiety and aggression, which are theoretically related to the stimuli we employed. Regarding Aim 2, we hypothesized that stronger avoidance biases should positively correlate with higher CW-BIS scores, whereas stronger approach biases should correlate with CW-BAS scores if task-based approach-avoidance biases are predictive for those

interindividual differences. Likewise, more task-based avoidance should also be associated with more trait anxiety, while more task-based approach should be associated with trait aggression. For all hypotheses, influences of valence are expected, e.g., trait anxiety should be especially relevant in the context of angry faces. State anxiety and depressive symptoms were investigated in addition, the former expected to relate to increased avoidance of negatively valenced stimuli, while the latter was expected to relate to overall inhibition, i.e., slower overall reaction times, based on previous findings (Bartoszek & Winer, 2015; Radke et al., 2014). Regarding the BIS and anxiety, it is important to note that the concepts are strongly linked in the revised reinforcement sensitivity theory by Gray and McNaughton (Gray & McNaughton, 2003). According to this theory, the detection of a goal conflict, i.e., an approach-avoidance, approach-approach or avoidance-avoidance conflict, will induce inhibition of current behavior and lead to an increase in state anxiety, while stable interindividual differences in BIS sensitivity should be related to observable differences in trait anxiety. This implies that BIS and trait anxiety self-report measures should correlate highly (as has for example been shown by Carver and White (1994)) as both are most likely reflections of the self-registered frequency and intensity of anxiety as an emotional state. However, we think that the distinction between BIS and trait/state anxiety is still relevant to a degree as questionnaires based on the BIS conceptualization of the original reinforcement sensitivity theory may be reflective of both, the BIS and the fight-flight-freeze system (Heym et al., 2008). To conclude, if the visual joystick and manikin task are differently suited to reflect these self-reported interindividual differences, the explained variance should differ between tasks. To offer perspective beyond the more established tasks, we also included the AACT as a less well-established paradigm. Previous research suggests a potential association between the AACT and trait anxiety and aggression (Vogel & Schwabe, 2019), although findings remain inconclusive as Bach et al. (2020) found no link between a different measure of anxiety and AACT outcome measures in adolescents. We therefore extended Aim 2 to exploratively include the relationship of AACT outcome measures of approach and avoidance with the before mentioned self-reported interindividual differences.

In addition to our preregistered aims above and considering the underreporting of reliability measures in the literature, we also assessed internal consistencies for the outcome measures of all three tasks as Aim 3 of our study and hope this practice becomes more commonplace in future research. This appears especially relevant as clinical studies utilize approach-avoidance tasks as possible interventions to alter behavioral tendencies (Asnaani et al., 2014; Bomyea et al., 2023; Sweet et al., 2021), implying the need for consistent measurement tools that can reliably capture participants' approach-avoidance behaviors.

In summary, we used a correlational within-subject design in which participants completed three behavioral approach-avoidance tasks, namely the visual joystick, manikin, and AACT, and answered several personality questionnaires. This allowed us to compare the visual joystick and manikin tasks and whether they map onto the same underlying constructs (Aim 1), compare their ability to predict several self-reported interindividual differences (Aim 2) and report their internal consistencies (Aim 3). For Aim 2 and 3, the AACT, a pharmacologically validated task-based measure of approach-avoidance tendencies during foraging was also investigated. The hypotheses and analyses were preregistered at osf.io/ahvzx.

4.3 METHODS

4.3.1 Participants

One hundred sixty-eight participants (81 self-identified men, 87 self-identified women, age: 18-56 years, mean: 22.85, SD: 4.90) with normal or corrected-to-normal vision and German as mother tongue or equivalent proficiency completed the study. A target sample size of at least 144 participants was supported by an a-priori power analysis (see preregistration at osf.io/ahvzx), allowing the discovery of medium-sized effects at an alpha error probability of .004 (alpha of .05 bonferroni-corrected for 12 planned comparisons) and a power of 80% for multiple linear regressions with four predictors

(G*Power 3.1.9.7; Faul et al., 2007; for details regarding the regression analyses, please refer to the Statistical Analysis section). Additional participants were tested due to being scheduled prior to reaching the target sample size. Participants provided written informed consent and student participants received partial course credit for participation. The study was approved by the local ethics committee (Ethikkommission der Medical School Hamburg, MSH-2019/79). All methods were performed in accordance with relevant guidelines, regulations and the Declaration of Helsinki.

4.3.2 Experimental Procedures

First, participants answered questionnaires assessing state and trait anxiety (STAI-S/T; Laux et al., 1981), trait aggression (DAF; Werner & von Collani, 2014), depressive symptoms in the past two weeks (BDI-II; Hautzinger et al., 2006), behavioral inhibition and approach (CW-BIS/BAS; Strobel et al., 2001) as well as chronic stress in the past three months (TICS; not reported here; Schulz et al., 2004). This was followed by the three behavioral tasks (visual joystick, manikin, and AACT) in counterbalanced order with short breaks in-between. Afterwards, participants answered Likert scale questions regarding drug use, gaming habits and current physical and psychological strain (not reported here). In the end, participants were debriefed about study procedures and informed about psychological help services in case of heightened depressive symptomatology ($BDI-II \geq 20$ or indicated suicidality). The experiment lasted approximately 100 minutes (SD: 13 minutes).

4.3.3 Visual Joystick and Manikin Task

The visual joystick and manikin task were adapted from Inquisit 5 templates (Millisecond Software, 2019a, 2019b). To enhance comparability, task designs were aligned as much as possible.

4.3.3.1 Stimulus Material

Emotional face images from the Karolinska Directed Emotional Faces (size: 562x762 px; Lundqvist et al., 1998) and Radboud Faces Database (size: 681x1024 px; Langner et al., 2010) were gray-scaled and rated based on their emotional valence, intensity and credibility of expression by three independent raters. Ninety-six images with angry/happy expressions of male/female faces (24 images each) were selected and divided evenly across the two tasks (see section 7.3).

4.3.3.2 Task design

Following 8 (manikin task) and 10 (visual joystick task) practice trials, participants performed 16 blocks of 12 trials (192 trials total) per task. Participants were instructed to either approach or avoid stimuli presented in the middle of a 22" computer screen as follows: Approach was implemented by pulling a joystick towards the participant (visual joystick task, Figure 4.1A) or by moving a manikin towards the stimulus by pressing the up (8-)key or down (2-)key on the num keyboard depending on the manikin's location (manikin task, Figure 4.1B). In contrast, participants were instructed to avoid by pushing a joystick away from the participant or moving the manikin away from the stimulus. In the visual joystick task, approach and avoidance were visually enhanced by real-time (i.e., proportional to the speed of the joystick movement) zoom-in/zoom-out effects of the stimulus on a white background. Initially, stimuli were scaled to fill 60% of the screen height and could be pushed to fill 10% or pulled to fill 100% of the screen height before disappearing. In the manikin task, animations of the manikin walking towards/away of the stimulus, which filled 40% of screen height on a black background, indicated approach and avoidance. Instructions varied block-wise between approach of happy/avoidance of angry faces (congruent) and approach of angry/avoidance of happy faces (incongruent). Congruency conditions of the first block were counterbalanced across participants and then switched after each block. Presentation order of stimuli was pseudo-randomized with all 48 stimuli within a task appearing twice per instruction with the limitations of only three stimuli in a row having the same valence or gender and stimuli only repeating after all 48 stimuli were displayed per instruction. In addition, the manikin appeared both above and below each stimulus once per instruction of the manikin task.

4.3.3.3 Indices (outcome parameters)

We recorded response correctness and reaction times (RT) for correct responses (visual joystick task: full extension of the joystick in correct direction; manikin task: press of 8- or 2-key on numpad). For RTs, values below 200 ms and above 1,500 ms were discarded. Values exceeding 3 SDs or more above/below the individual mean (of each specific valence/instruction combination) were subsequently removed. Moreover, data from two participants in the visual joystick and nine participants in the manikin task was excluded as more than 25% of trials were removed through the above steps. To ensure that post-error slowing in the visual joystick and manikin tasks had no effect on the respective association with outcome measures, we included the option to run the analysis with post-error-trials excluded in our analysis file (osf.io/ahvzx) as suggested by a reviewer. However, the results did not differ substantially from our main analysis.

Next, we constructed mean RT scores per task for all combinations of stimulus valence (happy/angry) and instruction (approach/avoid) as well as an overall mean RT score. Bias scores were then constructed by subtracting mean RTs of avoidance trials from approach trials per valence category. For example, the bias score for happy faces is the mean RT to make an approach movement towards happy faces minus the mean RT to make an avoidance movement away from happy faces. A negative score thus indicates faster approach, while a positive score indicates faster avoidance. Following reviewer suggestion, we additionally included a valence-unspecific bias measure as this is more in line with the phrasing of our hypotheses regarding general approach and avoidance biases. Moreover, we also included a global congruency measure in which reaction times in congruent trials, i.e., approaching happy and avoiding angry faces, were subtracted from reaction times in incongruent trials, i.e., avoiding happy and approaching angry faces.

In addition, so called D-Scores (Greenwald et al., 2003) were constructed for exploratory analyses as these are reportedly better suited measures of RT differences (Kersbergen et al., 2015). To construct these, the differences of mean RTs are divided

by their pooled standard deviation (irrespective of instruction) and data exclusion takes error rates into account by replacing error trials by the block RT mean +2 SD (irrespective of stimulus valance).

4.3.4 Approach-Avoidance Conflict Task

The AACT was adapted from Bach et al. (2014) in Python 3.2.5 using Pygame 1.9.2 (code available from osf.io/d69pr; Fricke et al., 2023).

4.3.4.1 Task design

For 160 trials (divided into four blocks), participants were instructed to forage for tokens on a 24x16 grid containing ten tokens in variable locations, a predator in one corner, and a safe space in the opposite corner. Avoidance motivation was induced by threat of the predator waking up, chasing participants and taking away the in-trial earned tokens (see Figure 4.1C). Threat level was manipulated by having high vs. low threat predator conditions (half of trials each) based on wake-up probability (60 vs. 20%). Initial threat distance was manipulated by placing participants either by the predator or the safe space (half of trials each). Trials lasted between 6 and 15 seconds and were extended by a 3.5 second chase-phase in case of predator wake-up. There was no monetary incentive for token collection. After task completion, participants estimated the predator wake-up probabilities. For a detailed description of the AACT, see the supplement of Fricke et al. (2023).

4.3.4.2 Indices (outcome parameters)

We selected ten previously established outcome parameters (Bach et al., 2014; Bach et al., 2018; Vogel & Schwabe, 2019). Three measures were per-trial measures (recorded once per trial): Foraging latency, i.e., time until the first button press, as measure of initial decision processes; sum of tokens retained (unless caught) to measure overall

performance; and failure to avoid threat (i.e., whether the participant got caught) as additional performance measure. Seven measures were in-trial measures (recorded every 500 ms): distance to closest wall, presence in safe quadrant of the board (12x8 field in which the safe place was located), presence in safe place, presence in dangerous quadrant of the board (12x8 field in which the predator was initially located), distance to predator, rate of token collection, and running speed on grid. All measures were averaged over trials (and time points for in-trial measures). As per reviewer's suggestion, we additionally increased resolution by separating the outcome parameters by initial threat distance (close, far) and threat level (low, high), leading to an additional 40 outcome parameters which were investigated in exploratory analyses that paralleled the statistical analyses regarding Aim 2 in the supplement (see supplementary section 7.3.1 Approach-Avoidance Conflict Task analyses including threat level and threat distance as variables). These analyses were initially not included as a prior study reported outcome measure interactions with threat level to be rather unreliable and that behavior became comparable over time for close and far initial threat distance (Bach et al., 2020).

4.3.5 Statistical analysis

All analyses were conducted in R (Version 4.3.1) and can be found, accompanied by the data, at osf.io/ahvzx. To compare the visual joystick and manikin task (Aim 1), we constructed Pearson correlation coefficients for all outcome measures (overall RT, overall accuracy, global congruency, approach-avoidance bias scores and exploratively D-Scores) of the visual joystick task with the respective outcome measure of the manikin task to investigate their similarities and differences.

To answer our main preregistered hypotheses, investigating the ability of all three tasks to predict self-reported interindividual differences (Aim 2), we first provided a correlation matrix (with probabilities not corrected for multiple comparisons) of all task outcome measures (of visual joystick, manikin, and AACT) with all questionnaire scores (CW-BIS/BAS, STAI-S/T, DAF subscales physical aggression, verbal

aggression, and anger, and BDI) as an overview. Then, we constructed multiple linear regression models to investigate how predictive the approach-avoidance tasks were of the personality variables measured by questionnaires. For both visual joystick and manikin task, we used the predictors overall RT, overall accuracy, valenced approach bias and avoidance bias scores as well as the control variables age and gender. The models were then compared to their respective baseline models containing only age and gender by testing whether the model fit was significantly improved. We tested for the assumption of independence with the Durbin-Watson-Test accepting values between one and three and for the assumption of no multicollinearity by variance inflation factors (VIF), checking whether the largest VIF would exceed a value of ten or the average VIF substantially exceeded a value of one (Bowerman & O'Connell, 2000). If studentized residuals were distributed non-normally as tested with a Shapiro-Wilk test, bias-corrected and accelerated bootstrapped confidence intervals based on 2,000 bootstrap repetitions are reported. The same procedure was then repeated for an alternative model in which potentially influential cases with standardized residuals exceeding two standard deviations away from the mean were excluded on the basis of Cook's distance exceeding a value of one, leverage values three times larger than the average leverage and/or the covariance ratio falling outside of one plus/minus three times the average leverage. In case of meaningful differences in models, i.e., only one of the models being a significantly better fit than the respective baseline model or predictors in models differing in their significance, findings of both models are reported. Outcome variables of the regression models were the CW-BIS/BAS, STAI-T and DAF (subscales: physical aggression; verbal aggression; anger) scores. Given the two tasks, this resulted in 12 multiple linear regression models that were corrected for multiple comparisons with the Benjamini-Hochberg procedure in line with our preregistered analysis strategy. The correction was separately applied for the standard model and the model with removed influential cases. In addition, exploratory models were constructed for STAI-S and BDI scores. These were corrected for multiple comparisons as the original 12 models by removing the four highest p-values of those 12 models and combining the remaining eight p-values with the four p-values of the STAI-S and BDI models. Following reviewer suggestion, we repeated the regression analyses with the additional predictors valence-unspecific bias and global congruency.

If the inclusion of the additional predictors resulted in more predictive models over the control models, we report the findings in addition to the original regression analyses.

Exploratively, we also constructed multiple regression models for the AACT as described for the other two tasks with the following changes: Since the ten predictor variables, i.e., the outcome measures of the AACT, had VIFs exceeding values of ten, we opted for parameter selection via least absolute shrinkage and selection operator regression before testing the selected parameters in the regression models described above. Age and gender were not included in the parameter selection, but added to the full models, which were compared against their respective baseline models containing only age and gender. We are aware that selecting variables that explain the most variance before for the regression models biases our data towards significant findings. Therefore, any findings should be interpreted with caution and tested with confirmatory hypotheses in the future. For the AACT, six models (Benjamini-Hochberg corrected) were generated for the outcome variables CW-BIS/BAS scores, STAI-T score and DAF-subscale physical aggression, verbal aggression and anger. In addition, exploratory models for STAI-S and BDI scores were corrected at the level of the original six models by removal of the two highest p-values.

To address Aim 3, we investigated internal consistencies of all task measures by separating trials based on task-factors first (visual joystick/manikin task: stimulus valance x instruction to approach or avoid; AACT: threat level x threat distance [x time in trial for in-trial variables, which were assessed every 500 ms]) and then splitting them in odd and even trials. We then averaged outcome measures per participant and calculated Pearson correlation coefficients for the aggregated odd and even values. We permuted our data set one thousand times (with the constraint of only permuting within block for visual joystick and manikin task) and repeated the procedure. Correlation coefficients were then averaged and 95% confidence intervals constructed based on the 25th and 975th highest correlation coefficient. Due to the task being split in half, Spearman-Brown prophecy formula-corrected consistencies were also reported. Similarly, we constructed split-half internal consistencies and Spearman-

Brown prophecy formula-corrected consistencies for all investigated questionnaires (or subscales). All reported *p*-values of our analyses are tested for significance at an alpha-level of 0.05.

In our preregistration, we intended to compare models across tasks by their Akaike Information Criterion (Anderson & Burnham, 2002). Given that task outcome parameters in our models were rarely influential, witnessed by no better model performance than the respective baseline model, we did not pursue direct comparisons of the three tasks. We also did not pursue an exploratory factor analysis, preregistered as exploratory analysis, across all task outcome measures to find commonalities between the tasks more directly due to an inadequate Kaiser-Meyer-Olkin factor (Kaiser, 1974) that could not be resolved without the exclusion of too many of our task outcome variables.

4.4 RESULTS

In the visual joystick task, participants averaged overall RT scores of 755 ms (SD: 78 ms) with an accuracy of 95% (SD: 4%). As expected, average bias scores indicated tendencies to approach happy faces (-36 ms) and avoid angry faces (2 ms, difference: $t_{165} = -5.78, p < .001$). The D-Scores showed a similar trend of happy face approach (-0.25) and angry face avoidance (0.023, difference: $t_{165} = -6.20, p < .001$). An ANOVA with valence (happy, angry) and instruction (approach, avoid) as within-subject factors, i.e., including the global congruency effect, showed a significant interaction of valence and instruction ($F_{1,165} = 37.89, p < .001, \eta^2G = .014$), which was qualified post hoc by

an approach bias towards happy faces ($F_{1,165} = 59.10, p < .001, \eta^2G = .043$), but no significant avoidance bias of angry faces.

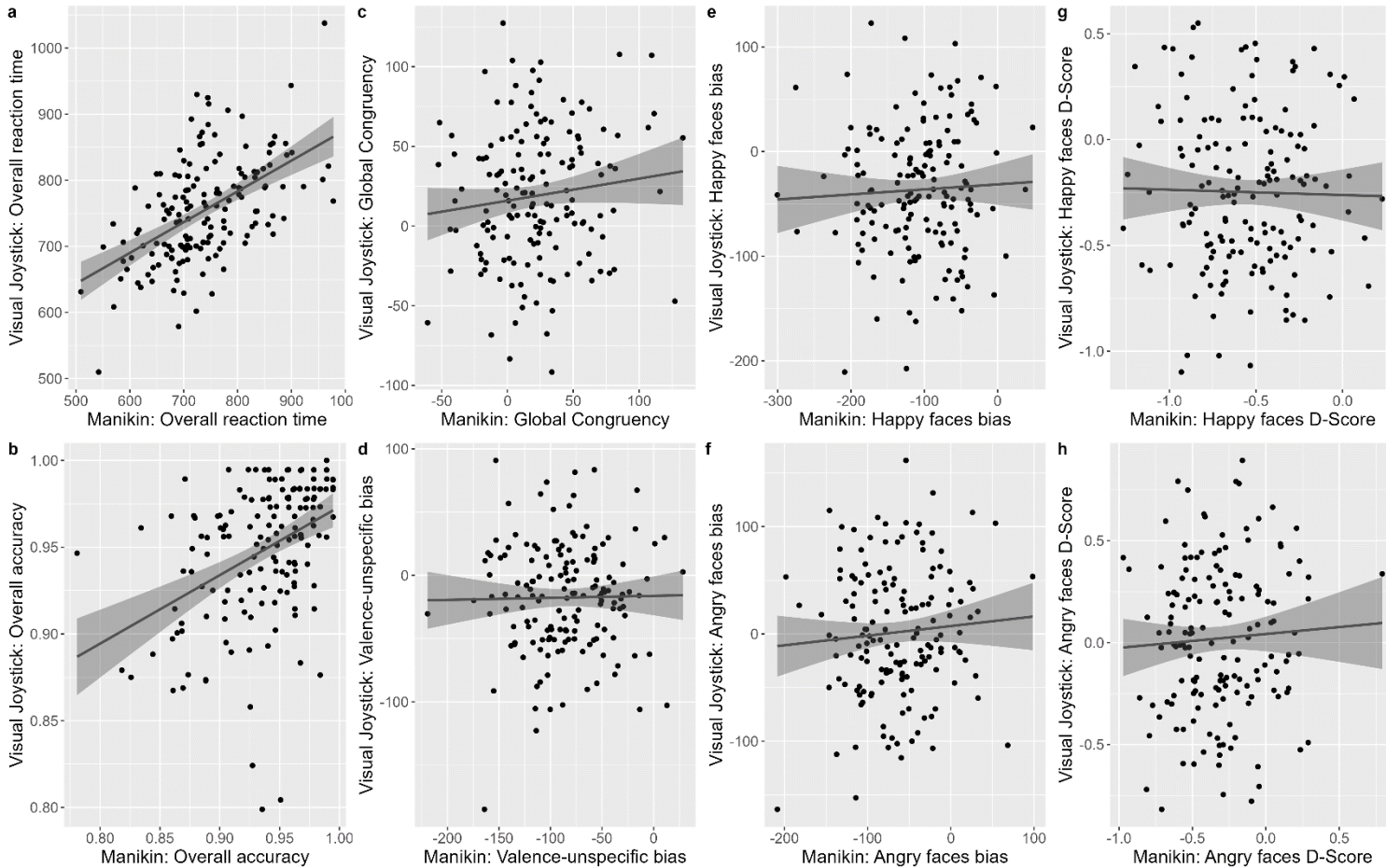


Figure 4.2. Correlations of visual joystick and manikin task measures a) overall reaction time ($r_{156} = .53, p < .001$), b) overall accuracy ($r_{156} = .41, p < .001$), c) global congruency ($r_{156} = .12, p = .135$), d) valence-unspecific bias ($r_{156} = .02, p = .844$), e) happy faces bias ($r_{156} = .05, p = .551$), f) angry faces bias ($r_{156} = .08, p = .339$), g) happy faces D-Score ($r_{156} = -.02, p = .796$) and h) angry faces D-Score ($r_{156} = .05, p = .495$). Line indicates linear regression over all data points with 95% confidence interval.

In the manikin task, participants averaged overall RT scores of 739 ms (SD: 90 ms) with an accuracy of 94% (SD: 4%). As in the visual joystick task, bias scores and D-Scores could be differentiated based on stimulus category (bias – happy faces: -108 ms, angry faces: -63 ms, difference: $t_{158} = -7.69, p < .001$; D-Score – happy faces: -0.55, angry faces: -0.32, difference: $t_{158} = -7.42, p < .001$) and indicated stronger approach

for happy than angry faces. A valence x instruction ANOVA showed a significant interaction ($F_{1,158} = 57.65$, $p < .001$, $\eta^2G = .014$), which was qualified post hoc by approach biases towards happy ($F_{1,158} = 478$, $p < .001$, $\eta^2G = .224$) and to a lesser degree angry faces ($F_{1,158} = 182$, $p < .001$, $\eta^2G = .082$).

Regarding Aim 1, the comparison of visual joystick and manikin task outcome measures revealed no correlations between bias and D-Scores of the two tasks, while overall reaction time ($r_{156} = .53$, $p < .001$) and accuracy ($r_{156} = .41$, $p < .001$) were moderately correlated (see Figure 4.2). Participants were therefore comparably fast and accurate in both tasks, but bias and D-Scores were unrelated, indicating that the tasks are not comparable operationalizations of the same underlying construct despite ostensibly similar measures of approach and avoidance.

Table 4.1. Mean, standard deviation, range and internal consistency estimates of all self-reported measures per gender.

Questionnaire Scale	men		women		Internal consistency estimate (SB)
	mean (sd)	range (min; max)	mean (sd)	range (min; max)	
CW-BIS	2.73 (0.53)	2.57 (1.14; 3.71)	3.16 (0.56)	2.29 (1.71; 4)	0.69 (0.82)
CW-BAS	3.15 (0.37)	1.85 (2.15; 4)	3.15 (0.35)	1.61 (2.31; 3.92)	0.56 (0.72)
STAI S	36.28 (6.49)	31 (22; 53)	36.51 (7.52)	48 (23; 71)	0.75 (0.85)
STAI T	38.69 (9.15)	46 (22; 68)	41.44 (10.91)	44 (24; 68)	0.85 (0.92)
DAF physical aggression	15.53 (5.1)	20 (9; 29)	11.7 (3.63)	20 (9; 29)	0.76 (0.86)
DAF verbal aggression	11.28 (2.42)	12 (7; 19)	10.32 (2.31)	11 (6; 17)	0.40 (0.58)
DAF anger	12.99 (3.66)	18 (7; 25)	12.63 (4.13)	17 (7; 24)	0.68 (0.81)
BDI	8.67 (6.99)	39 (0; 39)	10.47 (8.28)	35 (0; 35)	0.81 (0.90)

Notes. SB = Spearman-Brown-corrected.

Concerning interindividual differences, the sample showed sufficient variance for all self-reported questionnaire scores (see Table 4.1; for boxplots/density plots, see Figure 7.3.1). Compared to (non-clinical) norm samples, values were normal to slightly elevated for trait anxiety and depressive symptoms. CW-BIS and CW-BAS were comparable to the published norm (Strobel et al., 2001). Internal consistencies of the questionnaires were mostly acceptable with only CW-BAS and verbal aggression

seemingly subpar (see Table 4.1). Figure 4.3 shows the correlation matrix (uncorrected probabilities) of all task outcome measures with all questionnaire scores (Aim 2).

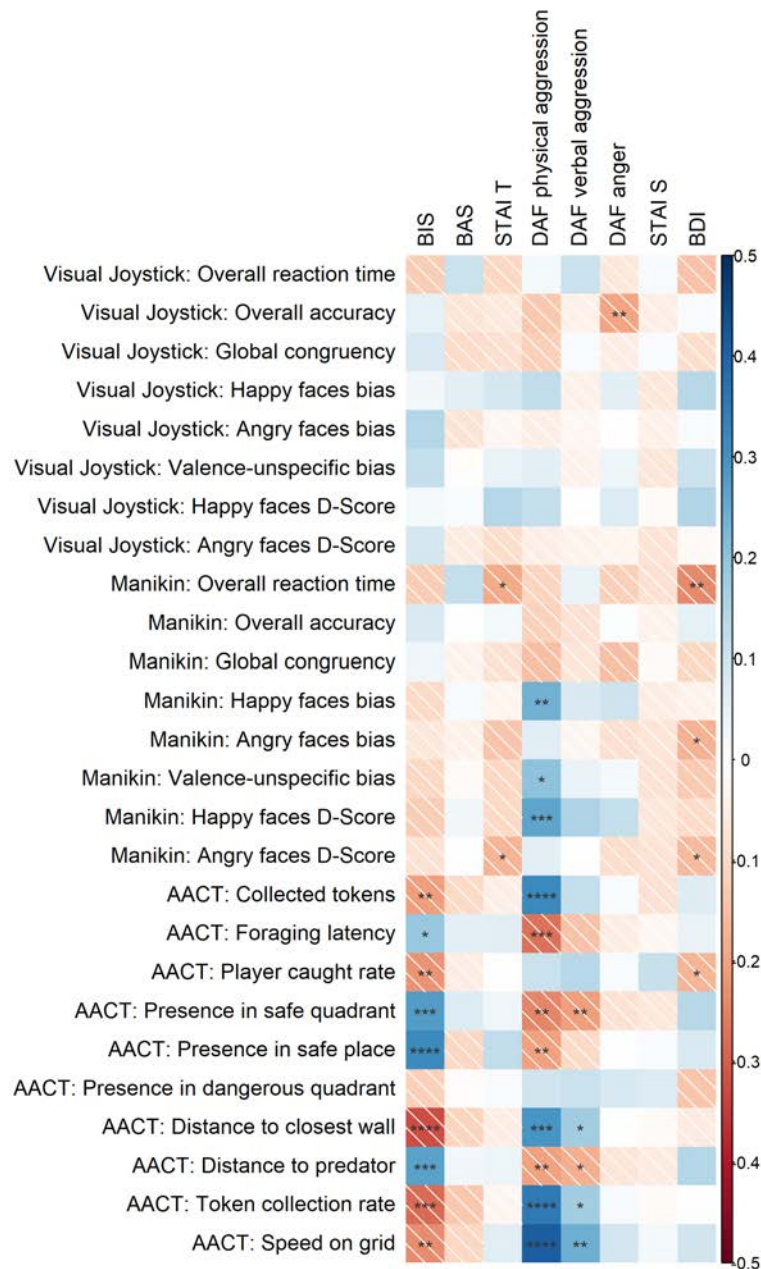


Figure 4.3. Correlation matrix of all questionnaire scores with task outcome measures. Color intensity indicates strength of correlation, color and shade indicate direction of effect (blue/no shade = positively correlated; red/ shaded = negatively correlated). p-values are uncorrected for multiple comparisons. Significance codes: **** p < .0001, *** p < .001, ** p < .01, * p < .05.

In contrast to our hypotheses, bias and D-Scores of the visual joystick task were not significantly correlated with any self-reported questionnaire scores. In the manikin task, physical aggression was related to stronger avoidance of happy faces (bias: $r_{157} = .24$, $p = .003$; D-Score: $r_{157} = .26$, $p < .001$) and valence-unspecific avoidance ($r_{157} = .20$, $p = .010$), whereas trait anxiety (D-Score: $r_{157} = -.17$, $p = .035$) and depressive symptoms (bias: $r_{155} = -.17$, $p = .029$; D-Score: $r_{155} = -.16$, $p = .049$) related to the approach of angry faces. Higher depressive symptom scores ($r_{155} = -.24$, $p = .003$) and trait anxiety ($r_{157} = -.19$, $p = .017$) were additionally associated with significantly faster overall reaction times. These findings regarding the visual joystick task and the manikin task were not in line with our hypotheses.

For the AACT, plausible clusters of correlations emerged for the BIS, physical aggression and, to a lesser degree, verbal aggression. A higher CW-BIS score was related to more cautious behavior, more precisely, initiating foraging later ($r_{166} = .19$, $p = .016$), collecting fewer tokens (total tokens: $r_{166} = -.21$, $p = .007$; collection rate: $r_{166} = -.28$, $p < .001$), being caught less frequently by the predator ($r_{166} = -.22$, $p = .004$), staying more in safe areas (safe quadrant: $r_{166} = .28$, $p < .001$; safe place: $r_{166} = .32$, $p < .001$) and therefore farther away from the predator ($r_{166} = .27$, $p < .001$), staying closer to the walls ($r_{166} = -.32$, $p < .001$), and moving generally slower throughout the task ($r_{166} = -.23$, $p = .002$). The opposite pattern was true for physical and verbal aggression, which led to faster initiation of foraging (physical: $r_{166} = -.27$, $p < .001$), collecting more tokens (physical: total tokens: $r_{166} = .32$, $p < .001$; collection rate: $r_{166} = .41$, $p < .001$; verbal: collection rate: $r_{166} = .24$, $p = .024$), staying more outside safe areas (physical: safe quadrant: $r_{166} = -.24$, $p = .001$; safe place: $r_{166} = -.20$, $p = .008$; verbal: safe quadrant: $r_{166} = -.21$, $p = .007$), closer to the predator (physical: $r_{166} = -.20$, $p = .008$; verbal: $r_{166} = -.18$, $p = .020$), further away from the walls (physical: $r_{166} = .29$, $p < .001$; verbal: $r_{166} = .17$, $p = .023$) and moving generally faster during the task (physical: $r_{166} = .41$, $p < .001$; verbal: $r_{166} = .24$, $p = .001$). These clusters in the AACT convincingly indicate more approach tendencies in more aggressive individuals and more avoidance tendencies in participants with stronger behavioral inhibition, which was in line with theoretical expectations.

Regression models including visual joystick and manikin task outcome measures had no incremental predictive value for any investigated questionnaire scores beyond age and gender alone ($p > .099$). This was also the case for models including the additional predictors valence-unspecific bias and global congruency. In contrast, AACT regression models predicting BIS, BAS, physical aggression, verbal aggression and depressive symptom scores performed significantly better than their respective baseline models including only age and gender (see Table 4.2 for a list of the significant models and their predictors). In particular, less presence in the safe place was predictive of higher CW-BAS scores and higher speed on grid predictive of higher physical aggression and depressive symptom scores. Gender was a significant predictor for several models despite being also included in the respective baseline models with women scoring higher in BIS and depressive symptoms, but lower in physical aggression. It is important to keep in mind that these regression models on AACT data warrant independent replication as they were constructed based on preselected predictors explaining the most variance to reduce multicollinearity, thereby increasing the likelihood of significant findings.

Table 4.2. Significantly better multiple regression models of the AACT compared to baseline models (with predictors)

Questionnaire	Predictor Variables	Original Model	Alternative Model
		Model fit / sig. β estimates	Model fit / sig. β estimates
CW-BIS			adj. $R^2 = .20$, $F(6,156) = 7.772$, $p < .001$
	Gender		0.410***
	Age		.
	Presence in safe quadrant		.
	Presence in safe place		.
	Distance to closest wall		.
	Token Collection Rate		.
CW-BAS		adj. $R^2 = .06$, $F(7,160) = 2.534$, $p = .017$	adj. $R^2 = .08$, $F(7,154) = 2.920$, $p = .007$
	Gender	.	.
	Age	.	.
	Player caught rate	.	.

4 | COMPARISON OF TWO REACTION-TIME-BASED AND ONE FORAGING-BASED BEHAVIORAL APPROACH-AVOIDANCE TASKS IN RELATION TO INTERINDIVIDUAL DIFFERENCES AND THEIR RELIABILITY

	Presence in safe place	-4.400***	-4.574***
	Presence in dangerous quadrant	.	.
	Distance to closest wall	.	.
	Token Collection Rate	.	.
<hr/>			
physical aggression		adj. R ² = .19, F(4,163) = 10.970, p <.001	adj. R ² = .25, F(4,157) = 14.070, p <.001
	Gender	-2.260 ^a	-2.622**
	Age	.	.
	Presence in safe quadrant	.	.
	Speed on grid	2.716*	2.041 ^a
<hr/>			
verbal aggression			adj. R ² = .08, F(4,159) = 4.510, p =.002
	Gender	.	.
	Age	.	.
	Presence in safe quadrant	.	.
	Speed on grid	.	.
<hr/>			
BDI		adj. R ² = .08, F(6,159) = 3.541, p =.003	adj. R ² = .06, F(6,153) = 2.650, p =.018
	Gender	3.414 ^a	.
	Age	.	.
	Foraging latency	.	.
	Player caught rate	.	.
	Presence in safe quadrant	.	.
	Speed on grid	8.043**	5.435**

Notes. Alternative model: Model without cases with standardized residuals exceeding two standard deviations away from the mean and Cook's distance exceeding a value of one, leverage values three times larger than the average leverage and/or a covariance ratio outside of one plus/minus three times the average leverage. Significant predictors are in bold. ^aNot significant based on bootstrapped confidence interval. Significance codes: *** p < 0.001, ** p < 0.01, * p < 0.05

Finally, and regarding Aim 3, the internal consistencies of all visual joystick and manikin task approach-avoidance measures (global congruency, bias and D-Scores) were subpar (all $r \leq .52$ / Spearman-Brown-corrected (SB): $r \leq .69$), indicating low consistency for both tasks (see Figure 4.4). Only the consistency of general performance measures was good (overall reaction time ($r \geq .95$ / SB: $r \geq .97$); accuracy ($r \geq .69$ / SB: $r \geq .82$), but these are not specific to approach-avoidance. Internal consistencies for the AACT can be considered good to excellent (all $r \geq .81$ / SB: $r \geq .90$), indicating that participants behaved consistently throughout the task, a finding that was already suggested by Bach et al. (2014).

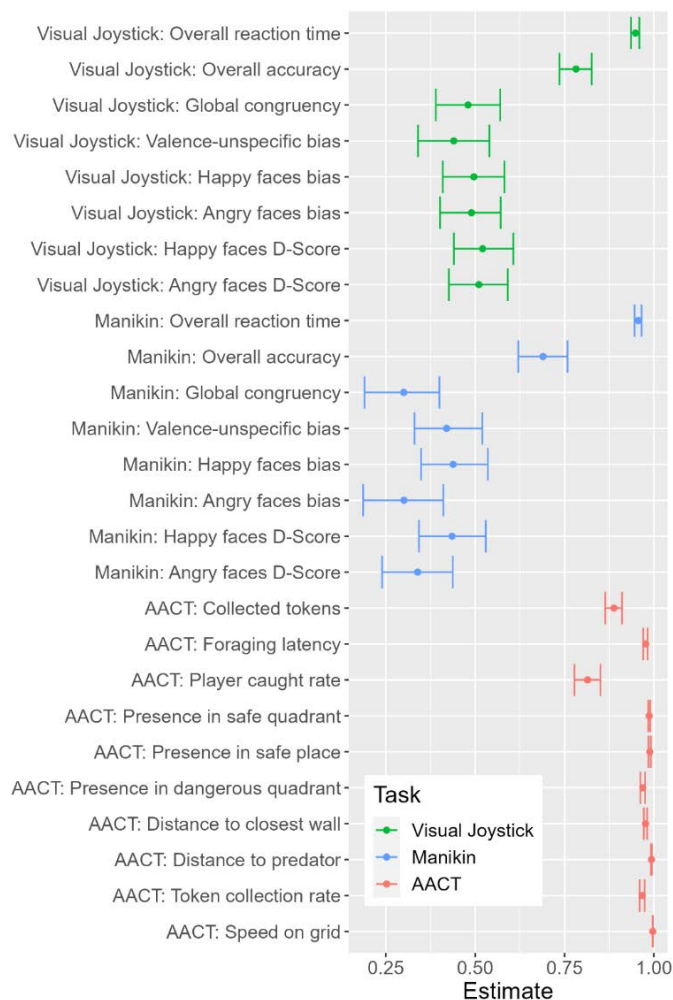


Figure 4.4. Internal consistency estimates for all outcome measures sorted by task. Bars indicate the confidence interval based on the 25th and 975th value based on thousand randomly permuted datasets (for restrictions see Methods section).

4.5 DISCUSSION

Approach-avoidance tasks, such as the visual joystick and manikin tasks, are one way to operationalize approach-avoidance tendencies that are widely used in research. However, although these reaction-time-based tasks aim to measure the same underlying constructs, it remains unclear whether they are actually comparable. Additionally, concerns have been raised regarding the ability of these tasks to predict interindividual differences which are theoretically strongly associated with approach-avoidance tendencies (Fricke & Vogel, 2020). To address these issues, the present study sought to compare proposed indices of approach-avoidance tendencies between the visual joystick and manikin tasks (Aim 1). Furthermore, the explanatory power of both tasks and the AACT, a pharmacologically validated approach-avoidance task developed in the context of anxiety, were assessed for several self-report measures, which are theoretically related to approach and avoidance (Aim 2). Internal consistencies of the tasks were also examined as reliability measures of the tasks are seldom given, but relevant, for example, in interindividual differences research and the context of clinical studies (Aim 3).

4.5.1 Visual joystick and manikin tasks: Convergent validity and association with self-report questionnaires

The bias measures of the visual joystick and manikin tasks, supposedly indexing approach-avoidance tendencies, were not correlated with each other. This lack of association is surprising as the sample was sufficiently large and heterogenous, the task designs of both tasks comparable (e.g., stimuli, trial number, blocks), the outcome measures analogue, and the statistical analyses identical. One potential explanation for the missing correlations could be that the tasks differed in their salience. The visual joystick task adopts a self-related frame of reference, i.e., pulling and pushing towards/away from oneself, and includes real time zoom-in/-out effects of the stimuli,

which prevent recategorizing of the joystick movements (Phaf et al., 2014). In comparison, in the manikin task approach-avoidance behavior was more representational by moving a manikin toward/away from the stimulus per button press and receiving visual feedback only after the response is made. Due to the different framing, the manikin task may appear considerably less salient and therefore have introduced less approach-avoidance conflict in the incongruent condition. However, even with differences in saliency, associations beyond general performance measures would have been expected if both tasks measure the same underlying constructs. In addition, the potential increase in saliency in the visual joystick task did not translate into stronger associations with self-report measures (see below) rendering interpretations difficult. Saliency might have been especially lacking for angry face stimuli, which did not elicit avoidance biases in either task averaged across participants. Nevertheless, it is important to note that the commonly examined outcome measures in the existing literature primarily focus on the differences in bias between distinct stimulus categories (e.g., happy vs. angry faces), which were indeed present in our data. Moreover, the absence of avoidance bias on group level does not negate that variance in approach-avoidance tendencies between participants should have led to between-task associations if the measures were related. We conclude that, at least for the emotional facial stimuli presented here, the tasks' bias measures do not assess the same underlying constructs of approach and avoidance, which warrants further investigation in the future.

In regard to self-reported measures of interindividual differences, outcome measures of the visual joystick task did not explain any significant variability. For the manikin task, correlations indicated avoidance tendencies for happy faces in participants with higher physical aggression and approach tendencies for angry faces in trait anxious and depressive individuals, which seems hard to reconcile with theoretical accounts (Barlow et al., 2004; Carver & Harmon-Jones, 2009). Given that the constructed regression models did not explain interindividual differences better than age and gender alone, we conclude that both tasks did not provide incremental information on self-reported differences. Importantly, various explanations are conceivable for this lack of findings. For once, it is possible that self-reported

interindividual differences had low convergence with task outcomes due to measuring different aspects of approach-avoidance tendencies or being not suited to assess facets of approach-avoidance tendencies in general. We find the latter unlikely as self-reported interindividual differences had mostly sufficient reliabilities and in part related to the AACT in ways that could be plausibly interpreted in terms of approach-avoidance. Another reason could be the so-called “reliability paradox”: Hedge et al. (2018) investigated seven classical cognitive tasks and reported “surprisingly low” reliabilities (Hedge et al., 2018, p. 1166). They propose that experimental tasks become popular due to their ability to create replicable, homogenous intraindividual task effects across participants, which is achieved by keeping interindividual variability low. However, this reduced interindividual variability makes it harder to achieve robust correlations with external measures such as self-reported questionnaire scores. The visual joystick and manikin tasks have both been designed to elicit reliable differences between approach and avoidance of a particular stimulus category (and especially in contrast to another stimulus category), which might therefore make them less suited for correlational studies which rely on interindividual variability. This interpretation is in line with the subpar split-half consistencies for the bias measures of both tasks. These low reliability estimates hamper correlations of task variables with external measures. For this reason, Goodhew and Edwards (2019) suggested that if studying interindividual differences with experimental tasks, researchers should include accounts of reliability for all measures. We agree that this practice should become commonplace in approach-avoidance research as it may aid understanding under which circumstances interindividual differences can and cannot be measured in approach-avoidance tasks (Fricke & Vogel, 2020).

In this context, another recommendation from Goodhew and Edwards (2019) should be considered, as they suggested that task conditions or versions should be used that lead to the greatest interindividual variation within task outcome measures. It is possible that our task design, for example, the decision to use many blocks of switching instructions with few stimuli each or the usage of grayscale happy and angry faces as in prior studies (Tyborowska et al., 2024; Volman et al., 2016) may have reduced interindividual variation. To find task versions and stimuli that are optimal in

interindividual differences research, consequences of different task design choices have to be investigated systematically and should be critically reconsidered in future studies. The same is true for the selection of outcome measures. Here, we did not find any meaningful differences between bias scores and D-Scores, but the choice of outcome measure may nonetheless be highly relevant. For example, difference scores, i.e., approach-avoidance biases and D-measures, have generally less reliability than the underlying individual measures, i.e., separate approach and avoidance scores, as measurement error is added up and between-participant variability reduced (Hedge et al., 2018). Individual measures or other scoring procedures may therefore be more advantageous when researching interindividual differences with approach-avoidance tasks.

4.5.2 The Approach-Avoidance Conflict task: Robust outcome measures relate to behavioral inhibition and physical aggression

In contrast to the visual joystick and manikin tasks, AACT outcome measures related to self-reported behavioral inhibition, physical aggression and verbal aggression, forming clusters of correlations (with uncorrected probabilities) that appear more in line with theoretical predictions. Physical and verbal aggression led to a riskier, but successful strategy (more collected tokens overall) that involved the collection of tokens in the middle of the field, further away from the safe place. For individuals with higher behavioral inhibition scores, the opposite was true. These findings are in line with a prior reporting of cautiousness and daringness correlating with AACT performance (Bach et al., 2020). Further, as the BIS is proposed to be sensitive to uncertainty in Gray's reinforcement sensitivity theory, a stronger relation of the BIS to the AACT with its looming threat compared to the visual joystick and manikin tasks in which the results of one's own behavior are more certain, i.e., either a zooming in or out of the stimulus or a short clip of the manikin moving towards/away from the

stimulus, appears theoretically plausible. Why the other self-reported interindividual differences (behavioral activation, state/trait anxiety, anger and depressive symptoms) did not correlate with task outcomes is unclear given theoretical expectations and comparable internal consistencies (see Table 4.1). Especially anxiety measures were expected to correlate with the AACT as the task has been validated with anxiolytics in the past, showing that the intake of anxiolytics compared to a placebo led to less anxious behavior, i.e., the participants spending less time in the safe areas (Bach et al., 2018; Korn et al., 2017). Considering that trait anxiety and BIS are both conceptually strongly related as detailed in the introduction, it is surprising that only CW-BIS (and not STAI-T) correlated with AACT behavior. It is possible that this is due to both questionnaires measuring different aspects of (trait) anxiety, for example more items related to anxious apprehension in the CW-BIS and more items related to (the absence of) anxious arousal or anhedonia in the STAI-T. It is therefore possible that a subscore of selected STAI-T items may have been more informative and that content analyses of questionnaires at item-level can be a promising next step to improve associations between traits and specific experimental measures in general (Brandt & Mueller, 2022). Moreover, it has been discussed that the STAI-T might not be a specific measure of anxiety per se, but rather a non-specific measure of tendency for negative affect (Knowles & Olatunji, 2020). It could thus be discussed that the CW-BIS may be a stronger measure of trait anxiety as the output of the BIS, which would be in line with the pharmacologically validated sensitivity of the AACT towards anxiety (Bach et al., 2018; Korn et al., 2017). Although the reported correlations with uncorrected probabilities (displayed in Figure 4.3) should be interpreted with caution, especially since variance might partially be explained by gender differences (Bach et al., 2020; Fricke et al., 2023), some of them would remain significant even if conservative comparison corrections had been applied. Additionally, regression analyses that controlled for gender resulted in models including task outcomes as significant predictors for behavioral activation, physical aggression and depressive symptoms.

Despite its advantages, the AACT presents a different challenge in that it offers numerous possible outcome parameters. Here, we selected ten outcome measures based on prior studies (Korn et al., 2017; Vogel & Schwabe, 2019), some of which

shared substantial variance with one another (see Table 7.3.1). Notably, Bach et al. (2020) included 38 outcome parameters in their analyses, illustrating the potential complexity of parameter selection. Consequently, one of the primary challenges for the AACT lies in identifying the most promising parameters, which may depend on the specific interindividual differences being investigated and warrants further exploration in future studies. Furthermore, it is essential to gain better insight into which aspects of approach-avoidance conflicts are related to which outcome parameters, even if this might be difficult as the task scenario is ambiguous and approach and avoidance not clearly separable by design. Differentiating trials based on threat level and initial threat distance (see supplementary section 7.3.1 Approach-Avoidance Conflict Task analyses including threat level and threat distance as variables) as well as not only tracing averaged in-trial measures, but looking at their dynamics over time might aid in these efforts (Bach et al., 2020). Moreover, unlike the other tasks, which can be easily customized by selecting relevant stimuli for different scenarios, the AACT lacks this adaptability, limiting its scope. Despite these challenges, the AACT appears to be a promising task to measure interindividual differences in approach-avoidance tendencies, which is further supported by the good to excellent reliability of its task outcome measures. In the future, it might be interesting to see how the AACT compares to other types of foraging tasks, for example by Kolling et al. (2012), and whether these foraging tasks are more similar in the elicitation of goal-conflict. Direct comparisons with the reaction-time-based tasks presented here were not possible due to an inadequate Kaiser-Meyer-Olkin factor, indicative of the three tasks' outcome measures not being suited for shared factor analyses in this sample.

4.5.3 Differences in goal conflict elicitation and further task design choices

Differences between the three tasks, especially the AACT in comparison to the visual joystick and manikin tasks, should be briefly addressed to gain more insight into the different results. We have already discussed some conjectures in the above sections, for example, that the visual joystick and manikin tasks were developed to induce a

main congruency effect which may come at the cost of being less reliable in tracking interindividual differences. In addition, it is likely that the tasks differ in their potential to elicit goal-conflicts because of conceptual differences, i.e., visual joystick and manikin tasks measuring automatic approach-avoidance tendencies and the AACT inducing more explicit approach-avoidance conflicts. The tasks differing on the dimension of implicit vs. explicit may be one contributing factor to our findings. Self-report measures are inherently explicit and would therefore be expected to yield higher correlations with other explicit measures compared to more automatic measures due to overlapping response modalities, possibly giving the visual joystick and manikin task a slight disadvantage to find the expected associations. Further, in the visual joystick and manikin tasks, congruent and incongruent actions were manipulated in a block-wise design. While the frequent switching between congruency (16 blocks of 12 trials each) and the zooming effect (visual joystick task) / manikin motion after the button press (manikin task) should have strengthened the elicitation of approach-avoidance conflicts, it is possible that this was in part prevented by proactive or strategic mechanisms of action regulation and cognitive control that reduced conflict by reframing it (Asanowicz et al., 2022; Lange et al., 2022; Strack et al., 2013). A reduced goal-conflict would in turn lead to less activation of the BIS, i.e., generate less anxiety, which in turn could reduce associations with self-reported BIS and anxiety measures. To increase goal-conflict in future research, tasks could include stimulus-irrelevant instructions, e.g., to approach all landscape format stimuli and avoid all portrait format stimuli, as this would allow presenting congruent and incongruent trials in random succession. However, it should also be considered that these more implicit instructions may lead to reduced goal-conflicts, if stimuli are largely processed based on features irrelevant to the research question. In the review by Fricke and Vogel, it remained unclear whether stimulus-relevant or -irrelevant task versions were more predictive of interindividual differences as both types of tasks resulted in heterogeneous findings (Fricke & Vogel, 2020). The AACT, in contrast, induces approach-avoidance conflicts which likely varied in strength between trials due to differences in threat level and initial threat distance as well as experiences in prior trials. This stronger induction of goal-conflict may therefore be one reason why the AACT related to the self-report measures investigated here.

4.6 CONCLUSION

In conclusion, our findings indicate that the visual joystick and manikin task measures are not comparable operationalizations of the same underlying constructs and have limited associations with the self-reported interindividual differences examined in this study. This is noteworthy considering our sufficiently large and heterogeneous sample, the identical structure of both tasks, the use of similar stimuli, and the application of identical analysis procedures. Furthermore, the approach-avoidance bias measures in both tasks showed subpar reliability. Conversely, the AACT seems to be associated with several interindividual differences and demonstrated good to excellent split-half reliabilities.

Our study highlights the need for further research to determine the most promising task-based measures of approach and avoidance tendencies when investigating interindividual variability. Besides improving prediction (of individual differences), we would like to emphasize that our findings also have repercussions for much-needed studies using experimental approaches to better understand the precise mechanisms governing approach avoidance behaviors. For instance, for both reaction-time-based tasks, reliabilities should consistently be reported per study and efforts should be made to improve them. Stimulus selection may be especially of relevance as higher reliabilities were achieved with different stimulus sets (images of spiders; Krieglmeier & Deutsch, 2010; Rinck & Becker, 2007). Stimulus saliency may also be increased, for example, by testing approach-avoidance tendencies in more immersive and ecologically valid virtual reality settings (Lange & Pauli, 2019). As the tasks do not appear to measure the same construct, it might be of interest to further investigate why the tasks differ from one another. Alternative tasks such as the AACT might be advantageous, but have their own shortcomings such as potentially more rigid designs and, in most cases, limited literature to support their efficacy. To effectively measure individual differences in approach-avoidance tendencies operationalized by behavioral tasks with high criterion validity, careful consideration of task selection, stimulus materials, and ensuring sufficient reliability will be required.

5 DISCUSSION

Approach and avoidance behaviors play a fundamental role in our interaction with the environment (Gray, 1975). As the underlying systems are hypothesized to govern most of our behavior and are relevant to several psychopathologies (e.g., World Health Organization, 1992), it seems vital to understand these processes as well as possible. One possible avenue is the utilization of behavioral approach-avoidance tasks, which are designed to measure aspects of approach and avoidance tendencies or behaviors under standardized laboratory conditions. In the thesis at hand, I investigated how well current iterations of these tasks, especially the most popular ones in the field, are at correlating with measures of interindividual differences. This was achieved mainly via self-report questionnaires and a pharmacological intervention, but also patient groups and other types of interventions in the systematic review presented in Chapter 2. At a glance, both, the systematic literature review and the experiments presented in Chapters 3 and 4, indicate that there is little evidence regarding the capabilities of the most popular tasks, i.e., the joystick and manikin tasks, to reliably track most interindividual differences at the level of the individual. This finding is especially relevant in the context of task versions being used as cognitive behavioral modification interventions (for example, Schenkel et al., 2024). While the study by Schenkel et al. (2024) seems promising and showed significantly improved short term (i.e., 3 months) abstinence rates in patients with alcohol use disorders, the underlying tasks and what influences their sensitivity and reliability in correlating with interindividual differences is important to research and understand. This will ideally allow better, potentially individualized forms of approach-avoidance bias training in the future. The field has

also recognized the necessity of understanding the tasks better, for example, by investigating how different pre-processing decisions affect the reliability and validity of the approach-avoidance tasks (see Kahveci et al., 2023). In the following sections, I will briefly address and discuss the research objectives one-by-one as they have been posed in the introductory chapter of this thesis, before stating my final conclusions. For further ideas regarding the findings presented in this thesis, I would like to point to the respective discussion sections of Chapters 2-4.

5.1 DISCUSSION OF RESEARCH OBJECTIVES

5.1.1 Aim 1. Critical evaluation of current behavioral tasks that assess approach-avoidance behavior and their relationship with interindividual differences.

RQ 1.1 *Which interindividual differences impact task-based approach-avoidance behavior?*

In hindsight, the question should have probably been phrased as “Which interindividual differences are reliably measurable in behavioral approach-avoidance tasks?” as impact might be measurable under specific task-configurations that have not been utilized properly so far. Based on the evidence presented in this thesis, most interindividual differences seem to lead to ambiguous patterns of correlation with task-based outcome measures. In Chapter 2, only specific phobias seemed to reliably elicit avoidance behavior by participants with that specific phobia, while other interindividual differences resulted in either hypothesis-congruent effects or no significant effects. The studies that resulted in significant and non-significant findings, respectively, did not differ in any systematic way, but could be investigated in more detail in the future. For example, based on Goodhew and Edwards (2019), it seemed likely that group designs would have an edge over correlational designs as the classical approach-avoidance tasks had been originally developed to measure differences

between congruent and incongruent conditions on the group level, but this does not seem to be the case based on our analysis.

Within the experimental studies conducted for this thesis, evidence also appears conflicting. In the intervention study in Chapter 3, designed to elicit a pharmacological stress response by targeting two of the most prominent stress mediators, no hypothesized effects of hydrocortisone and yohimbine on behavior were found. Further, the self-report measures (trait anxiety, sensation seeking, subscales of trait anger) did not show any significant relationship with the task outcomes in the approach-avoidance-conflict task (AACT) utilized in the study. In Chapter 4, the two classical tasks, i.e., the joystick and the manikin task, did not correlate with questionnaire scores in the expected way. In contrast, the AACT correlated with physical (and to a lesser degree verbal) aggression and behavioral inhibition, but not trait anxiety or behavioral activation. Therefore, the results for physical (and verbal) aggression appear contradictory as they differ between Chapter 3 and 4. Given the ambiguity in findings presented in Chapter 2, this is not necessarily surprising, but should raise awareness that even the task that had been most successful in relating to self-reported interindividual differences in the task-comparison study as well as showing significant effects of trait anxiety and aggression in Vogel and Schwabe (2019) does not necessarily show consistency in correlations with interindividual differences. One explanation may be the difference in power between the two studies as the comparison study had more than twice the participants than the pharmacological study. For trait anxiety, only the study by Vogel and Schwabe (2019) found effects in interaction with stress, while the studies presented here did not. Attention should also be given to the fact that interindividual differences as measured by self-report are often trait measures intended to be estimated over a longer duration and multiple situations, while the tasks at hand measure behavior during one specific situation at one point in time (Brandt & Mueller, 2022). This is the difference in the level of abstraction, which I had referred to in the abstract. Longitudinal studies with several timepoints at which approach-avoidance behavior is assessed may alleviate this problem partially and also aid in the investigation of differences in current state such as feeling stressed. To answer the research question, based on the evidence presented in this thesis, I feel only

confident to judge specific phobias to be reliably measurable in approach-avoidance tasks to this date. For other interindividual differences, research efforts will have to be made into task design choices as well as other factors that differentiate the studies that had either significant findings or null findings. Evidence is further obfuscated by the fact that many tasks are only utilized in few studies, making it harder to evaluate those tasks.

RQ 1.2 *Which tasks are specifically sensitive to interindividual differences?*

As mentioned in the previous paragraph, the fact that most tasks appear to have been used in just a few studies makes evaluation within the systematic review rather difficult. For the experiments that were conducted for this thesis, the direct comparison in sensitivities based on self-report measures (behavioral activation and inhibition; trait anxiety, state/trait aggression, and depressive symptoms) appears to favor the AACT compared to the most commonly used tasks in approach-avoidance tendency assessment. While the joystick and manikin task did not correlate in expected ways with self-report measures, the AACT showed correlations (as detailed in the answer to RQ 1.1 above). Further, internal consistencies suggest that measures of the AACT are also far more reliable than those commonly used in joystick in manikin task. On the surface, the AACT thus appears favorable, especially since it has been pharmacologically validated with anxiolytics (e.g., Bach et al., 2018). However, the joystick and manikin task are more flexible in their task design, which may offer advantages depending on the research question. If experimenters were to create procedures in which stimuli are individualized based on imagery that is evaluated as especially rewarding or punishing for the participant, it may reduce measurement errors and allow for stronger associations with the interindividual differences of interest. For example, the stimulus sets used in Chapter 4 of this thesis contain both happy and angry faces of male and female actors. Which faces elicit strong tendencies of approach and avoidance, however, may be dependent on the participants prior experiences in life. Tasks can also be further adapted in a variety of other ways as, for example, discussed in Chapter 4. In conclusion, the AACT appears to be the most

sensitive task out of the three tasks investigated in Chapter 4 to assess interindividual differences, but this finding should not be considered set in stone by any means.

RQ 1.3 How do approach-avoidance tasks differ? Which best practices should be adopted as scientific standards?

In regard to how approach-avoidance tasks differ from one another, this thesis also cannot offer any definite assessment. While it is possible to descriptively compare the variety of tasks that were employed in the systematic literature review and the studies presented here and to theorize how they differ in their assessment of approach-avoidance behaviors, it was not feasible to compare them directly. During the planning of the study presented in Chapter 4, the factor analysis of task outcome measures from all three tasks had been intended, but was not realized. The decision to omit the factor analysis was made due to comparable approach-avoidance outcome measures in the joystick and manikin task not correlating with one another, leading to a low likelihood of measures converging on shared factors. While this may be due to both tasks measuring different aspects of approach-avoidance tendencies, namely once from one's own perspective and once taking the perspective of the manikin, the task designs were harmonized in a way that both tasks should have been similar enough to find at least some shared variance. Further, the outcome parameters of all three tasks were rarely influential in models aimed at explaining interindividual differences. A third reason was the inadequate Kaiser-Meyer-Olkin factor within our data (Kaiser, 1974). Similarly, due to the low reliability of outcome measures in the joystick and manikin tasks, best practice recommendations within the tasks seem difficult at this point. More standardized experimentation will be needed to figure out task configurations (e.g., task length, number of blocks, implicit vs. explicit designs) that are beneficial for the assessment of interindividual differences. One general recommendation one could give is to not only describe the experimental protocol with as much detail as possible, but to also report validity and reliability measures, if not make the data available online for those analyses.

5.1.2 Aim 2. Critical evaluation of the role of acute stress in approach-avoidance related behaviors.

RQ 2.1 *What is the specific role of the central stress mediators cortisol and noradrenaline in the balance of approach-avoidance behavior?* and RQ 2.2 *How do the acute stress mediators cortisol and noradrenaline moderate personality or sex-based differences of approach-avoidance behavior?*

Similar to Aim 1, the research questions of Aim 2 can also only be answered with some level of uncertainty. In the studies reviewed in Chapter 2, cortisol was mainly encountered as measure of overall stress, while there is little evidence found in the way of noradrenaline (usual measurements include heart-rate and blood pressure, which may be taken as proxy for the activity of the sympathetic nervous system). Curiously, there are relatively few studies in general explicitly investigating the influences of stress on approach-avoidance behaviors. Early studies show correlations between higher cortisol concentrations in primates (Sapolsky, 1990), rats (Cavigelli et al., 2007), and 6-month old infants (Buss et al., 2003) and increased avoidance behavior. It is therefore surprising that stress can have seemingly opposing effects in different studies of laboratory stress induction. For example, accelerated approach of angry faces under stress could be observed in psychogenic non-epileptic seizure patients, but not healthy controls (Bakvis et al., 2011), while avoidance of social threat stimuli was observed in social anxiety disorder patients, but not PTSD patients, i.e., patients suffering from posttraumatic stress, or healthy controls (Roelofs, van Peer, et al., 2009). Another study indicated that healthy participants that responded with a high cortisol response to a social stressor, displayed diminished approach and avoidance towards positive and negative stimuli respectively, therefore suggesting no increased avoidance behavior either (Roelofs et al., 2005). Administration of cortisol, however, led to increased avoidance of threatening stimuli in highly avoidant participants, but not in low avoidant participants (van Peer et al., 2007). In a correlational study, increased approach behavior and substance use were correlated at high levels of stress (Hinnant et al., 2017). Combined, these studies do not clearly indicate increased avoidance as a

result of stress, but rather different responses dependent on the investigated population and stimuli (for further studies of approach-avoidance behavior in experimental tasks, see the results section on laboratory stress in Chapter 2).

In Chapter 3, correlations and hierarchical regressions including personality traits, cortisol and noradrenaline as well as their interactions as variables did not show significant influences of cortisol and/or noradrenaline on approach-avoidance outcome measures. For this reason, during the investigation of gender and sex hormones, cortisol and noradrenaline were not included as factors. Due to the null findings presented here, research questions RQ 2.1 and RQ 2.2 cannot be answered with confidence. At this point, it appears that either the release of additional or other stress mediators or a subjective experience of stress need to be present to influence approach-avoidance tendencies consistently during task-based approach-avoidance behavior measurements.

5.2 CONCLUSION AND OUTLOOK

The work presented in this thesis demonstrates the complexity and the numerous open questions that are still present when considering how to measure approach-avoidance behaviors experimentally under standardized laboratory conditions, especially in the context of relating the behaviors to interindividual differences. Not only does the literature show ambiguity in most fields besides specific phobias, but the experiments were unable to establish robust correlations for most task/interindividual difference combinations aside from behavioral inhibition and aggression in the AACT (the latter also shown in Vogel & Schwabe, 2019). Given the growing interest in employing classical approach-avoidance tasks for cognitive bias modification (e.g., Asnaani et al., 2014; Bomyea et al., 2023; Schenkel et al., 2024; Sweet et al., 2021), it becomes imperative to study the nuanced dynamics of task-based approach-avoidance behaviors and their interplay with interindividual differences in more detail. This scrutiny is essential to ensure the reliability and efficacy of the intended interventions and markers of change.

Moving forward, it appears to me that the drawbacks and uncertainties presented here may outweigh the benefits of understanding these tasks better and adapting them to the point where interindividual differences can be assessed reliably. Instead, research efforts may be directed towards novel, more immersive ways of measurement. Virtual reality is one avenue in which the environment can elicit life-like responses of the participants (and also the according measures such as eye tracking, movements of separate body segments and rotations), while affording researchers precise control of the environments. Recent investigations in the realm of approach-avoidance behaviors in recent years underscore the potential of virtual reality in this regard (for example, see Biedermann et al., 2017; Kiser et al., 2022; Lange et al., 2022; Sporrer et al., 2023).

Approach-avoidance behaviors are among the most evolutionary conserved mechanisms and are relevant for the survival of almost all lifeforms. Despite their conceptual simplicity, i.e., approaching rewarding and avoiding punishing stimuli, measuring these behaviors in the laboratory can still be refined in the future. Advances in the field depend on the evaluation, whether currently prominent tasks have room to be improved meaningfully, and on utilizing novel tasks. By addressing the methodological challenges outlined in this thesis and embracing innovative approaches, researchers can contribute to a more nuanced and comprehensive understanding of approach-avoidance behaviors and their implications for human cognition, behavior and health.

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7 APPENDIX

7.1 SUPPLEMENT – CHAPTER 2

Task-based exclusion criteria. The following is a detailed description of our task-based exclusion criteria.

During our systematic search, we encountered papers that may be considered approach-avoidance related, but did not fit our definition of a behavioral approach-avoidance task. For example, tasks were required to have a tangible approach-avoidance conflict, thus hypothetical tasks in which a negative or positive outcome has to be imagined were not considered in our review. This also holds true for tasks with hypothetical questions asked about approach-avoidance towards a given scenario or stimulus. Tasks had to have a behavioral component, thus pure eye-tracking tasks and similar tasks were excluded. Further, we focused on behavioral results and not on neuroimaging outcomes of studies. The reason for this decision is that there were not enough reconcilable findings to make informed statements about the neurobiology underlying interindividual differences, partially due to the overall low amount of neuroimaging studies and additionally due to articles focusing on different and non-overlapping regions of interest. In a similar manner, articles using frontal asymmetry as outcome measure for behavioral approach-avoidance were not considered due to their low number and a continuous discussion among scholars about their explanatory power (Kuper et al., 2019). Lastly, there is an extensive body of research using approach-avoidance tasks for cognitive bias modification (CBM) trainings. Exploring the differences of CBM trainings was not considered to be an interindividual difference and therefore only articles that had a control group and a patient population with a native comparison of their approach-avoidance behaviors were considered for the review.

Table 7.1.1: Articles that fulfilled criteria but were not included in results section of the review

STUDY	TASK TYPE	INTERINDIVIDUAL DIFFERENCES EXPLORED
BACH, GUITART-MASIP ET AL., 2014	Other	Hippocampus lesions
BACH, KORN ET AL., 2018	Other	Administration of Valproate; Pregabalin
BAQUEDANO, VERGARA ET AL., 2017	Visual Joystick Task (im)	Subjective realism
BEADMAN, DAS ET AL., 2015	Manikin Task (ex)	Emotion Regulation
BERAHA, SALEMINK ET AL., 2018	Visual Joystick Task (im)	Administration of Baclofen
BERTSCH, KRAUCH ET AL., 2018	Visual Joystick Task (ex)	Borderline personality disorder
BERTSCH, ROELOFS ET AL., 2018	Visual Joystick Task (ex)	Borderline personality disorder
BOFFO, SMITS ET AL., 2018	Visual Joystick Task (im)	High risk gambling
BROCKMEYER, HAHN ET AL., 2015	Visual Joystick Task (im)	Trait and state food craving
CAPOZZA, DI BERNARDO ET AL., 2017	Manikin Task (ex)	Priming (humanization)
CAVALLET, CHAIM-AVANCINI ET AL., 2016	Manikin Task (im)	Attention deficit hyperactivity disorder
CHEVAL, AUDRIN ET AL., 2017	Manikin Task (ex)	Hunger and food wanting
CHEVAL, RADEL ET AL., 2016	Manikin Task (ex)	Homophobia
CHEVAL, SARRAZIN ET AL., 2014	Manikin Task (ex)	Non-exercise activity thermogenesis
CHRYSIKOU, GOREY ET AL., 2017	Other	Trait anxiety; Transcranial direct current stimulation
CLUDIUS, KULZ ET AL., 2017	Visual Joystick Task (im)	Obsessive compulsive disorder

DE LA ASUNCION, DOCX ET AL., 2015	Visual Joystick Task (ex)	Schizophrenia
DECKERS, ROELOFS ET AL., 2014	Visual Joystick Task (im)	Autism spectrum disorder
DEGNER, ESSIEN ET AL., 2016	Manikin Task (ex)	Ingroup/outgroup behavior
DI LEMMA, DICKSON ET AL., 2015	Manikin Task (ex)	Emotional Priming
DUBEY, ROPAR ET AL., 2018	Other	Autism traits (healthy participants)
ENTER, COLZATO ET AL., 2012	Visual Joystick Task (im)	Genetic variation (DAT gene polymorphism)
ERNST, LUTZ ET AL., 2013	Visual Joystick Task (ex)	Genetic variation (MAOA-L VS MAOA-H)
FLEURKENS, VAN MINNEN ET AL., 2018	Visual Joystick Task (im)	Genetic variation (5-HTTLPR polymorphism); Childhood trauma
GARCIA-SORIANO, ROSELL-CLARI ET AL., 2016	Other	Obsessive compulsive disorder
HOOFS, CARSTEN ET AL., 2018	Manikin Task (im)	Incentive type priming
JUERGENSEN AND LECKFOR, 2018	Visual Joystick Task (im)	Facebook addiction
KAKOSCHKE, KEMPS ET AL., 2015	Visual Joystick Task (im)	Food consumption
KAMPMANN, EMMELKAMP ET AL., 2018	Visual Joystick Task (im)	Exposure therapy
KOBELEVA, SEIDEL ET AL., 2014	Joystick Task (im)	Borderline personality disorder
KOOPMANN-HOLM AND TSAI, 2014	Visual Joystick Task (ex)	Cultural differences
KORN, VUNDER ET AL., 2017	Other	Amygdala lesions; administration of Lorazepam
KRIEGLMEYER AND DEUTSCH, 2013	Manikin Task (ex)	Goal motifs (affiliation, aggression)

KUYPERS, DE LA TORRE ET AL., 2018	Visual Joystick Task (im)	Administration of MDMA; Ketanserin
LANGE, SALEMINK ET AL., 2010	Visual Joystick Task (im)	Priming (modified stimulus interpretation)
LANSU, CILLESSEN ET AL., 2012	Visual Joystick Task (im)	Gender; Popularity
LINKE AND WESSA, 2017	Visual Joystick Task (im)	Mental imagery
LOMBARDO, ASHWIN ET AL., 2012	Other	Fetal testosterone
LY, HUYS ET AL., 2014	Other	Body freezing during task
MAAS, KEIJSERS ET AL., 2014	Visual Joystick Task (im)	Dieting
MAAS, KEIJSERS ET AL., 2017	Visual Joystick Task (im)	Habitual snacking
MATSUDA, OKANOYA ET AL., 2013	Other	Approach-tendencies; Fear-tendencies; Shyness
MAY, NOCK ET AL., 2018	Visual Joystick Task (im)	Physical exercise
MILLER, ZIELASKOWSKI ET AL., 2012	Joystick Task (ex)	Prejudice; Emotional priming
MOGG, BRADLEY ET AL., 2012	Manikin Task (ex)	Administration of D3 receptor antagonist
MULLER AND ROTHERMUND, 2017	Joystick Task (im)	Implicit motive and goal-pursuit
NAJMI, KUCKERTZ ET AL., 2010	Visual Joystick Task (im)	Obsessive compulsive disorder
NASRIN, RIMES ET AL., 2017	Visual Joystick Task (im)	Behavioral activation
NEO AND MCNAUGHTON, 2011	Other	Gender; Neuroticism
NORBURY, KURTH-NELSON ET AL., 2015	Other	D2 receptor antagonist; Sensation seeking
OLIVER AND KEMPS, 2018	Manikin Task (ex)	Incidental physical activity
PAPIES, BARSALOU ET AL., 2011	Visual Joystick Task (im)	Mindful attention

PIQUERAS-FISZMAN, KRAUS ET AL., 2014	Joystick Task (im)	Hunger
PITTIG, ALPERS ET AL., 2015	Other	State anxiety
RADKE, PFERSMANN ET AL., 2015	Joystick Task (im)	Schizophrenia
REDDY, GREEN ET AL., 2016	Visual Joystick Task (im)	Schizophrenia
RODRIGUEZ, SACK ET AL., 2018	Visual Joystick Task (ex)	Trait sexual excitation/inhibition; transcranial magnetic stimulation
SCHUCK, KEIJSERS ET AL., 2012	Visual Joystick Task (im)	Pathological skin picking
SILVA, DA FONSECA ET AL., 2015	Visual Joystick Task (im)	Autism spectrum disorder
SNAGOWSKI AND BRAND, 2015	Visual Joystick Task (ex)	Cybersex addiction
STAATS AND BURNS, 1982	Joystick Task (ex)	Trait religiousness
STARK, KRUSE ET AL., 2017	Visual Joystick Task (im)	Sexual motivation
TALLEY, FLEMING ET AL., 2018	Visual Joystick Task (im)	Sexual orientation self-concept ambiguity
THEWISSEN, HAVERMANS ET AL., 2007	Manikin Task (ex)	Conditioned smoking
TIPPLES, 2018	Joystick Task (ex)	Gender
VAN BEUGEN, MAAS ET AL., 2016	Visual Joystick Task (im)	Alopecia; Psoriasis
VAN CAUWENBERGE, SONUGA-BARKE ET AL., 2017	Other	Attention deficit hyperactivity disorder
VAN GUCHT, VANSTEENWEGEN ET AL., 2008	Manikin Task (ex)	Chocolate craving and extinction
WEIDACKER, KARGEL ET AL., 2018	Visual Joystick Task (ex)	Pedophilia

WIERS, RINCK ET AL., 2009	Visual Joystick Task (im)	Genetic variation (OPRM1)
ZHOU, LI ET AL., 2012	Visual Joystick Task (ex)	Heroin use
ZLOMUZICA, MACHULSKA ET AL., 2018	Visual Joystick Task (im)	Genetic variation (DRD2 Taq1B polymorphism)

Please note: im = implicit task version; ex = explicit task version; for an explanation of the different task types, please see Box 2 in Chapter 2

Table 7.1.2: Interindividual differences not addressed in results section in articles that fulfilled criteria and were included for a different individual difference in the results section of the review

STUDY	TASK TYPE	INTERINDIVIDUAL DIFFERENCES EXPLORED	INCLUDED IN PAPER FOR:
BIEDERMANN, BIEDERMANN ET AL., 2017	Other	Administration of Yohimbine; Lorazepam	Trait anxiety
COUSIJN, LUIJTEN ET AL., 2014	Visual Joystick Task (im)	Emotional priming	Substance use: Alcohol
DE CARLI, RIEM ET AL., 2017	Visual Joystick Task (im)	Emotional priming	Trauma
EFFTING, SALEMINK ET AL., 2016	Manikin Task (im)	Working memory capacity	Specific phobias
KOTYNSKI AND DEMAREE, 2017	Visual Joystick Task (im)	Focus training	Approach/Inhibition questionnaires
MACCALLUM, SAWDAY ET AL., 2015	Visual Joystick Task (im)	Emotional priming	Depression
PITTIG, SCHULZ ET AL., 2014	Other	State anxiety	Trait anxiety
SIMONS, MAISTO ET AL., 2016	Visual Joystick Task (ex)	Physical exercise	Substance use: Alcohol
SLEUWAEGEN, HULSTIJN ET AL., 2018	Visual Joystick Task (ex)	Emotional control	Approach/Inhibition questionnaires

TURNER, WITTEKIND ET AL., 2018	Visual Joystick Task (im)	Trait sexual excitation/inhibition (SES/SIS)	Approach/Inhibition questionnaires
VONCKEN, RINCK ET AL., 2012	Visual Joystick Task (im)	State anxiety	Trait anxiety

Please note: im = implicit task version; ex = explicit task version; for an explanation of the different task types, please see Box 2 in Chapter 2

7.2 SUPPLEMENT – CHAPTER 3

7.2.1 Detailed inclusion and exclusion criteria

Participants had to be between the ages of 18 and 35 years with normal or corrected-to-normal vision, normal body weight (body mass index: 18.5 to 26.5 kg/m²), a regular sleep-wake cycle, German as mother tongue or equivalent proficiency and naïve to both experimental tasks. Participant's health status was assessed in a standardized telephone screening prior to participation. Individuals were excluded if they had any physical, psychiatric, neurological, endocrine, cardiovascular or internal conditions, osteoporosis, asthma or glaucoma. Individuals were further excluded if they had been vaccinated within the last month, had used medication within the last month affecting stress reactivity or reported other events that potentially affected their stress response. Drinking more than 15 glasses of wine (or an equivalent alcohol consumption) per week as well as prior or past illicit drug use led to exclusion. An exception was made for cannabis use if at least 2 months in the past and with a frequency below once per month as well as the singular consumption of other illicit drugs more than 6 months ago without withdrawal symptoms. To keep hypothalamus-pituitary-adrenal (HPA) axis responsiveness comparable, smokers were excluded if they smoked more than five cigarettes a week (Rohleder & Kirschbaum, 2006). Similarly, pregnant or breastfeeding women as well as women on hormonal contraceptives within the last 3 months were excluded. Women additionally needed to have a regular menstrual cycle and were scheduled for the laboratory visit during their luteal phase in order to avoid effects of the menstrual cycle (Kirschbaum et al., 1999).

Participants were recruited via advertisement at our university as well as through an online recruitment platform and included both students and non-students. Two male participants were excluded from all analyses due to fulfilling exclusion criteria (determined in post-experiment conversation and initially not disclosed) and displaying non-compliance during the study, respectively, leading to a total sample size of $n = 94$ out of 96 initially recruited.

7.2.2 Vital sign measures and saliva sampling

Vital signs were measured with an automated wrist monitor (RS2, OMRON, the Netherlands). Each assessment was performed twice and mean values were used for analyses. Saliva was collected via Salivettes® (Sarstedt, Germany) to assess cortisol concentration and alpha amylase activity. In total, vital signs and saliva via Salivettes were collected five times throughout the experiment. In addition, native saliva was collected via microtubes with a straw for the assessment of testosterone and estrogen concentrations (directly after the first and fourth collection of saliva via Salivette). Collection time of native saliva varied based on the participants' ability to produce native saliva.

The saliva samples were frozen and stored at -18 °C (-0.4 °F) immediately after testing and later moved to a -80 °C (-112 °F) unit for long-term storage until shipping to Dresden Lab Service GmbH for analysis. After thawing, Salivettes were centrifuged at 3,000 rpm for 5 min, which resulted in a clear supernatant of low viscosity. Salivary cortisol concentrations were measured using commercially available chemiluminescence immunoassay with high sensitivity (IBL International, Hamburg, Germany). The intra- and interassay coefficients were below 4.3% and 5%, respectively. Activity of salivary alpha-amylase was measured by an enzyme kinetic method as described by Rohleder et al. (2006). The intra- and interassay coefficients were below 4.1% and 4.4%, respectively. Participants for which at least one sample did not contain sufficient saliva were excluded from analyses involving salivary cortisol (n=6; placebo: n=2, hydrocortisone: n=2, yohimbine: n=1, hydrocortisone and yohimbine: n=1) or salivary alpha-amylase (n=8; placebo: n=3, hydrocortisone: n=2, yohimbine: n=2, hydrocortisone and yohimbine: n=1), respectively.

The native saliva samples were similarly frozen and stored at -18 °C (-0.4 °F) immediately after testing and later moved to a -80 °C (-112 °F) unit for long-term storage until shipping to Dresden Lab Service GmbH for analysis. After thawing, samples were centrifuged at 12,000 rpm for 5 min and 200 µL supernatant injected into a liquid chromatography–tandem mass spectrometry system to determine

testosterone and estradiol concentrations as described in Gao et al. (2015). Intra-and inter-assay coefficients of variance were between 4.3% and 10.8%.

7.2.3 Detailed description of the approach-avoidance task and additional outcome parameters investigated

7.2.3.1 Approach-Avoidance conflict task (AACT)

To assess approach and avoidance behavior, we employed an adapted version of the AACT (programmed in Python 3.2.5 using Pygame 1.9.2; see Vogel & Schwabe, 2019), originally developed by Bach et al. (2014; see Figure 3.1). The task was inspired by anxiety research in rodents to investigate human behavior in approach-avoidance conflicts and induced behavioral inhibition and passive avoidance as shown before in analogue tasks in non-human animals (Bach et al., 2014; for a more general discussion on the use of non-human behavioral paradigms in psychiatric research, see for instance: Geyer & Markou, 1995; Shemesh & Chen, 2023) . Moreover, the task was pharmacologically validated using anxiolytics such that intake of lorazepam, valproate or pregabalin reduced anxious behavior in approach-avoidance conflicts (Bach et al., 2018; Korn et al., 2017).

The AACT is trial-based and played on a 24 x 16 grid presented on a standard computer monitor. The grid contained 1) a player-controlled green triangle, 2) 10 diamond-shaped yellow tokens of which one randomly changed location every two seconds (and a new token appeared in a random location if participants collected one), and 3) a predator (initially a grey circle) that could wake up during a trial to chase the player and was initially located in a randomly chosen corner opposite to 4) a black square, representing a safe space in which the player could not be caught by the predator. The green triangle was controlled with the arrow keys of a keyboard to a maximum speed of 8 blocks/s, whereas the predator was at minimum 2.5 times faster than the player at a constant 20 blocks/s. Therefore, escaping the awoken predator was only possible if participants were in the proximity of the safe place. Participants were instructed to collect as many tokens as possible without being caught by the

predator as random trials would be selected to determine additional monetary compensation.

Trials could differ on several accounts. Participants could start either in the safe place (50% of trials; passive avoidance to stay away from threat) or in the same location as the predator (active avoidance to escape the threat first and passive avoidance later). Threat level could be high (50% of trials; 60% chance for the predator to wake up) or low (20% chance), and was represented by the initial grid border color (orange or blue; color-threat level association was randomized over participants), but not explicitly instructed. The predator assumed the color of the border in case of wake-up, and the border turned red to clearly indicate the active threat. Trials without predator wake-up could last 6, 7.5, 9, 10.5, 12, 13.5, or 15 s. For trials with active predator, the predator woke up after the same durations and had to be avoided for 3.5 seconds. These trials ended either after 3.5 seconds or when the player was caught beforehand.

In total, participants played 160 trials, evenly divided into four blocks and separated by self-paced breaks, taking 42 minutes on average. The 50% split between the two threat levels and starting positions was maintained within each block as well as the distribution of trial durations. Due to a programming error, however, threat level and threat distance were not balanced in regard to each other. This led to task blocks in which there were missing combinations of threat level x threat distance x wake-up of threat for individual participants. After the AACT, participants were asked to estimate the wake-up probabilities for both predators.

7.2.3.2 Supplemental outcome parameters

Recently, Bach et al. (Bach et al., 2020) assessed test-retest reliability of AACT outcome variables over 11-32 months in 567 participants (aged 14-24 years). Several variables reached a sufficient test-retest coefficient of above 0.6: average number of tokens retained after predator wake-up (or end of trial if predator did not wake up; 0.689), average token collection (0.686), decrease in token collection over time in trial (0.771), average speed when on grid (0.681), and decrease in speed when on grid (0.608). Of

note, no interactions with threat level displayed sufficient test-retest reliability (all coefficients < 0.173). Given these findings, we included the remaining four of these five variables with high test-retest reliability (tokens retained was covered in our primary analyses) in additional analyses to enhance comparability with the work of Bach and colleagues. Finally, we also included mixed-design ANOVAs for six outcome variables over time-in-trial (e.g., time spent in safe space; speed; token collection rate; see Figure 7.2.2 and Table 7.2.1) to enhance comparability with previous findings (e.g., Bach et al., 2014; Bach et al., 2018; Korn et al., 2017).

7.2.4 Influence of time of recruitment on participant characteristics

Analysis: Given that recruitment was spread over a longer time period, which contained the onset of the Covid-19 pandemic, we explored whether our recruitment might be biased over time such that only certain individuals partook in our study as the pandemic progressed. To this end, we explored trait anxiety and sensation seeking scores over time of recruitment in linear regressions.

Results: Regarding changes in sample composition over time (experimental period: 11.11.2019 to 21.06.2021) as the pandemic developed and progressed, there was a slight increase in trait anxiety scores (adj. $R^2 = .04$, $F(1,92) = 4.72$, $p = .032$), while sensation seeking scores did not change (adj. $R^2 = -.01$, $F(1,92) = 0.08$, $p = .780$), suggesting that the covid-19 pandemic had no major effects on the type of participants who volunteered for our experiment (see Figure 7.2.1).

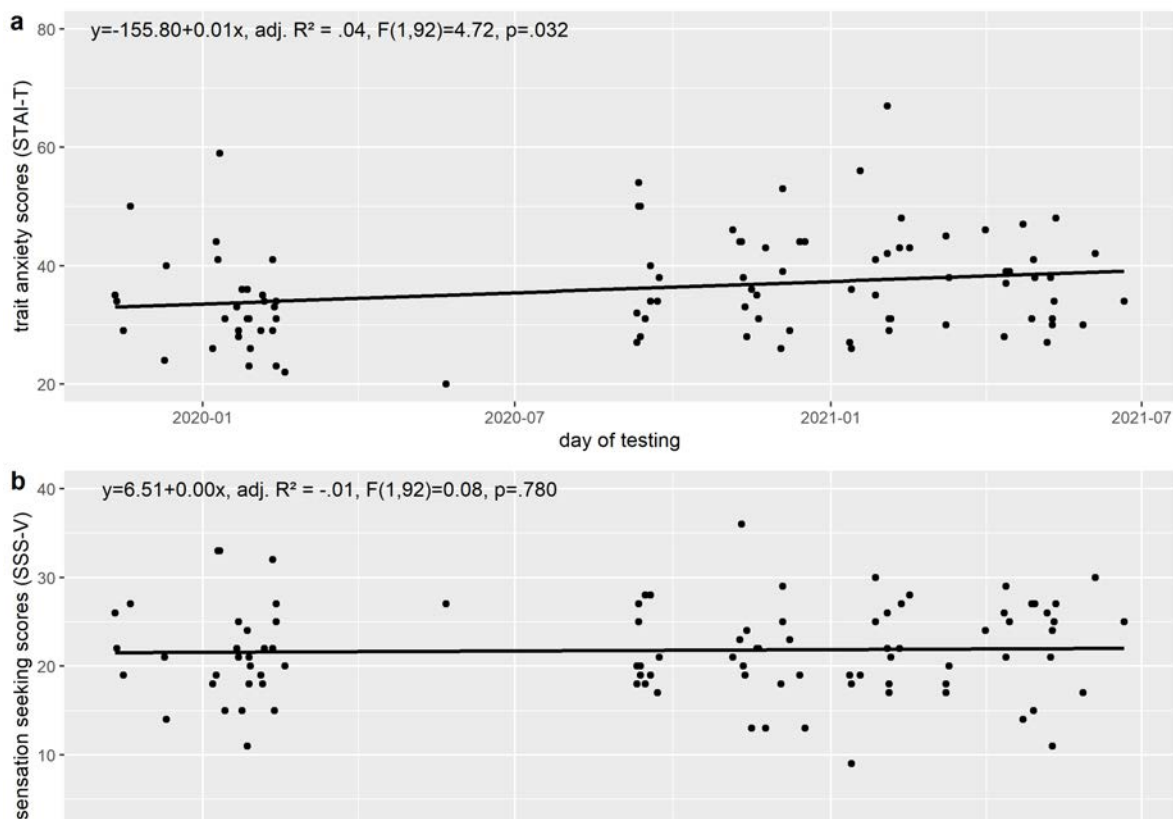


Fig 7.2.1. Trait anxiety scores (a) and sensation seeking scores (b) of participants over day of testing to see if participant population was influenced by covid-19 pandemic onset

7.2.5 Analyses and results of additional test-retest reliable parameters and time-over-trial parameters

Due to the rich possibilities in parameterization of the AACT, it is possible that relevant outcome parameters have been missed in our main analyses. Therefore, we investigate both additional test-retest reliable parameters and time-over-trial parameters in this section. For future research, it will be vital to understand which approach-avoidance task features index which cognitive component, are comparable with other tasks and potentially link with personality or psychiatric disorders. This would aid in the reconciliation of ambiguous findings in the current approach-avoidance literature and thus allow better understanding of underlying cognitive processes.

7.2.5.1 Test-retest reliable Parameters:

Analysis: For the parameters with high test-retest reliability identified above (decrease in token collection, decrease in speed, average speed, average token collection; Bach et al., 2020) – see section 7.2.3, we conducted mixed-design ANOVAs with the within-subject factor initial threat distance (long vs. short) and the between-subject factors hydrocortisone, yohimbine and gender. Bonferroni-Holm correction was applied for four outcome variables. Initial threat distance was included due to a recent study reporting the dependence of stress effects in task-based approach-avoidance to depend on it (Vogel & Schwabe, 2019).

We additionally carried out linear hierarchical regressions as described for the sum of tokens retained in the main text for the high test-retest reliable parameters aside from removing speed on grid as predictor, since two of the variables were directly related to speed during the AACT. In blockwise fashion, the following mean-centered variables were introduced: 1) The control variables gender, age, followed by 2) the interventions (hydrocortisone, yohimbine) as well as their interaction, 3) the

personality trait measures (trait anxiety by STAI-T total score (Laux et al., 1981), sensation seeking by SSSV total score (Beauducel et al., 2003) and aspects of trait aggression by four subscales of the DAF, namely physical aggression, verbal aggression, anger and mistrust (Werner & von Collani, 2014)), and finally 4) the interactions of personality trait measures with the interventions.

Results - Test-retest reliable parameters are not influenced by hydrocortisone or yohimbine: For the test-retest reliable parameters (aside retained tokens, which has been covered in the main text), ANOVAs focusing on the initial distance of threat due to the importance of threat distance for approach-avoidance behavior in recent studies (Fung et al., 2019; Vogel & Schwabe, 2019) were conducted. We found effects of gender as male participants collected more tokens on average (average token collection per 500ms: 0.37 vs. 0.303; $F(1,86) = 27.663$, $p < 0.001$, $\eta^2G = 0.238$) and kept a higher average speed compared to female participants (average speed per 500ms: 2.99 vs. 2.50; $F(1,86) = 40.702$, $p < 0.001$, $\eta^2G = 0.318$). Initial threat distance also mattered as starting in the immediate vicinity of the predator led to increases in both, average token collection (starting location: 0.348 vs. 0.323.; $F(1,86) = 122.806$, $p < 0.001$, $\eta^2G = 0.04$) and slope of the token collection (starting location: 0.0000167 vs. 0.0000121; $F(1,86) = 70.555$, $p < 0.001$, $\eta^2G = 0.066$). No significant effects were found for the slope of speed. However, yohimbine and hydrocortisone did not show any significant main effects or interactions for any of the four parameters.

Regarding the hierarchical regression models for the test-retest reliable parameters, none of the regression models including personality traits, intervention or their interactions performed better than their respective control models, indicating no advantage of adding those effects to the model.

7.2.5.2 Time-Over-Trial Parameters:

As seen in previous studies and to enhance comparability (e.g., Bach et al., 2014; Bach et al., 2018; Korn et al., 2017), we also included mixed-design ANOVAs for six outcome variables over time-in-trial. To analyze intervention effects on behavior over time-in-trial we used ANOVAs as described for our summary variables in the main text, and included the factor time-in-trial but omitted the factor block. Bonferroni-Holm correction was applied for six outcome variables. Figure 7.2.2 displays the trajectories of the averaged trials in each of the groups divided by starting close or far away from threat. Table 7.2.1 (placed at the end of section 7.2 due to its length) displays the results of the Over-Trial ANOVAs. Please note that these analyses revealed no or minimal effects of yohimbine and hydrocortisone on behavior over time-in-trial also.

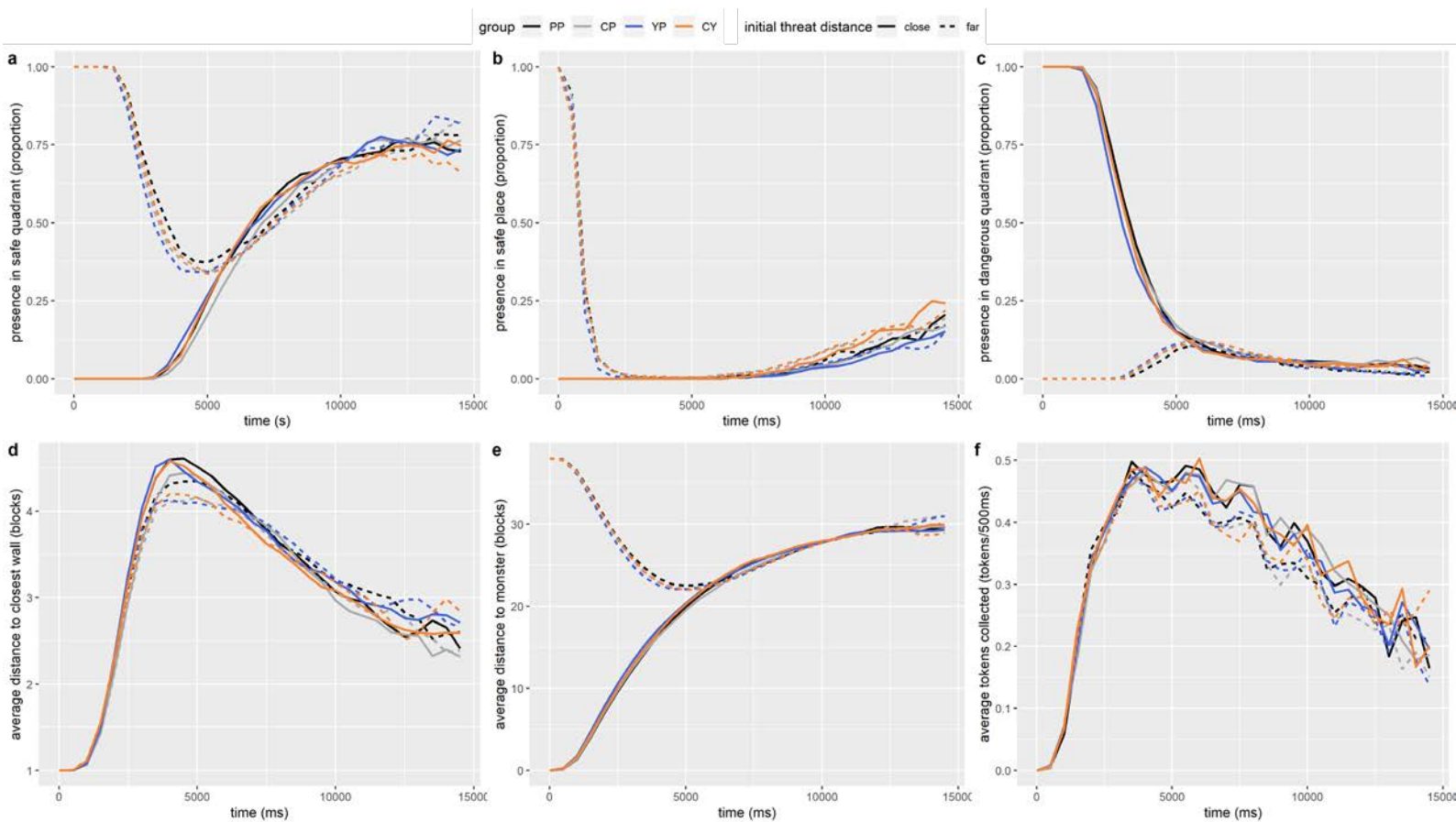


Fig 7.2.2. Averaged measurements over time in trial (each 500ms) for (a) presence in safe quadrant, (b) presence in safe place, (c) presence in dangerous quadrant, (d) average distance to closest wall, (e) average distance to predator and (f) average tokens collected, split according to initial threat distance. Groups: placebo (PP), hydrocortisone (CP), yohimbine (YP), hydrocortisone and yohimbine (CY)

7.2.6 Analyses and results regarding the influences of threat overestimation on summary outcome measures

In the results section Participants overestimate low threat condition in the approach-avoidance conflict task, we noted that women overestimated threat more than men (mean overestimation of wake-up probability 12.0% vs. 7.7%, $F_{1,86}=5.454$, $p=.022$, $\eta^2G=.019$, see Figure 7.2.3). As advised by a reviewer, it is interesting to exploratively investigate in how far threat overestimation predicts our summary outcome measures and if this is based on either gender or testosterone effects. To this end, we first correlated gender, testosterone, threat overestimation and our summary outcome variables (sum of collected tokens, average foraging latency, catch rate). The correlations can be found in Table 7.2.2. Average threat overestimation was moderately correlated to two outcome variables, such that individuals who overestimated threat more retained less tokens and were more inhibited (i.e. had longer foraging latencies).

We additionally carried out linear hierarchical regressions for all three summary variables, once with and once without gender and testosterone added as control variables. In blockwise fashion, the following mean-centered variables were introduced: 1) The control variables age and speed during the task and optionally gender and basal testosterone level, followed by 2) the individual overestimation of threat (averaged over high and low threat conditions). These regressions did not show any advantage of adding the average overestimation to the model independent of whether gender and testosterone were included or not. Further, speed during the task was the only significant predictor in all models. For readers that are interested in further analyses, we recommend exploring the data set as well as the accompanying analysis files available at <https://osf.io/d69pr/>.

Table 7.2.2. Correlations of threat overestimation, gender, testosterone level and outcome measures

	1	2	3	4	5	6	7	8
1. gender	-							
2. testosterone	.68**	-						
3. overestimation (average)	-.23*	-.23*	-					
4. overestimation (high-threat)	-.22*	-.09	.64**	-				
5. overestimation (low-threat)	-.03	-.18	.51**	-.33**	-			
6. sum of collected tokens	.58**	.50**	-.31**	-.09	.28**	-		
7. average foraging latency	.47**	.41**	.33**	.09	.30**	-.73**	-	
8. catch rate	-.13	-.09	-.03	-.01	-.03	-.10	.01	-

Note. Gender coding: woman = 0 and man = 1. * $p < .05$. ** $p < .01$.

Supplemental Figures

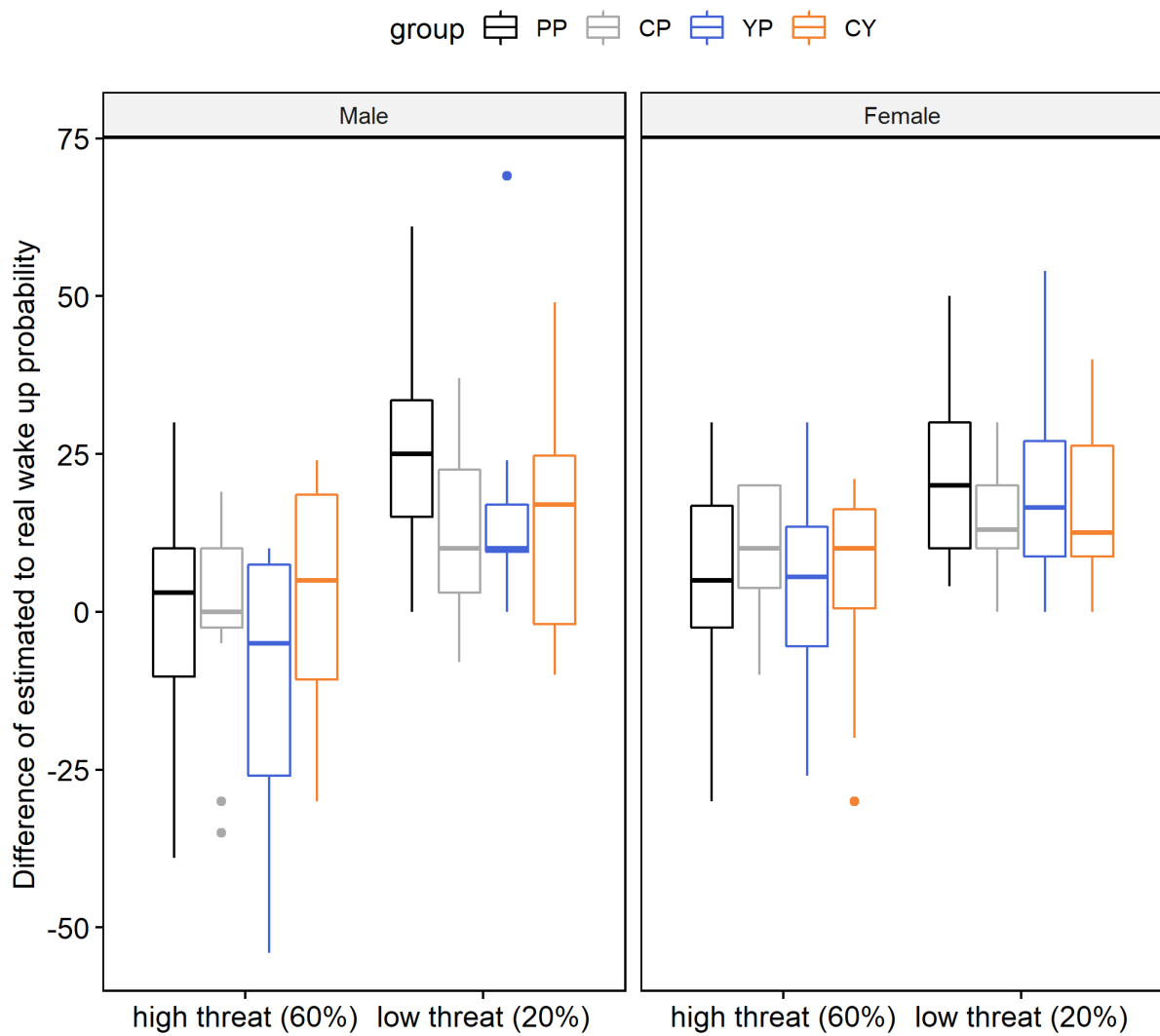


Fig 7.2.3. Differences in over-/underestimation of wake-up rates based on pharmacological intervention and gender. Groups: placebo (PP), hydrocortisone (CP), yohimbine (YP), hydrocortisone and yohimbine (CY)

Supplementary Tables

Table 7.2.3. Sample Characteristics

	PP (N=24)	CP (N=23)	YP (N=23)	CY (N=24)	F-value	p value
age					0.764	.517 ¹
Mean (SD)	25.42 (5.12)	24.78 (4.24)	23.57 (3.62)	24.25 (4.30)		
Lower CI (95%)	23.25	22.95	22.00	22.44		
Upper CI (95%)	27.58	26.62	25.13	26.06		
BMI					0.945	.423 ¹
Mean (SD)	23.05 (2.12)	22.59 (2.48)	22.38 (1.81)	22.07 (1.82)		
Lower CI (95%)	22.16	21.52	21.59	21.31		
Upper CI (95%)	23.95	23.66	23.16	22.84		
trait anxiety					0.651	.584 ¹
Mean (SD)	34.54 (7.19)	38.04 (9.10)	36.61 (10.22)	35.88 (8.40)		
Lower CI (95%)	31.51	34.11	32.19	32.33		
Upper CI (95%)	37.58	41.98	41.03	39.42		
physical aggression					0.468	.705 ¹
Mean (SD)	13.17 (3.60)	14.22 (3.91)	13.09 (3.13)	13.29 (4.04)		
Lower CI (95%)	11.65	12.53	11.73	11.59		
Upper CI (95%)	14.68	15.91	14.44	15.00		
verbal aggression					0.969	.411 ¹
Mean (SD)	10.04 (2.46)	10.96 (2.6)	11.35 (3.02)	10.79 (2.7)		
Lower CI (95%)	9.00	9.83	10.04	9.65		
Upper CI (95%)	11.08	12.08	12.66	11.93		
anger					0.104	.957 ¹
Mean (SD)	12.29 (3.61)	12.83 (3.83)	12.43 (3.42)	12.71 (3.85)		
Lower CI (95%)	10.77	11.17	10.95	11.08		
Upper CI (95%)	13.81	14.48	13.91	14.33		
mistrust					0.617	.606 ¹
Mean (SD)	13.08 (4.09)	14.30 (3.69)	14.26 (3.51)	13.54 (3.27)		
Lower CI (95%)	11.36	12.71	12.74	12.16		
Upper CI (95%)	14.81	15.90	15.78	14.92		
sensation seeking					1.496	.221 ¹
Mean (SD)	20.00 (6.34)	22.35 (5.22)	21.70 (4.91)	23.04 (4.11)		
Lower CI (95%)	17.32	20.09	19.57	21.31		

Upper CI (95%) 22.68 24.60 23.82 24.78

Note. Degrees of freedom are 3 and 90 for all tests. Groups: placebo (PP), hydrocortisone (CP), yohimbine (YP), hydrocortisone and yohimbine (CY). [†]Linear Model ANOVA.

Table 7.2.4. Characteristics of MDBF and VAS

	PP (N=24)	CP (N=23)	YP (N=23)	CY (N=24)
MDBF awake-tired 1				
Mean (CI)	16.333 (15.644, 17.023)	15.609 (14.576, 16.641)	15.739 (14.744, 16.734)	15.833 (14.736, 16.931)
MDBF awake-tired 2				
Mean (CI)	15.167 (14.091, 16.243)	15.348 (14.199, 16.496)	14.739 (13.586, 15.892)	14.458 (13.135, 15.782)
MDBF awake-tired 3				
Mean (CI)	13.875 (12.718, 15.032)	13.609 (12.294, 14.924)	13.348 (11.824, 14.872)	13.792 (12.232, 15.352)
MDBF calm-restless 1				
Mean (CI)	16.542 (15.697, 17.386)	15.870 (14.513, 17.226)	16.000 (14.709, 17.291)	15.917 (14.906, 16.928)
MDBF calm-restless 2				
Mean (CI)	16.292 (14.886, 17.698)	16.348 (14.910, 17.786)	14.261 (12.207, 16.315)	14.875 (13.222, 16.528)
MDBF calm-restless 3				
Mean (CI)	15.792 (14.242, 17.342)	14.913 (13.473, 16.353)	13.261 (11.393, 15.129)	13.208 (11.580, 14.837)
MDBF good-bad 1				
Mean (CI)	17.375 (16.479, 18.271)	16.652 (15.689, 17.616)	17.043 (16.108, 17.979)	17.000 (16.085, 17.915)
MDBF good-bad 2				
Mean (CI)	17.250 (16.422, 18.078)	16.783 (15.708, 17.857)	16.217 (14.826, 17.609)	16.083 (14.569, 17.598)
MDBF good-bad 3				
Mean (CI)	16.917 (16.011, 17.822)	16.652 (15.411, 17.893)	16.304 (14.891, 17.717)	16.125 (14.645, 17.605)
VAS anxious 1				
Mean (CI)	1.375 (1.102, 1.648)	1.826 (1.219, 2.433)	1.870 (1.312, 2.427)	1.458 (1.210, 1.707)
VAS anxious 2				
Mean (CI)	1.333 (1.095, 1.572)	1.304 (1.063, 1.546)	1.652 (1.046, 2.258)	1.417 (1.141, 1.693)
VAS anxious 3				
Mean (CI)	1.333 (1.012, 1.655)	1.304 (0.974, 1.635)	1.826 (1.005, 2.647)	1.417 (1.141, 1.693)
VAS upset 1				
Mean (CI)	2.708 (2.145, 3.272)	2.783 (2.144, 3.421)	3.000 (2.298, 3.702)	2.542 (2.060, 3.024)
VAS upset 2				
Mean (CI)	2.125 (1.592, 2.658)	1.783 (1.371, 2.194)	2.696 (1.690, 3.701)	2.208 (1.743, 2.674)
VAS upset 3				
Mean (CI)	1.875 (1.388, 2.362)	2.435 (1.772, 3.097)	2.739 (1.965, 3.513)	2.708 (1.916, 3.501)
VAS stressed 1				
Mean (CI)	1.792 (1.463, 2.121)	2.565 (1.763, 3.367)	2.043 (1.398, 2.689)	2.167 (1.500, 2.833)
VAS stressed 2				

Mean (CI)	1.792 (1.279, 2.305)	1.826 (1.192, 2.460)	2.304 (1.465, 3.144)	2.000 (1.472, 2.528)
VAS stressed 3				
Mean (CI)	2.000 (1.472, 2.528)	2.217 (1.730, 2.704)	2.696 (1.846, 3.545)	2.542 (1.618, 3.465)

Note. Average and 95% confidence interval of the Mehrdimensionaler Befindlichkeitsfragebogen (MDBF (Steyer et al., 1994)) and three visual analogue scales. Bonferroni-Holm corrected ANOVAs for 6 variables with the between-variables hydrocortisone and yohimbine and the within-variable time point (1: at the begin of the experiment, 2: 45 minutes after intake of medication, or 3: at end of experiment) did not show changes in mood based on pharmacological intervention. Across groups, MDBF awake-tired ($F(1.81, 162.82) = 28.428, p < .001, \eta^2G = .100$), MDBF calm-restless ($F(2, 180) = 13.319, p < .001, \eta^2G = .045$) and VAS upset ($F(2, 180) = 5.684, p = .016, \eta^2G = .023$) significantly varied over time points. Groups: placebo (PP), hydrocortisone (CP), yohimbine (YP), hydrocortisone and yohimbine (CY).

Table 7.2.1. Results of Over-Trial Outcome Variable ANOVAs

Effect	Outcome Variable	F-value with DF(n,d)	p	p<.05	p.a dj	p.a dj <.05 ges
hydrocortisone	tokens collected	F(1,84)=0	0.994		1.000	<0.01
hydrocortisone:threatlevel	tokens collected	F(1,84)=0.082	0.775		1.000	<0.01
hydrocortisone:threatdistance	tokens collected	F(1,84)=0.711	0.401		1.000	<0.01
hydrocortisone:threatdistance:threatlevel	tokens collected	F(1,84)=1.484	0.227		1.000	<0.01
hydrocortisone:gender	tokens collected	F(1,84)=0	0.992		1.000	<0.01
hydrocortisone:gender:threatlevel	tokens collected	F(1,84)=0.19	0.664		1.000	<0.01
hydrocortisone:gender:threatdistance	tokens collected	F(1,84)=0.187	0.667		1.000	<0.01
hydrocortisone:gender:threatdistance:threatlevel	tokens collected	F(1,84)=0.484	0.488		1.000	<0.01
hydrocortisone:gender:time	tokens collected	F(9.03,758.43)=0.385	0.943		1.000	0.001
hydrocortisone:gender:time:threatlevel	tokens collected	F(10.76,903.57)=1.413	0.163		0.978	0.003
hydrocortisone:gender:time:threatdistance	tokens collected	F(13.32,1118.94)=0.663	0.804		1.000	0.001
hydrocortisone:gender:time:threatdistance:threatlevel	tokens collected	F(13.18,1107.26)=0.583	0.871		1.000	0.001
hydrocortisone:time	tokens collected	F(9.03,758.43)=0.72	0.692		1.000	0.002
hydrocortisone:time:threatlevel	tokens collected	F(10.76,903.57)=1.228	0.264		0.792	0.003
hydrocortisone:time:threatdistance	tokens collected	F(13.32,1118.94)=1.483	0.114		0.684	0.003
hydrocortisone:time:threatdistance:threatlevel	tokens collected	F(13.18,1107.26)=0.788	0.676		1.000	0.001
hydrocortisone:yohimbine	tokens collected	F(1,84)=0.069	0.793		1.000	<0.01
hydrocortisone:yohimbine:threatlevel	tokens collected	F(1,84)=0.095	0.759		1.000	<0.01
hydrocortisone:yohimbine:threatdistance	tokens collected	F(1,84)=2.496	0.118		0.708	<0.01
hydrocortisone:yohimbine:threatdistance:threatlevel	tokens collected	F(1,84)=0.085	0.771		1.000	<0.01
hydrocortisone:yohimbine:gender	tokens collected	F(1,84)=0.609	0.437		1.000	0.002
hydrocortisone:yohimbine:gender:threatlevel	tokens collected	F(1,84)=3.574	0.062		0.372	0.001
hydrocortisone:yohimbine:gender:threatdistance	tokens collected	F(1,84)=2.188	0.143		0.715	<0.01
hydrocortisone:yohimbine:gender:threatdistance:threatlevel	tokens collected	F(1,84)=2.164	0.145		0.435	<0.01
hydrocortisone:yohimbine:gender:time	tokens collected	F(9.03,758.43)=1.276	0.246		1.000	0.004
hydrocortisone:yohimbine:gender:time:threatlevel	tokens collected	F(10.76,903.57)=0.494	0.905		1.000	0.001
hydrocortisone:yohimbine:gender:time:threatdistance	tokens collected	F(13.32,1118.94)=1.783	0.040 *		0.200	0.003
hydrocortisone:yohimbine:gender:time:threatdistance:threatlevel	tokens collected	F(13.18,1107.26)=1.167	0.298		0.894	0.002
hydrocortisone:yohimbine:time	tokens collected	F(9.03,758.43)=1.027	0.417		1.000	0.003
hydrocortisone:yohimbine:time:threatlevel	tokens collected	F(10.76,903.57)=1.38	0.179		1.000	0.003
hydrocortisone:yohimbine:time:threatdistance	tokens collected	F(13.32,1118.94)=1.485	0.114		0.342	0.003
hydrocortisone:yohimbine:time:threatdistance:threatlevel	tokens collected	F(13.18,1107.26)=0.955	0.495		1.000	0.002
threatlevel	tokens collected	F(1,84)=15.34	<0.01 *		0.001 *	0.003
threatdistance	tokens collected	F(1,84)=83.246	<0.01 *		<0.01 *	0.007
threatdistance:threatlevel	tokens collected	F(1,84)=1.556	0.216		0.432	<0.01
gender	tokens collected	F(1,84)=14.406	<0.01 *		0.002 *	0.036
gender:threatlevel	tokens collected	F(1,84)=0.639	0.426		1.000	<0.01

gender:threatdistance	tokens collected	F(1,84)=2.161	0.145	0.435	<0.01
gender:threatdistance:threatlevel	tokens collected	F(1,84)=1.1	0.297	1.000	<0.01
gender:time	tokens collected	F(9.03,758.43)=6.18	<0.01 *	<0.01 *	0.018
gender:time:threatlevel	tokens collected	F(10.76,903.57)=0.708	0.729	1.000	0.001
gender:time:threatdistance	tokens collected	F(13.32,1118.94)=1.137	0.322	0.322	0.002
gender:time:threatdistance:threatlevel	tokens collected	F(13.18,1107.26)=1.547	0.093	0.558	0.003
time	tokens collected	F(9.03,758.43)=289.839	<0.01 *	<0.01 *	0.469
time:threatlevel	tokens collected	F(10.76,903.57)=1.43	0.156	0.156	0.003
time:threatdistance	tokens collected	F(13.32,1118.94)=3.417	<0.01 *	<0.01 *	0.006
time:threatdistance:threatlevel	tokens collected	F(13.18,1107.26)=1.284	0.215	0.860	0.002
yohimbine	tokens collected	F(1,84)=0.007	0.932	1.000	<0.01
yohimbine:threatlevel	tokens collected	F(1,84)=0.486	0.488	0.976	<0.01
yohimbine:threatdistance	tokens collected	F(1,84)=0.144	0.705	1.000	<0.01
yohimbine:threatdistance:threatlevel	tokens collected	F(1,84)=1.659	0.201	0.804	<0.01
yohimbine:gender	tokens collected	F(1,84)=1.946	0.167	1.000	0.005
yohimbine:gender:threatlevel	tokens collected	F(1,84)=0	0.982	1.000	<0.01
yohimbine:gender:threatdistance	tokens collected	F(1,84)=6.815	0.011 *	0.066	0.001
yohimbine:gender:threatdistance:threatlevel	tokens collected	F(1,84)=2.038	0.157	0.942	<0.01
yohimbine:gender:time	tokens collected	F(9.03,758.43)=0.758	0.656	1.000	0.002
yohimbine:gender:time:threatlevel	tokens collected	F(10.76,903.57)=2.254	0.011 *	0.066	0.005
yohimbine:gender:time:threatdistance	tokens collected	F(13.32,1118.94)=1.257	0.231	0.924	0.002
yohimbine:gender:time:threatdistance:threatlevel	tokens collected	F(13.18,1107.26)=0.987	0.462	1.000	0.002
yohimbine:time	tokens collected	F(9.03,758.43)=0.786	0.630	1.000	0.002
yohimbine:time:threatlevel	tokens collected	F(10.76,903.57)=0.527	0.883	1.000	0.001
yohimbine:time:threatdistance	tokens collected	F(13.32,1118.94)=0.623	0.840	1.000	0.001
yohimbine:time:threatdistance:threatlevel	tokens collected	F(13.18,1107.26)=1.39	0.156	0.624	0.003
hydrocortisone	distance to monster	F(1,84)=0.006	0.939	1.000	<0.01
hydrocortisone:threatlevel	distance to monster	F(1,84)=0.155	0.695	1.000	<0.01
hydrocortisone:threatdistance	distance to monster	F(1,84)=0.006	0.940	1.000	<0.01
hydrocortisone:threatdistance:threatlevel	distance to monster	F(1,84)=0.167	0.683	1.000	<0.01
hydrocortisone:gender	distance to monster	F(1,84)=0.068	0.795	1.000	<0.01
hydrocortisone:gender:threatlevel	distance to monster	F(1,84)=0.071	0.790	1.000	<0.01
hydrocortisone:gender:threatdistance	distance to monster	F(1,84)=0.656	0.420	1.000	0.001
hydrocortisone:gender:threatdistance:threatlevel	distance to monster	F(1,84)=0.009	0.925	1.000	<0.01
hydrocortisone:gender:time	distance to monster	F(2.15,180.71)=0.076	0.937	1.000	<0.01
hydrocortisone:gender:time:threatlevel	distance to monster	F(3.51,295)=0.66	0.601	1.000	<0.01
hydrocortisone:gender:time:threatdistance	distance to monster	F(2.99,251.25)=0.359	0.782	1.000	0.001
hydrocortisone:gender:time:threatdistance:threatlevel	distance to monster	F(4.07,341.87)=0.632	0.643	1.000	<0.01
hydrocortisone:time	distance to monster	F(2.15,180.71)=0.109	0.909	1.000	<0.01
hydrocortisone:time:threatlevel	distance to monster	F(3.51,295)=2.336	0.064	0.320	0.002
hydrocortisone:time:threatdistance	distance to monster	F(2.99,251.25)=0.485	0.692	1.000	0.001

hydrocortisone:time:threatdistance:threatlevel	distance to monster	F(4.07,341.87)=0.797	0.530	1.000	<0.01
hydrocortisone:yohimbine	distance to monster	F(1,84)=0.002	0.965	1.000	<0.01
hydrocortisone:yohimbine:threatlevel	distance to monster	F(1,84)=0.832	0.364	1.000	<0.01
hydrocortisone:yohimbine:threatdistance	distance to monster	F(1,84)=0.032	0.858	1.000	<0.01
hydrocortisone:yohimbine:threatdistance:threatlevel	distance to monster	F(1,84)=0.295	0.589	1.000	<0.01
hydrocortisone:yohimbine:gender	distance to monster	F(1,84)=0.704	0.404	1.000	0.003
hydrocortisone:yohimbine:gender:threatlevel	distance to monster	F(1,84)=0.341	0.561	1.000	<0.01
hydrocortisone:yohimbine:gender:threatdistance	distance to monster	F(1,84)=1.636	0.204	0.715	0.002
hydrocortisone:yohimbine:gender:threatdistance:threatlevel	distance to monster	F(1,84)=11.628	0.001 *	0.006 *	0.001
hydrocortisone:yohimbine:gender:time	distance to monster	F(2.15,180.71)=1.008	0.372	1.000	0.003
hydrocortisone:yohimbine:gender:time:threatlevel	distance to monster	F(3.51,295)=1.198	0.312	1.000	0.001
hydrocortisone:yohimbine:gender:time:threatdistance	distance to monster	F(2.99,251.25)=1.057	0.368	1.000	0.002
hydrocortisone:yohimbine:gender:time:threatdistance:threatlevel	distance to monster	F(4.07,341.87)=2.252	0.062	0.310	0.001
hydrocortisone:yohimbine:time	distance to monster	F(2.15,180.71)=0.545	0.594	1.000	0.002
hydrocortisone:yohimbine:time:threatlevel	distance to monster	F(3.51,295)=0.812	0.505	1.000	0.001
hydrocortisone:yohimbine:time:threatdistance	distance to monster	F(2.99,251.25)=2.538	0.057	0.228	0.004
hydrocortisone:yohimbine:time:threatdistance:threatlevel	distance to monster	F(4.07,341.87)=0.99	0.414	1.000	0.001
threatlevel	distance to monster	F(1,84)=23.495	<0.01 *	<0.01 *	0.010
threatdistance	distance to monster	F(1,84)=1292.128	<0.01 *	<0.01 *	0.590
threatdistance:threatlevel	distance to monster	F(1,84)=7.783	0.007 *	0.036 *	0.001
gender	distance to monster	F(1,84)=0.002	0.964	1.000	<0.01
gender:threatlevel	distance to monster	F(1,84)=0.088	0.767	1.000	<0.01
gender:threatdistance	distance to monster	F(1,84)=5.553	0.021 *	0.126	0.006
gender:threatdistance:threatlevel	distance to monster	F(1,84)=0.017	0.898	1.000	<0.01
gender:time	distance to monster	F(2.15,180.71)=0.587	0.569	0.569	0.002
gender:time:threatlevel	distance to monster	F(3.51,295)=1.666	0.166	0.996	0.001
gender:time:threatdistance	distance to monster	F(2.99,251.25)=9.935	<0.01 *	<0.01 *	0.015
gender:time:threatdistance:threatlevel	distance to monster	F(4.07,341.87)=0.32	0.868	1.000	<0.01
time	distance to monster	F(2.15,180.71)=654.125	<0.01 *	<0.01 *	0.667
time:threatlevel	distance to monster	F(3.51,295)=6.17	<0.01 *	0.001 *	0.004
time:threatdistance	distance to monster	F(2.99,251.25)=2898.044	<0.01 *	<0.01 *	0.813
time:threatdistance:threatlevel	distance to monster	F(4.07,341.87)=1.221	0.302	0.906	0.001
yohimbine	distance to monster	F(1,84)=0.046	0.831	1.000	<0.01
yohimbine:threatlevel	distance to monster	F(1,84)=3.345	0.071	0.408	0.001
yohimbine:threatdistance	distance to monster	F(1,84)=1.504	0.223	1.000	0.002
yohimbine:threatdistance:threatlevel	distance to monster	F(1,84)=2.664	0.106	0.530	<0.01
yohimbine:gender	distance to monster	F(1,84)=0.049	0.825	1.000	<0.01
yohimbine:gender:threatlevel	distance to monster	F(1,84)=0.009	0.926	1.000	<0.01
yohimbine:gender:threatdistance	distance to monster	F(1,84)=0.015	0.901	1.000	<0.01
yohimbine:gender:threatdistance:threatlevel	distance to monster	F(1,84)=0.013	0.908	1.000	<0.01
yohimbine:gender:time	distance to monster	F(2.15,180.71)=0.423	0.671	1.000	0.001

yohimbine:gender:time:threatlevel	distance to monster	F(3,51,295)=1.167	0.324	1.000	0.001
yohimbine:gender:time:threatdistance	distance to monster	F(2,99,251.25)=0.312	0.816	1.000	<0.001
yohimbine:gender:time:threatdistance:threatlevel	distance to monster	F(4,07,341.87)=0.384	0.823	1.000	<0.001
yohimbine:time	distance to monster	F(2,15,180.71)=0.294	0.762	1.000	0.001
yohimbine:time:threatlevel	distance to monster	F(3,51,295)=1.217	0.304	1.000	0.001
yohimbine:time:threatdistance	distance to monster	F(2,99,251.25)=0.733	0.533	1.000	0.001
yohimbine:time:threatdistance:threatlevel	distance to monster	F(4,07,341.87)=1.943	0.102	0.612	0.001
hydrocortisone	distance to closest wall	F(1,84)=1.813	0.182	1.000	0.006
hydrocortisone:threatlevel	distance to closest wall	F(1,84)=1.124	0.292	1.000	<0.001
hydrocortisone:threatdistance	distance to closest wall	F(1,84)=0.161	0.689	1.000	<0.001
hydrocortisone:threatdistance:threatlevel	distance to closest wall	F(1,84)=0.009	0.923	1.000	<0.001
hydrocortisone:gender	distance to closest wall	F(1,84)=0.028	0.867	1.000	<0.001
hydrocortisone:gender:threatlevel	distance to closest wall	F(1,84)=1.076	0.302	1.000	<0.001
hydrocortisone:gender:threatdistance	distance to closest wall	F(1,84)=0.603	0.439	1.000	<0.001
hydrocortisone:gender:threatdistance:threatlevel	distance to closest wall	F(1,84)=0.1	0.752	1.000	<0.001
hydrocortisone:gender:time	distance to closest wall	F(3,27,274.36)=0.173	0.927	1.000	0.001
hydrocortisone:gender:time:threatlevel	distance to closest wall	F(5,47,459.21)=0.902	0.486	1.000	0.001
hydrocortisone:gender:time:threatdistance	distance to closest wall	F(6,503.67)=0.601	0.729	1.000	0.001
hydrocortisone:gender:time:threatdistance:threatlevel	distance to closest wall	F(7,16,601.72)=1.703	0.104	0.624	0.002
hydrocortisone:time	distance to closest wall	F(3,27,274.36)=0.396	0.773	1.000	0.002
hydrocortisone:time:threatlevel	distance to closest wall	F(5,47,459.21)=0.574	0.735	1.000	0.001
hydrocortisone:time:threatdistance	distance to closest wall	F(6,503.67)=0.981	0.437	1.000	0.001
hydrocortisone:time:threatdistance:threatlevel	distance to closest wall	F(7,16,601.72)=0.955	0.465	1.000	0.001
hydrocortisone:yohimbine	distance to closest wall	F(1,84)=0.057	0.811	1.000	<0.001
hydrocortisone:yohimbine:threatlevel	distance to closest wall	F(1,84)=0.104	0.748	1.000	<0.001
hydrocortisone:yohimbine:threatdistance	distance to closest wall	F(1,84)=0.57	0.453	1.000	<0.001
hydrocortisone:yohimbine:threatdistance:threatlevel	distance to closest wall	F(1,84)=6.655	0.012 *	0.072	0.001
hydrocortisone:yohimbine:gender	distance to closest wall	F(1,84)=0.713	0.401	1.000	0.002
hydrocortisone:yohimbine:gender:threatlevel	distance to closest wall	F(1,84)=3.522	0.064	0.372	0.001
hydrocortisone:yohimbine:gender:threatdistance	distance to closest wall	F(1,84)=0.16	0.690	0.715	<0.001
hydrocortisone:yohimbine:gender:threatdistance:threatlevel	distance to closest wall	F(1,84)=0.644	0.425	0.850	<0.001
hydrocortisone:yohimbine:gender:time	distance to closest wall	F(3,27,274.36)=1.269	0.285	1.000	0.005
hydrocortisone:yohimbine:gender:time:threatlevel	distance to closest wall	F(5,47,459.21)=0.911	0.480	1.000	0.001
hydrocortisone:yohimbine:gender:time:threatdistance	distance to closest wall	F(6,503.67)=1.097	0.363	1.000	0.001
hydrocortisone:yohimbine:gender:time:threatdistance:threatlevel	distance to closest wall	F(7,16,601.72)=2.022	0.049 *	0.294	0.002
hydrocortisone:yohimbine:time	distance to closest wall	F(3,27,274.36)=0.503	0.696	1.000	0.002
hydrocortisone:yohimbine:time:threatlevel	distance to closest wall	F(5,47,459.21)=0.477	0.809	1.000	0.001
hydrocortisone:yohimbine:time:threatdistance	distance to closest wall	F(6,503.67)=0.603	0.728	0.728	0.001
hydrocortisone:yohimbine:time:threatdistance:threatlevel	distance to closest wall	F(7,16,601.72)=0.949	0.469	1.000	0.001
threatlevel	distance to closest wall	F(1,84)=19.337	<0.001 *	<0.001 *	0.008
threatdistance	distance to closest wall	F(1,84)=0.467	0.496	0.496	<0.001

threatdistance:threatlevel	distance to closest wall	F(1,84)=6.13	0.015 *	0.060	0.001
gender	distance to closest wall	F(1,84)=3.839	0.053	0.265	0.013
gender:threatlevel	distance to closest wall	F(1,84)=1.96	0.165	0.990	0.001
gender:threatdistance	distance to closest wall	F(1,84)=0.871	0.353	0.435	<0.01
gender:threatdistance:threatlevel	distance to closest wall	F(1,84)=0.087	0.768	1.000	<0.01
gender:time	distance to closest wall	F(3.27,274.36)=4.696	0.002 *	0.006 *	0.019
gender:time:threatlevel	distance to closest wall	F(5.47,459.21)=0.731	0.612	1.000	0.001
gender:time:threatdistance	distance to closest wall	F(6,503.67)=2.124	0.049 *	0.098	0.003
gender:time:threatdistance:threatlevel	distance to closest wall	F(7.16,601.72)=0.773	0.613	1.000	0.001
time	distance to closest wall	F(3.27,274.36)=508.708	<0.01 *	<0.01 *	0.674
time:threatlevel	distance to closest wall	F(5.47,459.21)=4.439	<0.01 *	0.001 *	0.006
time:threatdistance	distance to closest wall	F(6,503.67)=8.008	<0.01 *	<0.01 *	0.010
time:threatdistance:threatlevel	distance to closest wall	F(7.16,601.72)=0.715	0.662	1.000	0.001
yohimbine	distance to closest wall	F(1,84)=0.06	0.808	1.000	<0.01
yohimbine:threatlevel	distance to closest wall	F(1,84)=3.418	0.068	0.408	0.001
yohimbine:threatdistance	distance to closest wall	F(1,84)=0.245	0.622	1.000	<0.01
yohimbine:threatdistance:threatlevel	distance to closest wall	F(1,84)=0.008	0.929	1.000	<0.01
yohimbine:gender	distance to closest wall	F(1,84)=0.611	0.437	1.000	0.002
yohimbine:gender:threatlevel	distance to closest wall	F(1,84)=0.001	0.979	1.000	<0.01
yohimbine:gender:threatdistance	distance to closest wall	F(1,84)=5.699	0.019 *	0.095	0.001
yohimbine:gender:threatdistance:threatlevel	distance to closest wall	F(1,84)=0.414	0.522	1.000	<0.01
yohimbine:gender:time	distance to closest wall	F(3.27,274.36)=0.447	0.736	1.000	0.002
yohimbine:gender:time:threatlevel	distance to closest wall	F(5.47,459.21)=0.494	0.797	1.000	0.001
yohimbine:gender:time:threatdistance	distance to closest wall	F(6,503.67)=1.645	0.133	0.665	0.002
yohimbine:gender:time:threatdistance:threatlevel	distance to closest wall	F(7.16,601.72)=0.583	0.774	1.000	0.001
yohimbine:time	distance to closest wall	F(3.27,274.36)=1.486	0.216	1.000	0.006
yohimbine:time:threatlevel	distance to closest wall	F(5.47,459.21)=0.986	0.430	1.000	0.001
yohimbine:time:threatdistance	distance to closest wall	F(6,503.67)=1.252	0.278	1.000	0.002
yohimbine:time:threatdistance:threatlevel	distance to closest wall	F(7.16,601.72)=1.704	0.103	0.612	0.002
hydrocortisone	presence in dangerous quadrant	F(1,84)=0.572	0.452	1.000	0.001
hydrocortisone:threatlevel	presence in dangerous quadrant	F(1,84)=0.045	0.833	1.000	<0.01
hydrocortisone:threatdistance	presence in dangerous quadrant	F(1,84)=0.026	0.873	1.000	<0.01
hydrocortisone:threatdistance:threatlevel	presence in dangerous quadrant	F(1,84)=0.086	0.770	1.000	<0.01
hydrocortisone:gender	presence in dangerous quadrant	F(1,84)=0.877	0.352	1.000	0.002
hydrocortisone:gender:threatlevel	presence in dangerous quadrant	F(1,84)=1.289	0.260	1.000	<0.01
hydrocortisone:gender:threatdistance	presence in dangerous quadrant	F(1,84)=0.409	0.524	1.000	0.001
hydrocortisone:gender:threatdistance:threatlevel	presence in dangerous quadrant	F(1,84)=0.014	0.906	1.000	<0.01
hydrocortisone:gender:time	presence in dangerous quadrant	F(29,2436)=0.622	0.943	1.000	0.002
hydrocortisone:gender:time:threatlevel	presence in dangerous quadrant	F(29,2436)=0.75	0.830	1.000	0.001
hydrocortisone:gender:time:threatdistance	presence in dangerous quadrant	F(29,2436)=0.398	0.998	1.000	0.001
hydrocortisone:gender:time:threatdistance:threatlevel	presence in dangerous quadrant	F(29,2436)=0.611	0.949	1.000	0.001

hydrocortisone:time	presence in dangerous quadrant	F(29,2436)=0.347	1.000	1.000	0.001
hydrocortisone:time:threatlevel	presence in dangerous quadrant	F(29,2436)=1.279	0.146	0.584	0.001
hydrocortisone:time:threatdistance	presence in dangerous quadrant	F(29,2436)=0.272	1.000	1.000	0.001
hydrocortisone:time:threatdistance:threatlevel	presence in dangerous quadrant	F(29,2436)=0.836	0.715	1.000	0.001
hydrocortisone:yohimbine	presence in dangerous quadrant	F(1,84)=0.138	0.711	1.000	<0.001
hydrocortisone:yohimbine:threatlevel	presence in dangerous quadrant	F(1,84)=0.677	0.413	1.000	<0.001
hydrocortisone:yohimbine:threatdistance	presence in dangerous quadrant	F(1,84)=0.104	0.748	1.000	<0.001
hydrocortisone:yohimbine:threatdistance:threatlevel	presence in dangerous quadrant	F(1,84)=0.567	0.453	1.000	<0.001
hydrocortisone:yohimbine:gender	presence in dangerous quadrant	F(1,84)=0.401	0.528	1.000	0.001
hydrocortisone:yohimbine:gender:threatlevel	presence in dangerous quadrant	F(1,84)=1.099	0.297	1.000	<0.001
hydrocortisone:yohimbine:gender:threatdistance	presence in dangerous quadrant	F(1,84)=1.479	0.227	0.715	0.002
hydrocortisone:yohimbine:gender:threatdistance:threatlevel	presence in dangerous quadrant	F(1,84)=6.866	0.010 *	0.040 *	0.001
hydrocortisone:yohimbine:gender:time	presence in dangerous quadrant	F(29,2436)=0.774	0.800	1.000	0.002
hydrocortisone:yohimbine:gender:time:threatlevel	presence in dangerous quadrant	F(29,2436)=0.744	0.837	1.000	0.001
hydrocortisone:yohimbine:gender:time:threatdistance	presence in dangerous quadrant	F(29,2436)=0.41	0.998	1.000	0.001
hydrocortisone:yohimbine:gender:time:threatdistance:threatlevel	presence in dangerous quadrant	F(29,2436)=0.979	0.497	0.994	0.001
hydrocortisone:yohimbine:time	presence in dangerous quadrant	F(29,2436)=0.952	0.538	1.000	0.003
hydrocortisone:yohimbine:time:threatlevel	presence in dangerous quadrant	F(29,2436)=0.988	0.483	1.000	0.001
hydrocortisone:yohimbine:time:threatdistance	presence in dangerous quadrant	F(29,2436)=1.526	0.036 *	0.180	0.004
hydrocortisone:yohimbine:time:threatdistance:threatlevel	presence in dangerous quadrant	F(29,2436)=1.095	0.332	1.000	0.001
threatlevel	presence in dangerous quadrant	F(1,84)=1.592	0.210	0.210	<0.001
threatdistance	presence in dangerous quadrant	F(1,84)=1590.282	<0.001 *	<0.001 *	0.708
threatdistance:threatlevel	presence in dangerous quadrant	F(1,84)=0.422	0.518	0.518	<0.001
gender	presence in dangerous quadrant	F(1,84)=0.963	0.329	1.000	0.002
gender:threatlevel	presence in dangerous quadrant	F(1,84)=0.837	0.363	1.000	<0.001
gender:threatdistance	presence in dangerous quadrant	F(1,84)=3.439	0.067	0.268	0.005
gender:threatdistance:threatlevel	presence in dangerous quadrant	F(1,84)=1.617	0.207	1.000	<0.001
gender:time	presence in dangerous quadrant	F(29,2436)=2.581	<0.001 *	<0.001 *	0.007
gender:time:threatlevel	presence in dangerous quadrant	F(29,2436)=0.957	0.532	1.000	0.001
gender:time:threatdistance	presence in dangerous quadrant	F(29,2436)=5.888	<0.001 *	<0.001 *	0.016
gender:time:threatdistance:threatlevel	presence in dangerous quadrant	F(29,2436)=0.933	0.569	1.000	0.001
time	presence in dangerous quadrant	F(29,2436)=1650.631	<0.001 *	<0.001 *	0.827
time:threatlevel	presence in dangerous quadrant	F(29,2436)=1.552	0.030 *	0.060	0.002
time:threatdistance	presence in dangerous quadrant	F(29,2436)=2245.217	<0.001 *	<0.001 *	0.860
time:threatdistance:threatlevel	presence in dangerous quadrant	F(29,2436)=1.377	0.087	0.435	0.001
yohimbine	presence in dangerous quadrant	F(1,84)=0.499	0.482	1.000	0.001
yohimbine:threatlevel	presence in dangerous quadrant	F(1,84)=2.638	0.108	0.432	0.001
yohimbine:threatdistance	presence in dangerous quadrant	F(1,84)=2.72	0.103	0.618	0.004
yohimbine:threatdistance:threatlevel	presence in dangerous quadrant	F(1,84)=4.338	0.040 *	0.240	0.001
yohimbine:gender	presence in dangerous quadrant	F(1,84)=0.902	0.345	1.000	0.002

yohimbine:gender:threatlevel	presence in dangerous quadrant	F(1,84)=1.047	0.309	1.000	<0.01
yohimbine:gender:threatdistance	presence in dangerous quadrant	F(1,84)=0.002	0.961	1.000	<0.01
yohimbine:gender:threatdistance:threatlevel	presence in dangerous quadrant	F(1,84)=0.139	0.710	1.000	<0.01
yohimbine:gender:time	presence in dangerous quadrant	F(29,2436)=1.84	0.004 *	0.024 *	0.005
yohimbine:gender:time:threatlevel	presence in dangerous quadrant	F(29,2436)=1.043	0.403	1.000	0.001
yohimbine:gender:time:threatdistance	presence in dangerous quadrant	F(29,2436)=2.169	<0.01 *	0.002 *	0.006
yohimbine:gender:time:threatdistance:threatlevel	presence in dangerous quadrant	F(29,2436)=0.329	1.000	1.000	<0.01
yohimbine:time	presence in dangerous quadrant	F(29,2436)=0.893	0.630	1.000	0.003
yohimbine:time:threatlevel	presence in dangerous quadrant	F(29,2436)=0.355	0.999	1.000	<0.01
yohimbine:time:threatdistance	presence in dangerous quadrant	F(29,2436)=1.274	0.149	0.894	0.003
yohimbine:time:threatdistance:threatlevel	presence in dangerous quadrant	F(29,2436)=0.779	0.795	1.000	0.001
hydrocortisone	presence in safe place	F(1,84)=1.391	0.242	1.000	0.005
hydrocortisone:threatlevel	presence in safe place	F(1,84)=0.467	0.496	1.000	<0.01
hydrocortisone:threatdistance	presence in safe place	F(1,84)=0.924	0.339	1.000	<0.01
hydrocortisone:threatdistance:threatlevel	presence in safe place	F(1,84)=0.225	0.637	1.000	<0.01
hydrocortisone:gender	presence in safe place	F(1,84)=0.001	0.975	1.000	<0.01
hydrocortisone:gender:threatlevel	presence in safe place	F(1,84)=0.406	0.526	1.000	<0.01
hydrocortisone:gender:threatdistance	presence in safe place	F(1,84)=1.519	0.221	1.000	<0.01
hydrocortisone:gender:threatdistance:threatlevel	presence in safe place	F(1,84)=0.672	0.415	1.000	<0.01
hydrocortisone:gender:time	presence in safe place	F(1.41,118.23)=0.123	0.811	1.000	0.001
hydrocortisone:gender:time:threatlevel	presence in safe place	F(2.78,233.51)=0.595	0.606	1.000	0.001
hydrocortisone:gender:time:threatdistance	presence in safe place	F(4.51,378.68)=0.766	0.562	1.000	0.001
hydrocortisone:gender:time:threatdistance:threatlevel	presence in safe place	F(2.59,217.69)=1.604	0.196	0.980	0.001
hydrocortisone:time	presence in safe place	F(1.41,118.23)=1.094	0.320	1.000	0.006
hydrocortisone:time:threatlevel	presence in safe place	F(2.78,233.51)=0.624	0.588	1.000	0.001
hydrocortisone:time:threatdistance	presence in safe place	F(4.51,378.68)=0.486	0.768	1.000	0.001
hydrocortisone:time:threatdistance:threatlevel	presence in safe place	F(2.59,217.69)=0.317	0.784	1.000	<0.01
hydrocortisone:yohimbine	presence in safe place	F(1,84)=0.549	0.461	1.000	0.002
hydrocortisone:yohimbine:threatlevel	presence in safe place	F(1,84)=0.604	0.439	1.000	<0.01
hydrocortisone:yohimbine:threatdistance	presence in safe place	F(1,84)=0.108	0.743	1.000	<0.01
hydrocortisone:yohimbine:threatdistance:threatlevel	presence in safe place	F(1,84)=1.354	0.248	1.000	<0.01
hydrocortisone:yohimbine:gender	presence in safe place	F(1,84)=0.006	0.937	1.000	<0.01
hydrocortisone:yohimbine:gender:threatlevel	presence in safe place	F(1,84)=0.955	0.331	1.000	<0.01
hydrocortisone:yohimbine:gender:threatdistance	presence in safe place	F(1,84)=4.34	0.040 *	0.240	0.001
hydrocortisone:yohimbine:gender:threatdistance:threatlevel	presence in safe place	F(1,84)=0	0.983	0.983	<0.01
hydrocortisone:yohimbine:gender:time	presence in safe place	F(1.41,118.23)=0.164	0.771	1.000	0.001
hydrocortisone:yohimbine:gender:time:threatlevel	presence in safe place	F(2.78,233.51)=1.339	0.263	1.000	0.001
hydrocortisone:yohimbine:gender:time:threatdistance	presence in safe place	F(4.51,378.68)=1.78	0.124	0.496	0.002
hydrocortisone:yohimbine:gender:time:threatdistance:threatlevel	presence in safe place	F(2.59,217.69)=0.347	0.762	0.994	<0.01
hydrocortisone:yohimbine:time	presence in safe place	F(1.41,118.23)=0.601	0.494	1.000	0.003
hydrocortisone:yohimbine:time:threatlevel	presence in safe place	F(2.78,233.51)=0.594	0.607	1.000	0.001

hydrocortisone:yohimbine:time:threatdistance	presence in safe place	F(4.51,378.68)=1.14	0.338	0.676	0.001
hydrocortisone:yohimbine:time:threatdistance:threatlevel	presence in safe place	F(2.59,217.69)=0.434	0.700	1.000	<0.001
threatlevel	presence in safe place	F(1,84)=11.758	0.001 *	0.002 *	0.005
threatdistance	presence in safe place	F(1,84)=477.415	<0.001 *	<0.001 *	0.087
threatdistance:threatlevel	presence in safe place	F(1,84)=7.918	0.006 *	0.036 *	0.001
gender	presence in safe place	F(1,84)=0.78	0.380	1.000	0.003
gender:threatlevel	presence in safe place	F(1,84)=1.466	0.229	1.000	0.001
gender:threatdistance	presence in safe place	F(1,84)=4.032	0.048 *	0.240	0.001
gender:threatdistance:threatlevel	presence in safe place	F(1,84)=2	0.161	0.966	<0.001
gender:time	presence in safe place	F(1.41,118.23)=1.424	0.243	0.486	0.007
gender:time:threatlevel	presence in safe place	F(2.78,233.51)=0.918	0.427	1.000	0.001
gender:time:threatdistance	presence in safe place	F(4.51,378.68)=6.782	<0.001 *	<0.001 *	0.007
gender:time:threatdistance:threatlevel	presence in safe place	F(2.59,217.69)=0.518	0.643	1.000	<0.001
time	presence in safe place	F(1.41,118.23)=162.313	<0.001 *	<0.001 *	0.452
time:threatlevel	presence in safe place	F(2.78,233.51)=7.271	<0.001 *	0.001 *	0.006
time:threatdistance	presence in safe place	F(4.51,378.68)=737.547	<0.001 *	<0.001 *	0.450
time:threatdistance:threatlevel	presence in safe place	F(2.59,217.69)=3.18	0.031 *	0.186	0.002
yohimbine	presence in safe place	F(1,84)=0.041	0.839	1.000	<0.001
yohimbine:threatlevel	presence in safe place	F(1,84)=0	0.999	0.999	<0.001
yohimbine:threatdistance	presence in safe place	F(1,84)=1.508	0.223	1.000	<0.001
yohimbine:threatdistance:threatlevel	presence in safe place	F(1,84)=0.037	0.849	1.000	<0.001
yohimbine:gender	presence in safe place	F(1,84)=1.239	0.269	1.000	0.004
yohimbine:gender:threatlevel	presence in safe place	F(1,84)=1.355	0.248	1.000	0.001
yohimbine:gender:threatdistance	presence in safe place	F(1,84)=0.393	0.532	1.000	<0.001
yohimbine:gender:threatdistance:threatlevel	presence in safe place	F(1,84)=0.06	0.807	1.000	<0.001
yohimbine:gender:time	presence in safe place	F(1.41,118.23)=1.088	0.321	1.000	0.005
yohimbine:gender:time:threatlevel	presence in safe place	F(2.78,233.51)=0.912	0.430	1.000	0.001
yohimbine:gender:time:threatdistance	presence in safe place	F(4.51,378.68)=1.058	0.381	1.000	0.001
yohimbine:gender:time:threatdistance:threatlevel	presence in safe place	F(2.59,217.69)=0.663	0.554	1.000	<0.001
yohimbine:time	presence in safe place	F(1.41,118.23)=0.279	0.678	1.000	0.001
yohimbine:time:threatlevel	presence in safe place	F(2.78,233.51)=0.446	0.705	1.000	<0.001
yohimbine:time:threatdistance	presence in safe place	F(4.51,378.68)=0.87	0.493	1.000	0.001
yohimbine:time:threatdistance:threatlevel	presence in safe place	F(2.59,217.69)=0.878	0.441	1.000	0.001
hydrocortisone	presence in safe quadrant	F(1,84)=0.188	0.666	1.000	0.001
hydrocortisone:threatlevel	presence in safe quadrant	F(1,84)=0.001	0.982	1.000	<0.001
hydrocortisone:threatdistance	presence in safe quadrant	F(1,84)=0.35	0.556	1.000	<0.001
hydrocortisone:threatdistance:threatlevel	presence in safe quadrant	F(1,84)=0.003	0.957	1.000	<0.001
hydrocortisone:gender	presence in safe quadrant	F(1,84)=0.002	0.969	1.000	<0.001
hydrocortisone:gender:threatlevel	presence in safe quadrant	F(1,84)=0.104	0.748	1.000	<0.001
hydrocortisone:gender:threatdistance	presence in safe quadrant	F(1,84)=0.447	0.506	1.000	<0.001
hydrocortisone:gender:threatdistance:threatlevel	presence in safe quadrant	F(1,84)=0.43	0.514	1.000	<0.001

hydrocortisone:gender:time	presence in safe quadrant	F(29,2436)=0.119	1.000	1.000	<0.001
hydrocortisone:gender:time:threatlevel	presence in safe quadrant	F(29,2436)=0.619	0.944	1.000	0.001
hydrocortisone:gender:time:threatdistance	presence in safe quadrant	F(29,2436)=0.572	0.968	1.000	0.001
hydrocortisone:gender:time:threatdistance:threatlevel	presence in safe quadrant	F(29,2436)=0.614	0.947	1.000	0.001
hydrocortisone:time	presence in safe quadrant	F(29,2436)=0.296	1.000	1.000	0.001
hydrocortisone:time:threatlevel	presence in safe quadrant	F(29,2436)=1.899	0.003 *	0.018 *	0.002
hydrocortisone:time:threatdistance	presence in safe quadrant	F(29,2436)=1.207	0.206	1.000	0.002
hydrocortisone:time:threatdistance:threatlevel	presence in safe quadrant	F(29,2436)=0.637	0.933	1.000	0.001
hydrocortisone:yohimbine	presence in safe quadrant	F(1,84)=0.001	0.981	1.000	<0.001
hydrocortisone:yohimbine:threatlevel	presence in safe quadrant	F(1,84)=0.021	0.885	1.000	<0.001
hydrocortisone:yohimbine:threatdistance	presence in safe quadrant	F(1,84)=0.003	0.956	1.000	<0.001
hydrocortisone:yohimbine:threatdistance:threatlevel	presence in safe quadrant	F(1,84)=0.036	0.851	1.000	<0.001
hydrocortisone:yohimbine:gender	presence in safe quadrant	F(1,84)=0.35	0.556	1.000	0.001
hydrocortisone:yohimbine:gender:threatlevel	presence in safe quadrant	F(1,84)=0.554	0.459	1.000	<0.001
hydrocortisone:yohimbine:gender:threatdistance	presence in safe quadrant	F(1,84)=2.113	0.150	0.715	0.001
hydrocortisone:yohimbine:gender:threatdistance:threatlevel	presence in safe quadrant	F(1,84)=9.575	0.003 *	0.015 *	0.001
hydrocortisone:yohimbine:gender:time	presence in safe quadrant	F(29,2436)=0.548	0.976	1.000	0.002
hydrocortisone:yohimbine:gender:time:threatlevel	presence in safe quadrant	F(29,2436)=0.869	0.667	1.000	0.001
hydrocortisone:yohimbine:gender:time:threatdistance	presence in safe quadrant	F(29,2436)=1.603	0.022 *	0.132	0.003
hydrocortisone:yohimbine:gender:time:threatdistance:threatlevel	presence in safe quadrant	F(29,2436)=1.313	0.122	0.488	0.001
hydrocortisone:yohimbine:time	presence in safe quadrant	F(29,2436)=1.744	0.008 *	0.048 *	0.006
hydrocortisone:yohimbine:time:threatlevel	presence in safe quadrant	F(29,2436)=0.253	1.000	1.000	<0.001
hydrocortisone:yohimbine:time:threatdistance	presence in safe quadrant	F(29,2436)=2.503	<0.001 *	<0.001 *	0.004
hydrocortisone:yohimbine:time:threatdistance:threatlevel	presence in safe quadrant	F(29,2436)=0.985	0.488	1.000	0.001
threatlevel	presence in safe quadrant	F(1,84)=24.073	<0.001 *	<0.001 *	0.009
threatdistance	presence in safe quadrant	F(1,84)=910.062	<0.001 *	<0.001 *	0.338
threatdistance:threatlevel	presence in safe quadrant	F(1,84)=3.978	0.049 *	0.147	<0.001
gender	presence in safe quadrant	F(1,84)=0.038	0.845	1.000	<0.001
gender:threatlevel	presence in safe quadrant	F(1,84)=0.186	0.668	1.000	<0.001
gender:threatdistance	presence in safe quadrant	F(1,84)=1.645	0.203	0.435	0.001
gender:threatdistance:threatlevel	presence in safe quadrant	F(1,84)=0.013	0.909	1.000	<0.001
gender:time	presence in safe quadrant	F(29,2436)=2.409	<0.001 *	<0.001 *	0.008
gender:time:threatlevel	presence in safe quadrant	F(29,2436)=1.107	0.317	1.000	0.001
gender:time:threatdistance	presence in safe quadrant	F(29,2436)=6.682	<0.001 *	<0.001 *	0.011
gender:time:threatdistance:threatlevel	presence in safe quadrant	F(29,2436)=0.296	1.000	1.000	<0.001
time	presence in safe quadrant	F(29,2436)=396.83	<0.001 *	<0.001 *	0.558
time:threatlevel	presence in safe quadrant	F(29,2436)=3.339	<0.001 *	<0.001 *	0.004
time:threatdistance	presence in safe quadrant	F(29,2436)=882.829	<0.001 *	<0.001 *	0.596
time:threatdistance:threatlevel	presence in safe quadrant	F(29,2436)=0.768	0.807	1.000	0.001
yohimbine	presence in safe quadrant	F(1,84)=0.003	0.955	1.000	<0.001

yohimbine:threatlevel	presence in safe quadrant	F(1,84)=2.194	0.142	0.432	0.001
yohimbine:threatdistance	presence in safe quadrant	F(1,84)=1.339	0.251	1.000	0.001
yohimbine:threatdistance:threatlevel	presence in safe quadrant	F(1,84)=0.548	0.461	1.000	<0.001
yohimbine:gender	presence in safe quadrant	F(1,84)=0.094	0.760	1.000	<0.001
yohimbine:gender:threatlevel	presence in safe quadrant	F(1,84)=0.005	0.946	1.000	<0.001
yohimbine:gender:threatdistance	presence in safe quadrant	F(1,84)=0.002	0.961	1.000	<0.001
yohimbine:gender:threatdistance:threatlevel	presence in safe quadrant	F(1,84)=0.15	0.699	1.000	<0.001
yohimbine:gender:time	presence in safe quadrant	F(29,2436)=0.633	0.936	1.000	0.002
yohimbine:gender:time:threatlevel	presence in safe quadrant	F(29,2436)=0.601	0.954	1.000	0.001
yohimbine:gender:time:threatdistance	presence in safe quadrant	F(29,2436)=0.419	0.997	1.000	0.001
yohimbine:gender:time:threatdistance:threatlevel	presence in safe quadrant	F(29,2436)=0.615	0.947	1.000	0.001
yohimbine:time	presence in safe quadrant	F(29,2436)=0.476	0.992	1.000	0.002
yohimbine:time:threatlevel	presence in safe quadrant	F(29,2436)=0.766	0.810	1.000	0.001
yohimbine:time:threatdistance	presence in safe quadrant	F(29,2436)=1	0.466	1.000	0.002
yohimbine:time:threatdistance:threatlevel	presence in safe quadrant	F(29,2436)=0.667	0.911	1.000	0.001

Note. The six over-trial parameters in ANOVAs with the between variables yohimbine, hydrocortisone, and gender and the within variables time, threat level (high/low) and initial threat distance (close/far). * in $p < .05$ and $p_{adj} < .05$ indicates significance for uncorrected and Bonferroni-Holm corrected p-values. Ges is the generalized eta square

7.3 SUPPLEMENT – CHAPTER 4

Manikin Task Stimulus Set (from KDEF (Lundqvist et al., 1998) and Radboud Faces Databank (Langner et al., 2010))

Angry Male Faces	Angry Female Faces	Happy Male Faces	Happy Female Faces
AM17ANS	BF11ANS	AM04HAS	AF20HAS
AM28ANS	AF13ANS	AM16HAS	AF24HAS
BM05ANS	BF15ANS	AM23HAS	AF26HAS
BM15ANS	BF20ANS	BM10HAS	BF06HAS
BM17ANS	BF21ANS	BM20HAS	BF07HAS
BM25ANS	BF24ANS	BM22HAS	AF11HAS
BM27ANS	BF33ANS	BM32HAS	BF24HAS
BM28ANS	Rafd090_01_Caucasian_female_angry_frontal	Rafd090_07_Caucasian_male_happy_frontal	Rafd090_14_Caucasian_female_happy_frontal
BM34ANS	Rafd090_61_Caucasian_female_angry_frontal	Rafd090_25_Caucasian_male_happy_frontal	Rafd090_56_Caucasian_female_happy_frontal
Rafd090_05_Caucasian_male_angry_frontal	AF01ANS	Rafd090_33_Caucasian_male_happy_frontal	AF02HAS
Rafd090_23_Caucasian_male_angry_frontal	AF05ANS	Rafd090_46_Caucasian_male_happy_frontal	AF15HAS
Rafd090_28_Caucasian_male_angry_frontal	AF14ANS	Rafd090_71_Caucasian_male_happy_frontal	AF17HAS

Visual Joystick Task Stimulus Set (from KDEF and Radboud Faces Databank)

Angry Male Faces	Angry Female Faces	Happy Male Faces	Happy Female Faces
AM09ANS	AF21ANS	AM05HAS	AF19HAS
AM29ANS	AF25ANS	AM22HAS	AF22HAS
AM32ANS	AF33ANS	AM24HAS	AF33HAS
BM01ANS	BF01ANS	AM32HAS	BF02HAS
BM03ANS	BF16ANS	AM34HAS	BF17HAS
BM06ANS	BF17ANS	BM07HAS	BF22HAS
BM07ANS	BF29ANS	BM16HAS	AF27HAS
BM09ANS	Rafd090_16_Caucasian_female_angry_frontal	BM23HAS	BF30HAS
BM10ANS	AF07ANS	BM25HAS	BF31HAS
BM16ANS	AF13ANS	Rafd090_10_Caucasian_male_happy_frontal	BF33HAS
BM23ANS	AF16ANS	Rafd090_21_Caucasian_male_happy_frontal	Rafd090_04_Caucasian_female_happy_frontal
BM29ANS	AF17ANS	Rafd090_30_Caucasian_male_happy_frontal	BF11HAS

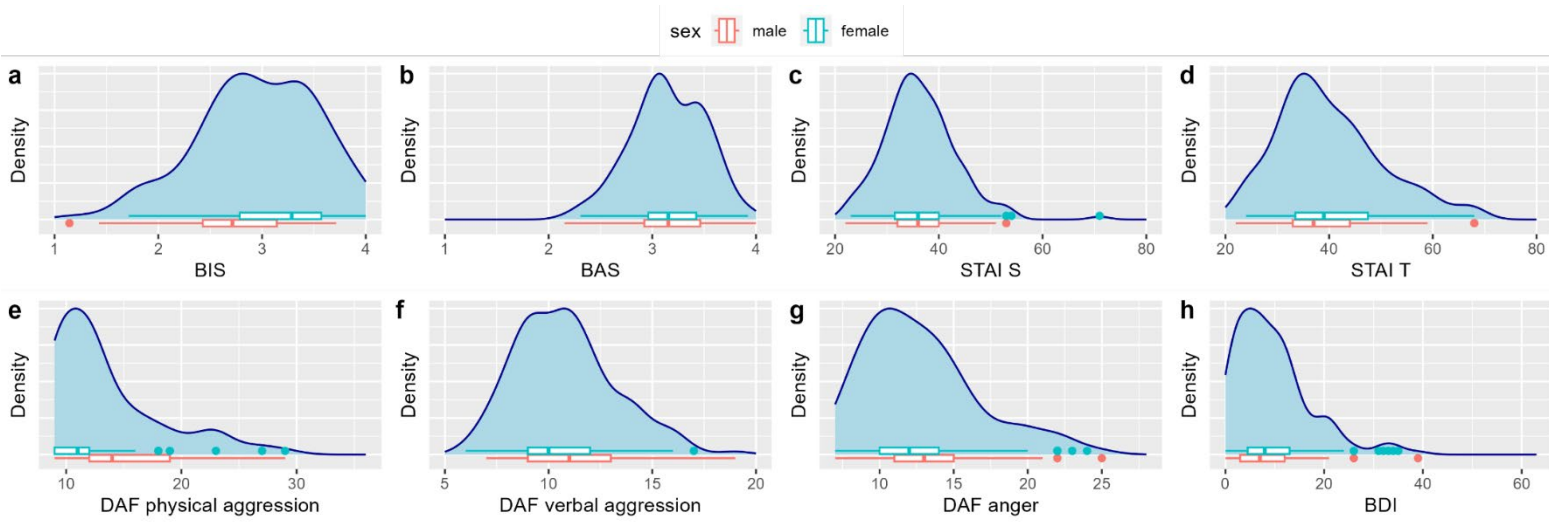


Figure 7.3.1. Density plots of (a) BIS, (b) BAS, (c) STAI S, (d) STAI T, (e) physical aggression, (f) verbal aggression, (g) anger, and (h) BDI scores with box-plots separated by gender.

Table 7.3.1. Approach avoidance conflict task outcome measure correlations with confidence intervals

Variable	1	2	3	4	5	6	7	8	9
1. Presence in safe quadrant									
2. Presence in safe place	.49**								
	[.37, .60]								
3. Distance to closest wall	-.72**	-.71**							
	[-.78, -.64]	[-.78, -.63]							
4. Speed on grid	-.40**	-.40**	.64**						
	[-.52, -.27]	[-.52, -.26]	[.54, .72]						
5. Presence	-.77**	-.23**	.42**	.05					

in dangerous quadrant	[-.83, -.70]	[-.37, -.09]	[.28, .54]	[-.11, .20]					
6. Distance to predator	.97** [.96, .98]	.53** [.41, .63]	-.71** [-.78, -.63]	-.32** [-.45, -.18]	-.86** [-.90, -.82]				
7. Token collection rate	-.56** [-.66, -.45]	-.52** [-.62, -.40]	.81** [.75, .86]	.81** [.75, .86]	.22** [.07, .36]	-.50** [-.61, -.38]			
8. Collected Tokens	-.23** [-.37, -.08]	-.36** [-.49, -.22]	.62** [.51, .70]	.79** [.72, .84]	-.09 [-.24, .06]	-.16* [-.31, -.01]	.91** [.88, .93]		
9. Foraging latency	.16* [.01, .31]	.31** [.16, .44]	-.46** [-.57, -.34]	-.67** [-.74, -.57]	.06 [-.09, .21]	.10 [-.06, .24]	-.57** [-.67, -.46]	-.61** [-.70, -.51]	
10. Player caught rate	-.82** [-.87, -.77]	-.46** [-.57, -.33]	.52** [.40, .62]	.08 [-.07, .23]	.74** [.67, .81]	-.86** [-.89, -.81]	.23** [.08, .37]	-.19* [-.33, -.04]	.10 [-.05, .25]

Note. Values in square brackets indicate the 95% confidence interval for each correlation. The confidence interval is a plausible range of population correlations that could have caused the sample correlation (Cumming, 2014). * indicates $p < .05$. ** indicates $p < .01$.

7.3.1 Approach-Avoidance Conflict Task analyses including threat level and threat distance as variables

To investigate potential influences of threat level and initial threat distance on the association between outcome parameters in the AACT and self-reported individual differences (see article), all ten parameters were split by threat level and initial threat distance, leading to 4x10 outcome parameters. These parameters were then subjected to the same analyses described for Aim 2 in the analysis section of Chapter 4. It is important to note that due to the process of the lasso regression variable selection, interpretations based on the data presented in the regression models (see Table 7.3.2) should be made carefully and with the strong intercorrelation of AACT variables in mind (see also Table 7.3.1). The correlations indicate that an increase in data resolution is especially relevant for threat distance as correlations are often found for either far or close initial threat distance (see Figure 7.3.2 and Table 7.3.3). Surprisingly, self-reported BIS did not seem to depend on the specific threat configuration, which might have been expected since the experienced approach-avoidance conflict depends on differences in initial threat distance and threat level. In the future, researcher could consider to also introduce an intermediate distance of threat, in which participants are placed in the middle of the field initially or find other ways to manipulate threat distance and threat level further.

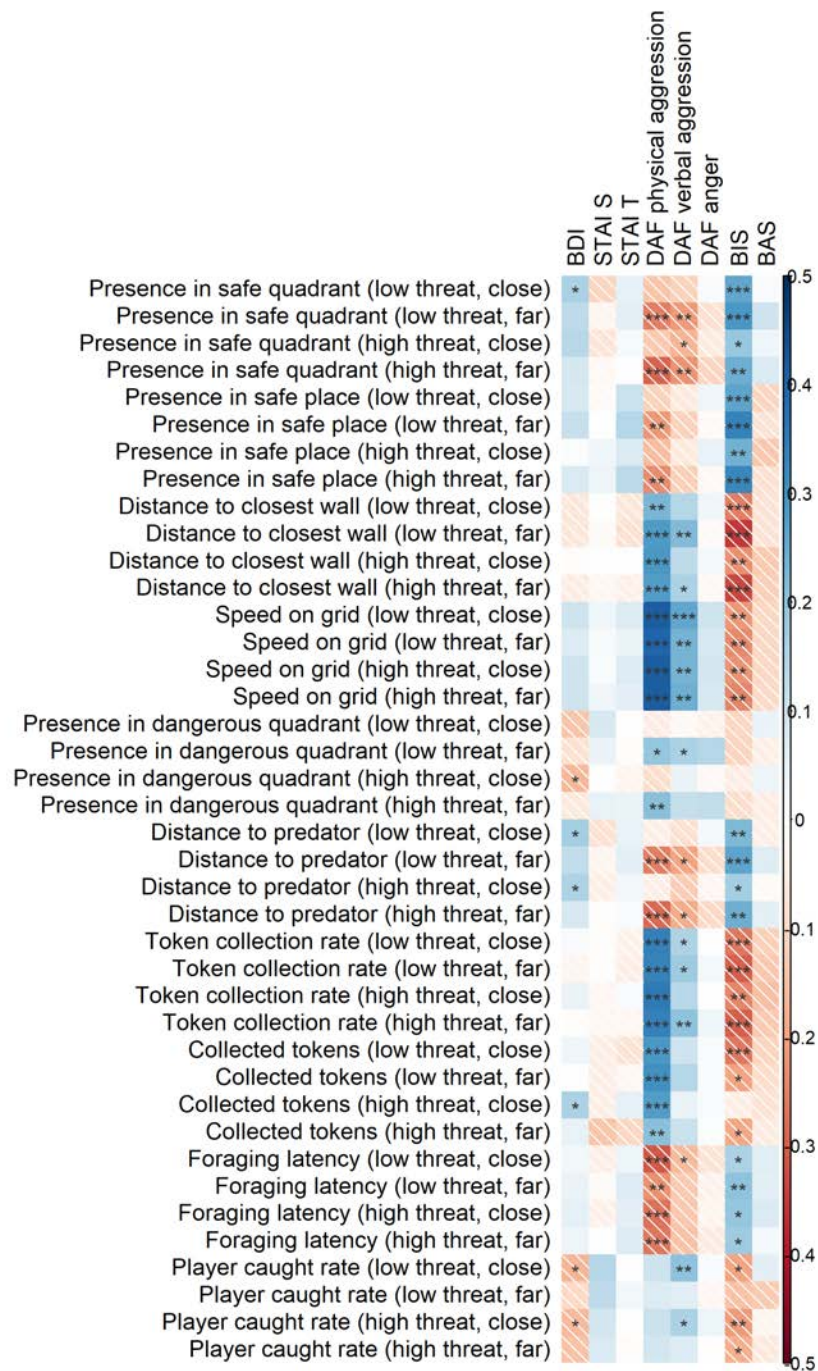


Figure 7.3.2. Correlation matrix of all questionnaire scores with AACT task outcome measures split by threat level (low/ high threat) and initial threat distance (close, far). Color intensity indicates strength of correlation, color and shade indicate direction of effect (blue/no shade = positively correlated; red/ shaded = negatively correlated). p-values are uncorrected for multiple comparisons. Significance codes: *** p < .001, ** p < .01, * p < .05.

Table 7.3.2. Significantly better multiple regression models including threat level and initial threat distance of the AACT compared to baseline models including only age and gender (with predictors)

Questionnaire	Predictor Variables	Original Model	Alternative Model
		Model fit / sig. β estimates	Model fit / sig. β estimates
BIS			adj. $R^2 = .19$, $F(6,156) = 6.568$, $p < .001$
	Gender		0.310**
	Age		.
	Collected Tokens (low threat, close)		.
	Presence in safe quadrant (low threat, close)		.
	Presence in safe place (low threat, far)		.
	Presence in safe place (high threat, far)		.
	Distance to closest wall (low threat, far)		.
BAS		adj. $R^2 = .10$, $F(9,158) = 2.986$, $p = .003$	adj. $R^2 = .13$, $F(9,152) = 3.656$, $p < .001$
	Gender	.	.
	Age	.	.
	Player caught rate (low threat, close)	.	.
	Player caught rate (low threat, far)	-0.416**	-0.342*
	Distance to predator (low threat, close)	.	.
	Presence in safe place (low threat, far)	.	.
	Presence in safe place (high threat, close)	.	-2.915*
	Distance to closest wall (high threat, close)	.	-0.315*
	Token Collection Rate (high threat, close)	.	-1.205*

verbal aggression	adj. R ² = .08, F(5,162) = 3.876, p = .002	adj. R ² = .10, F(5,158) = 4.494, p < .001
Gender	.	.
Age	.	.
Player caught rate (low threat, close)	1.921*	.
Speed on grid (low threat, close)	1.340** ^a	1.458*
Presence in safe quadrant (high threat, far)	.	.
BDI	adj. R ² = .10, F(10,155) = 2.788, p = .003	adj. R ² = .07, F(10,147) = 2.650, p = .018
Gender	3.447** ^a	.
Age	.	.
Player caught rate (low threat, close)	.	.
Distance to predator (low threat, far)	.	.
Presence in safe quadrant (low threat, far)	.	.
Presence in safe place (low threat, far)	.	.
Collected Tokens (high threat, close)	.	.
Foraging Latency (high threat, close)	0.008*	.
Presence in dangerous quadrant (high threat, close)	.	.
Speed on grid (high threat, far)	7.304**	5.759**

Notes. Alternative model: Model without cases with standardized residuals exceeding two standard deviations away from the mean and Cook's distance exceeding a value of one, leverage values three times larger than the average leverage and/or a covariance ratio outside of one plus/minus three times the average leverage. Low/high threat stands for the respective threat level, while far and close represent the initial threat distance. Significant predictors are in bold. ^aNot significant based on bootstrapped confidence interval.

Significance codes: *** p < 0.001, ** p < 0.01, * p < 0.05

Table 7.3.3. Correlations of AACT outcome measures including threat level and initial threat distance with self-report questionnaire scores


	BDI TOTAL	STAI S	STAI T	PHYSI CAL AGGR ESSIO N	VERBA L AGGR ESSIO N	ANGE R	BIS	BAS
PRESENCE IN SAFE QUADRANT (LOW THREAT, CLOSE)	r = 0.16, p = 0.04	r = -0.11, p = 0.157	r = 0.05, p = 0.509	r = -0.14, p = 0.08	r = -0.11, p = 0.141	r = 0.01, p = 0.862	r = 0.26, p = 0.001	r = 0.01, p = 0.855
PRESENCE IN SAFE QUADRANT (LOW THREAT, FAR)	r = 0.13, p = 0.105	r = -0.03, p = 0.727	r = 0.06, p = 0.469	r = -0.25, p = 0.001	r = -0.21, p = 0.006	r = -0.08, p = 0.307	r = 0.29, p < 0.001	r = 0.1, p = 0.188
PRESENCE IN SAFE QUADRANT (HIGH THREAT, CLOSE)	r = 0.14, p = 0.072	r = -0.07, p = 0.386	r = 0.02, p = 0.827	r = -0.13, p = 0.106	r = -0.17, p = 0.031	r = -0.05, p = 0.48	r = 0.19, p = 0.014	r = 0.03, p = 0.662
PRESENCE IN SAFE QUADRANT (HIGH THREAT, FAR)	r = 0.09, p = 0.265	r = -0.02, p = 0.82	r = 0, p = 0.977	r = -0.29, p < 0.001	r = -0.22, p = 0.004	r = -0.11, p = 0.159	r = 0.24, p = 0.001	r = 0.08, p = 0.33
PRESENCE IN SAFE PLACE (LOW THREAT, CLOSE)	r = 0.08, p = 0.291	r = -0.01, p = 0.896	r = 0.11, p = 0.175	r = -0.11, p = 0.141	r = -0.06, p = 0.462	r = 0.03, p = 0.696	r = 0.26, p = 0.001	r = -0.11, p = 0.172
PRESENCE IN SAFE PLACE (LOW THREAT, FAR)	r = 0.11, p = 0.153	r = 0, p = 0.99	r = 0.14, p = 0.065	r = -0.22, p = 0.004	r = -0.11, p = 0.153	r = -0.01, p = 0.89	r = 0.33, p < 0.001	r = -0.07, p = 0.342
PRESENCE IN SAFE PLACE (HIGH THREAT, CLOSE)	r = 0.01, p = 0.933	r = 0.03, p = 0.67	r = 0.08, p = 0.324	r = -0.15, p = 0.052	r = -0.06, p = 0.469	r = -0.05, p = 0.555	r = 0.24, p = 0.002	r = -0.13, p = 0.092
PRESENCE IN SAFE PLACE (HIGH THREAT, FAR)	r = 0.08, p = 0.315	r = 0.04, p = 0.634	r = 0.13, p = 0.092	r = -0.23, p = 0.003	r = -0.12, p = 0.128	r = -0.02, p = 0.822	r = 0.32, p < 0.001	r = -0.08, p = 0.304
DISTANCE TO CLOSEST WALL (LOW THREAT, CLOSE)	r = -0.06, p = 0.436	r = 0, p = 0.977	r = -0.06, p = 0.425	r = 0.23, p = 0.003	r = 0.14, p = 0.064	r = 0.03, p = 0.694	r = -0.25, p = 0.001	r = -0.07, p = 0.345
DISTANCE TO CLOSEST WALL (LOW THREAT, FAR)	r = -0.06, p = 0.412	r = -0.01, p = 0.849	r = -0.08, p = 0.327	r = 0.28, p < 0.001	r = 0.22, p = 0.004	r = -0.01, p = 0.885	r = -0.35, p < 0.001	r = -0.07, p = 0.366
DISTANCE TO CLOSEST WALL (HIGH THREAT, CLOSE)	r = -0.01, p = 0.908	r = 0, p = 0.974	r = 0, p = 0.984	r = 0.29, p < 0.001	r = 0.13, p = 0.106	r = 0.02, p = 0.779	r = -0.23, p = 0.003	r = -0.13, p = 0.099
DISTANCE TO CLOSEST WALL (HIGH THREAT, FAR)	r = -0.05, p = 0.547	r = -0.02, p = 0.776	r = -0.04, p = 0.65	r = 0.28, p < 0.001	r = 0.16, p = 0.042	r = -0.02, p = 0.816	r = -0.33, p < 0.001	r = -0.12, p = 0.131
SPEED ON GRID (LOW THREAT, CLOSE)	r = 0.1, p = 0.181	r = 0.03, p = 0.693	r = 0.07, p = 0.36	r = 0.41, p < 0.001	r = 0.26, p = 0.001	r = 0.1, p = 0.187	r = -0.22, p = 0.004	r = -0.1, p = 0.184
SPEED ON GRID (LOW THREAT, FAR)	r = 0.07, p = 0.344	r = 0.02, p = 0.812	r = 0.04, p = 0.57	r = 0.4, p < 0.001	r = 0.23, p = 0.002	r = 0.08, p = 0.28	r = 0.24, p = 0.002	r = -0.1, p = 0.188
SPEED ON GRID (HIGH THREAT, CLOSE)	r = 0.1, p = 0.198	r = 0.01, p = 0.865	r = 0.07, p = 0.362	r = 0.41, p < 0.001	r = 0.23, p = 0.002	r = 0.09, p = 0.242	r = -0.22, p = 0.004	r = -0.1, p = 0.187
SPEED ON GRID (HIGH THREAT, FAR)	r = 0.1, p = 0.192	r = 0.03, p = 0.678	r = 0.06, p = 0.476	r = 0.41, p < 0.001	r = 0.24, p = 0.001	r = 0.08, p = 0.288	r = -0.24, p = 0.001	r = -0.1, p = 0.211
PRESENCE IN DANGEROUS QUADRANT (LOW THREAT, CLOSE)	r = -0.14, p = 0.072	r = 0.08, p = 0.3	r = 0, p = 0.965	r = -0.05, p = 0.55	r = -0.02, p = 0.817	r = -0.03, p = 0.674	r = -0.1, p = 0.178	r = 0.04, p = 0.573
PRESENCE IN DANGEROUS QUADRANT (LOW THREAT, FAR)	r = -0.08, p = 0.32	r = 0.04, p = 0.576	r = -0.01, p = 0.925	r = 0.19, p = 0.012	r = 0.16, p = 0.038	r = 0.14, p = 0.065	r = -0.11, p = 0.157	r = -0.04, p = 0.581
PRESENCE IN DANGEROUS QUADRANT (HIGH THREAT, CLOSE)	r = -0.16, p = 0.036	r = 0, p = 0.973	r = -0.03, p = 0.738	r = -0.09, p = 0.258	r = 0.04, p = 0.577	r = -0.02, p = 0.84	r = -0.05, p = 0.553	r = 0.04, p = 0.627
PRESENCE IN DANGEROUS	r = -0.06, p = 0.451	r = 0.05, p = 0.554	r = 0.04, p = 0.574	r = 0.21, p = 0.007	r = 0.12, p = 0.124	r = 0.12, p = 0.118	r = -0.09, p = 0.272	r = -0.05, p = 0.554

QUADRANT (HIGH THREAT, FAR)								
DISTANCE TO PREDATOR (LOW THREAT, CLOSE)	r = 0.17, p = 0.031	r = -0.08, p = 0.325	r = 0.05, p = 0.55	r = -0.04, p = 0.596	r = -0.08, p = 0.313	r = 0.02, p = 0.782	r = 0.22, p = 0.004	r = -0.04, p = 0.597
DISTANCE TO PREDATOR (LOW THREAT, FAR)	r = 0.12, p = 0.122	r = -0.03, p = 0.738	r = 0.06, p = 0.471	r = -0.25, p = 0.001	r = -0.2, p = 0.01	r = -0.09, p = 0.247	r = 0.26, p = 0.001	r = 0.07, p = 0.389
DISTANCE TO PREDATOR (HIGH THREAT, CLOSE)	r = 0.15, p = 0.05	r = -0.04, p = 0.593	r = 0.03, p = 0.725	r = -0.04, p = 0.593	r = -0.12, p = 0.11	r = -0.02, p = 0.754	r = 0.17, p = 0.028	r = -0.01, p = 0.851
DISTANCE TO PREDATOR (HIGH THREAT, FAR)	r = 0.08, p = 0.293	r = -0.01, p = 0.901	r = 0.01, p = 0.872	r = -0.28, p < 0.001	r = -0.18, p = 0.019	r = -0.1, p = 0.215	r = 0.24, p = 0.002	r = 0.06, p = 0.446
TOKEN COLLECTION RATE (LOW THREAT, CLOSE)	r = 0.01, p = 0.877	r = -0.01, p = 0.932	r = -0.03, p = 0.696	r = 0.34, p < 0.001	r = 0.15, p = 0.048	r = 0, p = 0.994	r = -0.26, p = 0.001	r = -0.12, p = 0.125
TOKEN COLLECTION RATE (LOW THREAT, FAR)	r = -0.03, p = 0.743	r = -0.01, p = 0.914	r = -0.04, p = 0.588	r = 0.33, p < 0.001	r = 0.18, p = 0.023	r = 0.02, p = 0.785	r = -0.3, p < 0.001	r = -0.13, p = 0.087
TOKEN COLLECTION RATE (HIGH THREAT, CLOSE)	r = 0.04, p = 0.608	r = -0.02, p = 0.789	r = 0.01, p = 0.848	r = 0.35, p < 0.001	r = 0.14, p = 0.073	r = 0, p = 0.999	r = -0.24, p = 0.002	r = -0.15, p = 0.055
TOKEN COLLECTION RATE (HIGH THREAT, FAR)	r = -0.01, p = 0.916	r = -0.02, p = 0.775	r = -0.02, p = 0.779	r = 0.34, p < 0.001	r = 0.2, p = 0.009	r = 0.03, p = 0.676	r = -0.3, p < 0.001	r = -0.13, p = 0.104
COLLECTED TOKENS (LOW THREAT, CLOSE)	r = 0.03, p = 0.687	r = -0.04, p = 0.566	r = -0.07, p = 0.341	r = 0.29, p < 0.001	r = 0.1, p = 0.18	r = 0.01, p = 0.878	r = -0.26, p = 0.001	r = -0.11, p = 0.172
COLLECTED TOKENS (LOW THREAT, FAR)	r = 0, p = 0.953	r = -0.04, p = 0.597	r = -0.02, p = 0.794	r = 0.3, p < 0.001	r = 0.14, p = 0.062	r = 0.01, p = 0.893	r = -0.2, p = 0.011	r = -0.09, p = 0.248
COLLECTED TOKENS (HIGH THREAT, CLOSE)	r = 0.16, p = 0.045	r = -0.04, p = 0.566	r = 0.05, p = 0.489	r = 0.28, p < 0.001	r = 0.04, p = 0.566	r = 0.01, p = 0.862	r = -0.04, p = 0.568	r = -0.07, p = 0.346
COLLECTED TOKENS (HIGH THREAT, FAR)	r = 0.05, p = 0.562	r = -0.14, p = 0.076	r = -0.1, p = 0.178	r = 0.21, p = 0.007	r = 0.11, p = 0.172	r = 0.01, p = 0.91	r = -0.19, p = 0.012	r = -0.05, p = 0.498
FORAGING LATENCY (LOW THREAT, CLOSE)	r = 0.03, p = 0.715	r = -0.04, p = 0.598	r = 0.04, p = 0.62	r = -0.31, p < 0.001	r = -0.16, p = 0.043	r = -0.07, p = 0.336	r = 0.16, p = 0.04	r = 0.06, p = 0.418
FORAGING LATENCY (LOW THREAT, FAR)	r = 0.04, p = 0.571	r = -0.01, p = 0.862	r = 0.07, p = 0.336	r = -0.23, p = 0.003	r = -0.13, p = 0.095	r = -0.03, p = 0.678	r = 0.2, p = 0.009	r = 0.06, p = 0.448
FORAGING LATENCY (HIGH THREAT, CLOSE)	r = 0.05, p = 0.492	r = -0.04, p = 0.631	r = 0.06, p = 0.464	r = -0.27, p < 0.001	r = -0.13, p = 0.089	r = -0.03, p = 0.705	r = 0.19, p = 0.012	r = 0.08, p = 0.325
FORAGING LATENCY (HIGH THREAT, FAR)	r = 0.04, p = 0.611	r = 0, p = 0.983	r = 0.07, p = 0.367	r = -0.26, p = 0.001	r = -0.14, p = 0.062	r = -0.05, p = 0.485	r = 0.18, p = 0.023	r = 0.02, p = 0.762
PLAYER CAUGHT RATE (LOW THREAT, CLOSE)	r = -0.17, p = 0.033	r = 0.14, p = 0.061	r = 0, p = 0.969	r = 0.1, p = 0.196	r = 0.2, p = 0.008	r = 0.01, p = 0.856	r = -0.2, p = 0.01	r = 0.06, p = 0.452
PLAYER CAUGHT RATE (LOW THREAT, FAR)	r = -0.1, p = 0.209	r = 0.13, p = 0.096	r = 0.03, p = 0.714	r = 0.07, p = 0.339	r = 0.06, p = 0.419	r = -0.02, p = 0.785	r = -0.14, p = 0.067	r = -0.13, p = 0.094
PLAYER CAUGHT RATE (HIGH THREAT, CLOSE)	r = -0.16, p = 0.042	r = 0.09, p = 0.231	r = 0, p = 0.959	r = 0.11, p = 0.167	r = 0.16, p = 0.042	r = 0.04, p = 0.628	r = -0.21, p = 0.006	r = -0.03, p = 0.743
PLAYER CAUGHT RATE (HIGH THREAT, FAR)	r = -0.14, p = 0.066	r = 0.08, p = 0.305	r = -0.01, p = 0.932	r = 0.09, p = 0.227	r = 0.07, p = 0.363	r = 0, p = 0.981	r = -0.18, p = 0.021	r = -0.06, p = 0.474

Versicherung an Eides Statt zur Selbständigkeit

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