Dissertation zur Erlangung des akademischen Grades eines Doktors

der Naturwissenschaften (Dr. rer. nat.)

Dopamine Modulation of Individual Differences in Openness to Experience

A. M. Wiebke Käckenmester

Universität Hamburg

Fakultät für Psychologie und Bewegungswissenschaft

Institut für Psychologie

Vorgelegt am 05.02.2020

Tag der Disputation:	17.06.2020
Erstes Dissertationsgutachten:	Prof. Dr. Jan Wacker
Zweites Dissertationsgutachten:	Prof. Dr. Ulf Liszkowski
Disputationsvorsitz:	Prof. Dr. Martin Spieß
Erstes Disputationsgutachten:	PD Dr. Kirsten Hötting
Zweites Disputationsgutachten:	Prof. Dr. Tania Lincoln

Table of contents

List of figures

Publications

This dissertation is based on the following articles that have either been published or are currently under consideration for publication in peer-reviewed journals.

Käckenmester, W., Kroencke, L., & Wacker, J. (2018). Frontal asymmetry predicts the incentive value of perceptual information. *International Journal of Psychophysiology (134)*, 22-29.

Käckenmester, W., Bott, A., & Wacker J. (2019). Openness to experience predicts dopamine effects on divergent thinking. *Personality Neuroscience*, *2*(3), 1-7.

Käckenmester, W. & Wacker J. Are individual differences in openness and implicit sequence learning modulated by dopamine? Submitted to *Personality and Social Psychology Bulletin.*

“One of our pleasures was to enter our workshop at night; then, all around us we would see the luminous silhouettes of the beakers and capsules that contained our products. It was really a lovely sight and one always new to us.”

Marie Skłodowska Curie

Abstract

Individual differences in openness to experience have been theoretically linked to functions of the neuromodulator dopamine. Although a few trait characteristics have been connected to dopamine activity, causal connections with the broad domain still lack empirical evidence. In preparation for the first study, I developed a novel perceptual paradigm to examine the hypothesized association between openness and anticipation-related states with frontal EEG alpha asymmetry. The results yielded a main effect of state curiosity on left-lateralized activation and an interaction between openness and self-reported confidence, indicating that openness might explain individual differences in the responsiveness to perceptual uncertainty. The second study was conducted to directly assess the influence of dopamine on divergent thinking, a behavioral correlate of openness to experience. For this purpose, the dopamine receptor blocker sulpiride was administered in a placebo-controlled between-subjects design. The data yielded an interaction between openness to experience and substance group, indicating that the dopamine manipulation selectively affected divergent thinking as a function of openness to experience. The results provide novel empirical evidence for an association between dopamine activity and both openness to experience and divergent thinking. Performed in the same pharmacological design, the third study was conducted to assess the influence of dopamine activity on the relationship between openness and implicit learning. The hypothesized interaction between implicit learning and substance group, however, failed to reach statistical significance. In summary, evidence for the initial hypotheses was found in two of three studies. Implications of the present findings are discussed along with methodological considerations and future directions.

1 Introduction

Individual differences in human personality have been described and classified for more than 2000 years (Eysenck, 1964). Today, most modern researchers agree on five factors, commonly labelled the Five Factor Model or the "Big Five" (McCrae & Costa, 1997; Digman, 1990). Although characteristic patterns in human experience and behavior have been studied for a long time, their origins remained largely unknown. Despite an extensive amount of empirical research, most studies conducted during the past decades focus on describing rather than explaining individual differences in personality (DeYoung & Gray, 2009). Evidence for heritable factors in personality traits has been initially obtained from twin and adoption studies, suggesting that around 37 percent of the Big Five's trait variability are explained by genetic factors (Vukasović & Bratko, 2016). In order to explain the underlying biological mechanisms, Hans Eysenck (1967) and Jeffrey Gray (1970) proposed personality theories that focus on basic behavioral tendencies and their manifestations in neurophysiological functioning. Based on animal models and pharmacological studies, Gray (1987a) hypothesized that behavioral approach and inhibition reflect individual differences in impulsivity and anxiety, respectively. He connected Eysenck & Eysenck's (1969) biologically based concepts of extraversion and neuroticism with sensitivity to reward and sensitivity to punishment (Gray, 1987a). Among others, Gray's theory was further developed by Cloninger (1987), who assumed behavioral tendencies towards harm avoidance, novelty seeking, and reward dependence. Both theories further connect individual differences in behavioral approach to functions of the neurotransmitter dopamine (Cloninger, 1987; Gray 1987a).

1.1 Dopamine function in motivational control

Dopamine acts as a neurotransmitter and a neuromodulator in a widespread network in the human brain, including the striatum, the medial temporal lobe and the frontal cortex (Schultz, Dayan, & Montague, 1997). Dopamine function has been implicated in a variety of processes ranging from motor functioning to motivational drive and cognitive control (Bromberg-Martin, Matsumoto, & Hikosaka, 2010). The following assumptions are based on dopamine function in incentive motivation, specifically in reinforcement learning and salience processing (Schultz et al., 1997). Initially, it has been demonstrated that dopaminergic neurons respond to cues that signal appetitive stimuli (Schultz, Dayan, & Montague, 1997). More recently, Bromberg-Martin et al. (2010) proposed that different types of dopaminergic neurons support valence and salience coding. They proposed that dopaminergic valence coding neurons process cues that signal primary rewards (e.g., food, money) while salience coding neurons respond to both rewarding and aversive events of high motivational importance (Bromberg-Martin et al., 2010). Dopamine has thus been implicated not only in reward learning but also in salience coding that presumably facilitates orientation of attention and cognitive processing (Bromberg-Martin et al., 2010).

Depue & Collins (1999) initially connected dopamine function to trait variation in extraversion. From trait characteristics of the broad domain, they derived basic motivational tendencies that have been associated with dopamine activity. Essentially, they argued that dopamine and trait characteristics of extraversion are connected to the same motivational systems. Particularly, characteristic subtraits of extraversion (e.g., positive affect, sociability, achievement) have been theoretically associated with reward sensitivity and incentive motivation. Modulating incentive motivation, dopamine projections from the ventral tegmental area (VTA) might thus provide the neural substrate

of extraversion (Depue & Collins, 1999). Depue and Collin's (1999) theory has been investigated in humans using brain imaging techniques, electroencephalography (EEG), genetics, and pharmacological manipulations (Wacker & Smilie, 2015). For instance, individual differences in reward processing have been associated with extraversion spectrum traits (Mueller, Burgdorf, Chavanon, Schweiger, Wacker, Stemmler, 2014; Wu, Samanez-Larkin, Katovich, Knutson, 2014). Moreover, pharmacological manipulations with dopaminergic drugs provided important evidence for causal connections between extraversion and dopamine function (Depue, Luciana, Arbisi, Colins, Leon, 1994; Depue, 1995; Mueller et al., 2014; Wacker, Chavanon, & Stemmler, 2006; Wacker, Mueller, Pizzagalli, Hennig, Stemmler, 2013). Compared to the other Big Five domains, the neurobiological basis of extraversion has been comparably well studied and linked to individual differences in dopamine activity (DeYoung, 2013; Wacker & Smillie, 2015).

1.2 Openness to experience

Referring to Depue & Collins' (1999) reasoning, DeYoung, Peterson & Higgins (2005) theoretically linked dopamine function to another Big Five domain: openness to experience. The fifth factor of personality describes the tendency to notice and appreciate novel, complex, and unusual information in everyday experiences (DeYoung et al., 2014; McCrae, 1993). Highly open people describe themselves as creative, imaginative, and curious while less open people state that they are rather uncomfortable with complexities, favor conservative values, and tend to judge in conventional terms (Costa & McCrae, 1992, 1997). In an attempt to identify the underlying mechanisms, DeYoung (2010, p. 1169) described openness to experience as a tendency to "detect, explore, appreciate, and utilize patterns of abstract and sensory information". He presumed that the overarching motivational function behind openness to experience is cognitive exploration (DeYoung

et al., 2005; DeYoung, 2015). Labelled intellect, one aspect of the broad openness domain has been attributed the tendency to explore abstract information (DeYoung et al., 2010). The intellect aspect refers to lower-order traits that describe intellectual interests (e.g., in science or philosophy) as well as cognitive ability (DeYoung et al., 2010). The second aspect of the broad domain has been labelled openness, encompassing lower-order traits like artistic interests, imagination, and emotional engagement with music, poems, or nature. The openness aspect has been ascribed the tendency to explore patterns of perceptual information (DeYoung et al., 2010).

In line with DeYoung et al.'s (2005) assumptions, empirical findings indicate that highly open individuals have a wider attentional focus and process more information than less open people. Specifically, openness to experience has been negatively associated with latent inhibition, a low-level cognitive phenomenon relevant for shielding formerly ignored information from further processing (Peterson & Carson, 2000; Peterson, Smith, & Carson, 2002). Thus, highly open individuals might process more information that has previously been classified as task-irrelevant. Furthermore, openness to experience has been related to a wider range of inhibition of return, indicating a broader focus of spatial attention (Wilson, Lowe, Matthew, Ruppel, Pratt, & Ferber, 2016). Another study found openness to experience negatively related to inattentional blindness (i.e., the failure to consciously perceive unexpected stimuli; Kreitz, Schnuerch, Gibbons, & Memmert, 2015). Openness has been further associated with apophenia, the tendency to detect false positives in random patterns (Blain, Longenecker, Grazioplene, & DeYoung, 2019) and has been related to perceiving mixed images in a binocular rivalry paradigm (Antinori, Carter, & Smillie, 2017). The reviewed results overall support the hypothesis that openness to experience is connected to individual differences in processing sensory information.

1.3 The dopaminergic basis of openness to experience

Based on cognitive functions that have been associated with openness to experience and dopamine, respectively, DeYoung, Peterson & Higgins (2005) proposed that individual differences in openness to experience partly result from dopaminergic neurotransmission. Empirical evidence for this assumption has been suggested by Peterson & Carson (2000) who found openness to experience correlated with decreased latent inhibition (Peterson & Carson, 2000; Peterson, Smith, & Carson, 2002), a cognitive function that has previously been shown sensitive to dopaminergic drugs (Swerdlow, Stephany, Wasserman, Talledo, Sharp, & Auerbach, 2003; Weiner & Feldon, 1987; Weiner, Shadach, Tarrasch, Kidron, & Feldon, 1996). More direct evidence has been found for creativity, a central characteristic of the broad openness domain (DeYoung, 2013). For instance, creative thinking has been connected to dopamine D2 receptor density (although in a small sample; de Manzano, Cervenka, Karabanov, Farde, & Ullén, 2010) and mean diffusivity in dopamine-associated brain regions (Takeuchi et al., 2015). Moreover, creative thinking has been associated with eye blink rate (Akbari Chermahini & Hommel, 2010) and reduced latent inhibition (Carson, Higgins, & Peterson, 2003), both indicators of dopamine activity. Preliminary evidence for causal connections has been reported with Parkinson patients who increasingly engaged in creative activities with the introduction of dopaminergic medication, and reduced these activities after dose reductions (Lhommée et al., 2014). When treated with dopamine-increasing medication, Parkinson's patients have further demonstrated enhanced divergent thinking performance compared with non-medicated healthy controls (Faust-Socher, Kenett, Cohen, Hassin-Baer, & Inzelberg, 2014). Empirical links to individual differences in dopamine function have thus been demonstrated in creative thinking, a behavioral correlate of openness to experience.

Moreover, shared variance between extraversion and openness to experience might support an underlying dopamine mechanism (DeYoung, 2011). Although the Five Factor Model has been described as orthogonal (Costa & McCrae, 1992), extraversion and openness to experience have regularly been found moderately correlated (DeYoung, Peterson, & Higgins, 2002; Digman, 1997). Presumably facilitated by dopamine, extraversion might reflect a behavioral aspect and openness a cognitive aspect of exploration (DeYoung et al., 2005). Referring to Bromberg-Martin et al.'s (2010) theory, DeYoung (2013) suggested that extraversion might be linked to dopaminergic valence processing and openness to salience coding. He further presumed that extraversion connects to reward processing within a mesolimbic dopaminergic pathway and openness to salience processing within a mesocortical pathway (DeYoung et al., 2005). Supporting the latter suggestion, positive functional connectivity within mesocortical networks has been shown to correlate with self-reports of openness to experience (Passamonti et al., 2015).

Finally, personality traits have been connected to genetic polymorphisms that have been implicated in individual differences in dopaminergic neurotransmission (e.g., variants of the D4 dopamine receptor gene DRD4). However, the idea that a single-nucleotide polymorphism explains a meaningful proportion of variance in complex traits like personality must be considered outdated (Sanchez-Roige, Gray, McKillop, Chen, & Palmer, 2018). A promising approach towards the genetic basis of personality are genome-wide association studies (GWAS) that assume polygenetic effects by analyzing variations of hundreds to millions of singe-nucleotide polymorphisms. So far, the most consistent GWAS results were reported for neuroticism (Sanchez-Roige et al., 2018). However, reliable conclusions on the genetic basis of openness to experience cannot be

drawn from the existing literature. Since GWAS is a very young approach, the next years will probably bring more insight into the genetics of openness to experience.

1.4 The incentive value of information

A central assumption of DeYoung's (2013) theory on the biological basis of openness to experience focusses on the incentive value of information. Among others, empirical evidence for the idea has been provided by researchers who investigated the neural correlates of curiosity. Presenting abstract information via trivia questions (e.g.," What instrument was invented to sound like a human singing?"), Kang et al. (2009) found increased activity within the nucleus caudatus as a function of self-reported curiosity. Since the nucleus caudatus has previously been connected to reward anticipation, curiosity may share characteristics with the anticipation of external rewards (DeYoung, 2013; Kang et al., 2009). Within an almost identical design, Gruber, Gelman, & Ranganath (2014) also found dopamine-associated regions correlated with state curiosity, particularly the ventral striatum and midbrain regions. Similar fMRI findings on monetary reward anticipation (Adcock, Thangavel, Whitfield-Gabrieli, Knutson, & Gabrieli, 2006; Rademacher, Krach, Kohls, Irmak, Gründer, & Spreckelmeyer, 2010; Simon et al., 2010) support joint processes between anticipating primary reinforcers and information (DeYoung, 2013). Generalizing the framework of dopamine function in reward processing, DeYoung (2013) suggested that information itself holds an inherent reward value.

Using EEG, frontal asymmetry within the alpha frequency spectrum has been hypothesized to index emotional-motivational tendencies (Coan & Allen, 2004; Davidson, 1992, 2003). Most consistently, left-lateralized frontal activity has been shown to increase with reward anticipation (Gorka, Shan, & Shankman, 2015; Miller &

Tomarken, 2001; Sobotka, Davidson, & Senulis, 1992; Zinser, Fiore, Davidson, & Baker, 1999; but see Katz, Sarapas, Bishop, Patel, & Shankman, 2015). Compatible with the hypothesized involvement of dopamine in reward processing, dopamine function has also been associated with frontal asymmetry. In animal studies, DLPFC neurons displayed lateralized activation in modulating dopamine responses from the mesostriatal system (Molochnikov & Cohen, 2014). In humans, PET studies connected left-lateralized D2 receptor availability with trait incentive motivation (Tomer, Goldstein, Wang, Wong, & Nora, 2008) and task-dependent reward learning (Tomer et al., 2014). Moreover, associations between trait approach motivation and EEG frontal asymmetry have been altered by a pharmacological dopamine manipulation (Wacker et al., 2013). Taken together, left-lateralized frontal asymmetry provides an index of approach-motivation presumably modulated by dopamine. If information is inherently rewarding, the index probably applies to immediate rewards as well as to salient information.

2 The present research

Given the reviewed evidence, initial findings linked trait characteristics of openness to experience to dopamine function. However, support for a general framework connecting dopaminergic salience processing to openness to experiences is currently restricted to indirect associations. In a first approach, I developed a novel perceptual task to investigate EEG correlates of uncertainty-related states and its association with openness. In the second study, we used a pharmacological design to directly assess the effects of dopamine on divergent thinking, an established behavioral correlate of openness to experience. The third study was conducted within the same pharmacological study to test the effects of dopamine on the association between openness and implicit learning.

2.1 Study 1: Frontal asymmetry predicts the incentive value of perceptual information

The first study was designed to investigate the incentive value of information hypothesized by DeYoung (2013) and its association with trait levels of openness. DeYoung's hypothesis was previously supported by fMRI results that suggested similar neural correlates of curiosity and external reward anticipation (Kang et al., 2009; Gruber et al., 2014). We aimed to extend the approach by Kang et al. (2009) and Gruber et al. (2014) using EEG frontal asymmetry as an indicator of incentive motivation. Since the openness aspect of openness to experience has been characterized by perceptual sensibility (DeYoung, 2010), open individuals should be particularly responsive to ambiguous visual information. Therefore, we investigated individual differences in trait openness as a moderator of the association between perceptual uncertainty and frontal asymmetry. To our knowledge, a perceptual paradigm suitable for EEG or fMRI measurements has not been developed so far. Therefore, we designed a novel task that was pre-tested and consecutively administered in an EEG study. The task was designed to elicit and subsequently resolve varying levels of uncertainty during visual object recognition. In a first stimulus presentation, the detail of a photo was increasingly uncovered. Participants were asked how confident they were of having identified the object and how curious they are. After a short anticipation period, the photo's content was fully disclosed (see Figure 1). During the anticipation of the fully disclosed stimulus, frontal alpha asymmetry was analyzed as a function of self-reported confidence and curiosity.

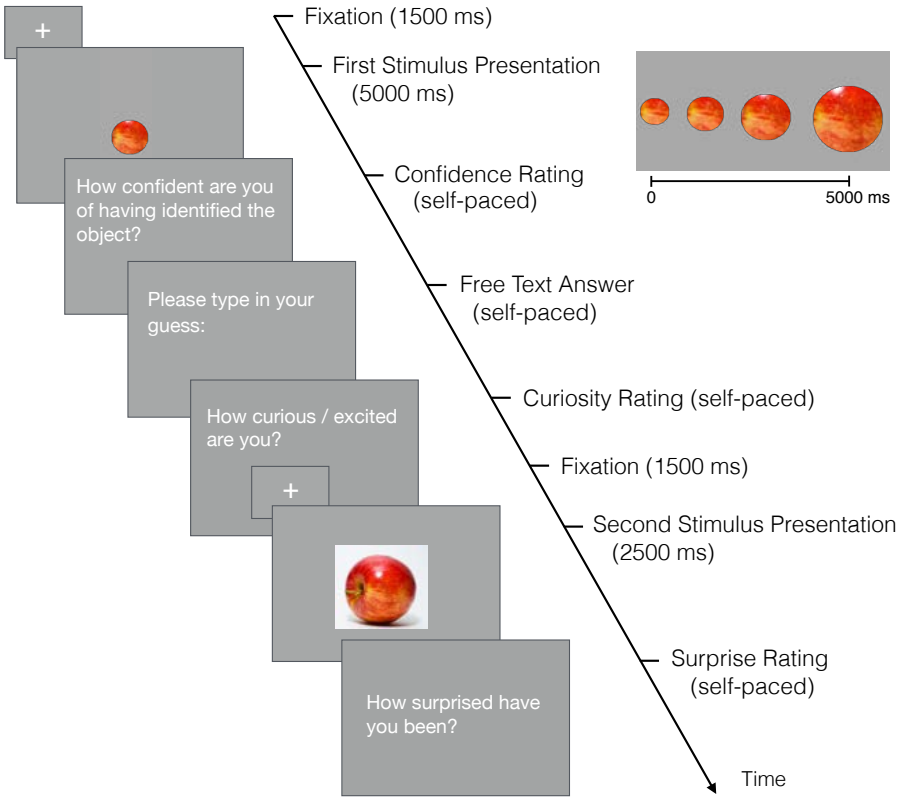


Figure 1. Trial sequence of the newly developed perceptual task. The first stimulus presentation is illustrated in the upper right corner: Within a grey surface, a circular aperture increased continuously, gradually revealing a photo in the background. Following self-reported confidence, free text answer and self-reported curiosity, the same photo was presented fully disclosed.

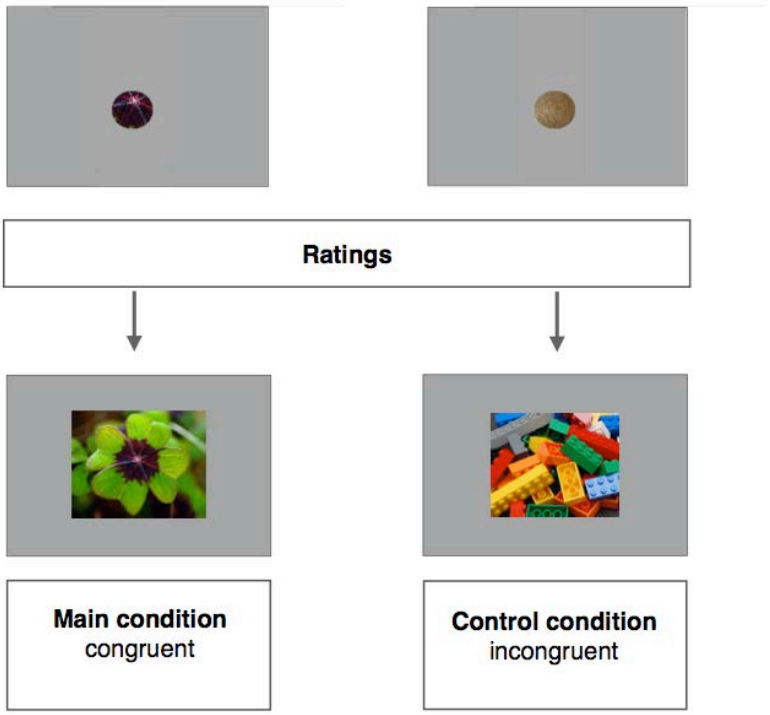


Figure 2. Illustration of the congruent and incongruent conditions. In congruent trials, the partly covered and the fully disclosed stimuli always depicted the same object. In the incongruent condition, they always depicted different objects.

Assuming that the prospect of information triggers incentive motivation, we hypothesized that left-lateralized frontal asymmetry increases with curiosity and with moderate levels of uncertainty. Furthermore, the correlations between frontal asymmetry and uncertainty/curiosity were expected to interact with openness. To test for the specificity of the effects in frontal asymmetry, a control condition was conducted in addition to the main condition (see Figure 2). The study was conducted by a total of 120 participants.

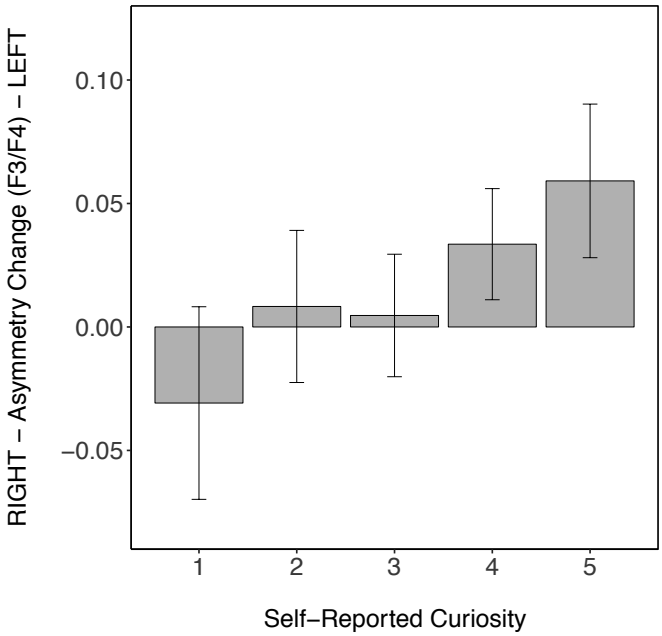


Figure 3. Task-related changes in frontal alpha asymmetry (F4/3) as a function of self-reported curiosity. Frontal asymmetry was calculated in congruent trails during anticipation periods (i.e., 1500 milliseconds prior to the onset of the fully disclosed stimuli). Error bars depict standard errors of the mean (SEM).

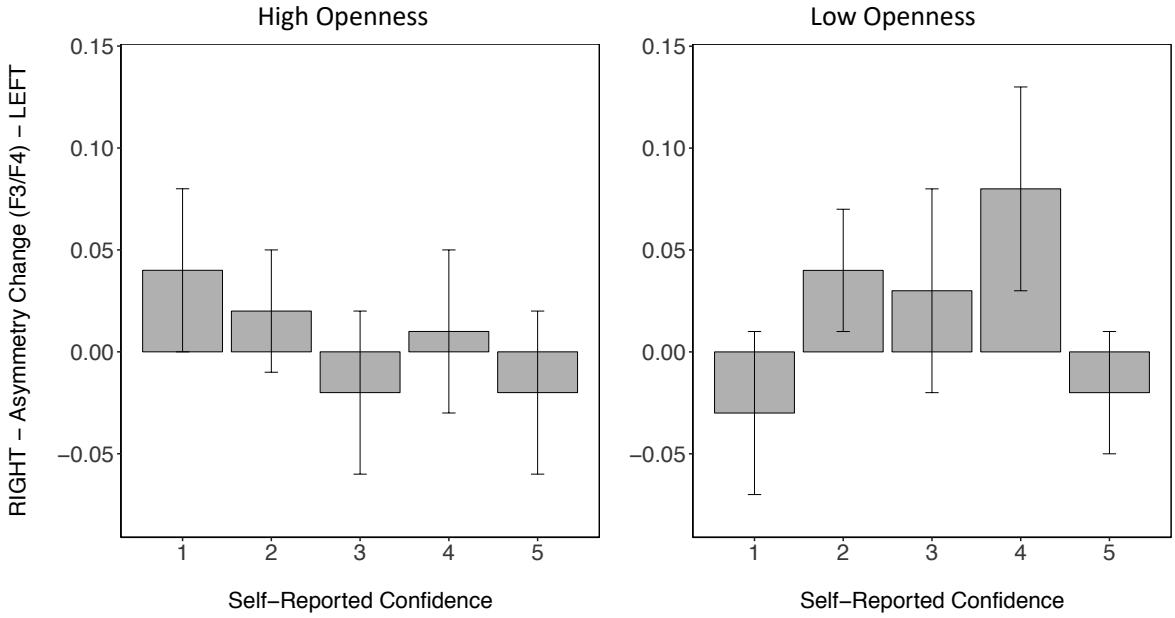


Figure 4. Task-related changes in frontal alpha asymmetry (F4/3) as a function of self-reported confidence and trait levels of openness. Participants were assigned to high and low openness groups by median split. Frontal asymmetry was calculated during anticipation periods in congruent trials (i.e., 1500 milliseconds prior to the onset of the fully disclosed stimuli). Error bars depict standard errors of the mean (SEM).

In the main condition, frontal alpha asymmetry was correlated with self-reported curiosity and confidence during the anticipation period. Particularly, highest levels of left-lateralized activation were associated with medium levels of confidence and with highest levels of curiosity (see Figure 3 and 4). Moreover, the curvilinear relationship with confidence was moderated by openness (see Figure 4). The interaction between congruent and incongruent condition, however, failed to reach statistical significance.

Overall, the first study provides empirical support for an incentive value of information and possible associations with trait levels of openness. The findings suggest that highly open people are more responsive to the rewarding aspects of uncertainty, as

indicated by increased left-lateralized activation during lower levels of confidence. Less open people, however, showed the highest levels of motivational activation when they were more confident (i.e., less uncertain). Since confidence ratings were positively associated with task performance, less open individuals might have been rather motivated by the expectation of positive feedback. Highly open individuals, on the other hand, might have been motivated by the expectation of information itself. Although these conclusions should be considered preliminary, the results provide initial evidence for openness-related individual differences in information processing. Furthermore, the novel task could be used in future research on the neurophysiological underpinnings of uncertainty-related motivational states and to investigate the role of dopamine in curious anticipation.

2.2 Study 2: Openness to experience predicts dopamine effects on divergent thinking

The second study was designed to directly assess the influence of dopamine on the relationship between openness to experience and divergent thinking. Divergent thinking was chosen as a behavioral correlate because its association with openness to experience has been frequently studied and empirically well established (Puryear, Kettler, & Rinn, 2017a). In a placebo-controlled between-subjects design, we administered the dopamine receptor blocker sulpiride or a placebo in two groups of healthy male participants. Sulpiride predominantly acts as a selective D2-receptor antagonist (Mauri, Bravin, Bitetto, Rudelli, & Invernizzi, 1996) and has been well tolerated by healthy participants in previous studies using a single dose of 200mg (Wacker, Mueller, Pizzagalli, Hennig, & Stemmler, 2013; Chavanon, Wacker, & Stemmler, 2013; Wacker, 2018). To assess divergent thinking, participants completed two verbal and two figural tasks from the inventiveness scale of the Berliner Intelligenzstruktur Test (BIS-4, Jäger at al., 1997; see

Figure 5 for an illustration of the object design task). The tasks were scored for ideational fluency (i.e., number of valid solutions) and ideational flexibility (i.e., number of categorically different valid solutions). Openness to experience was assessed beforehand using the NEO Personality Inventory (NEO-PI-3). The final sample consisted of 193 healthy male volunteers aged between 18 and 35 years. We hypothesized that manipulating dopamine activity alters the relationship between self-reported openness to experience and ideational fluency and flexibility.

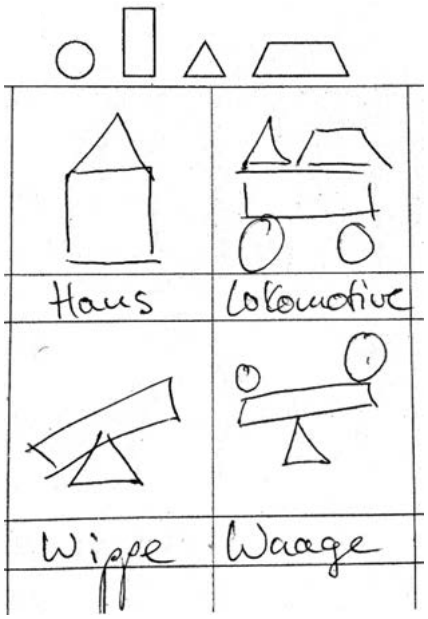


Figure 5. Object design task from the inventiveness scale of the Berliner Intelligenzstruktur Test (BIS 4). Participants are instructed to compose real-life objects using the above given elements.

The data revealed an interaction between openness to experience and substance group. Specifically, openness was more positively associated with both indicators of divergent thinking in the dopamine group (see Figure 6 for fluency). When comparing performance levels, highly open individuals in the dopamine blocker group reached the highest fluency scores (see Figure 7). Thus, sulpiride administration selectively affected divergent

thinking as a function of trait levels of openness to experience. Unexpectedly, the previously established correlation between openness to experience and divergent thinking was not found in the placebo group. The null finding might partly be attributed to unusual characteristics of the study sample. Despite this limitation, the results provide novel empirical evidence for an association between dopamine activity and both openness to experience and divergent thinking.

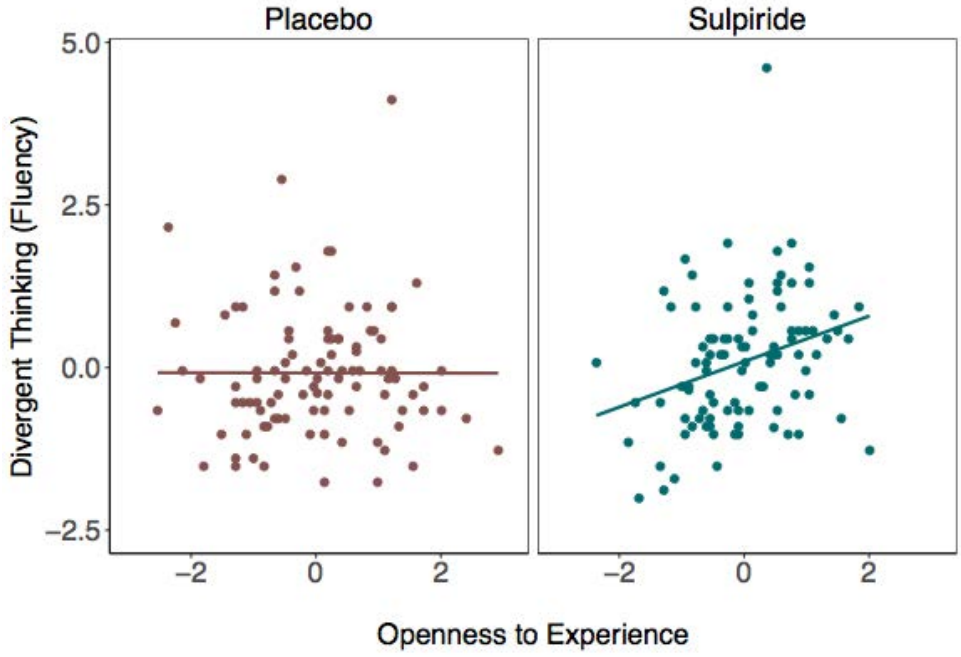


Figure 6. Relationship between openness to experience and divergent thinking in each substance group. Fluency scores (i.e., number of valid solutions) were z-transformed across the whole sample. Openness to experience scores were z-transformed within each experimental group.

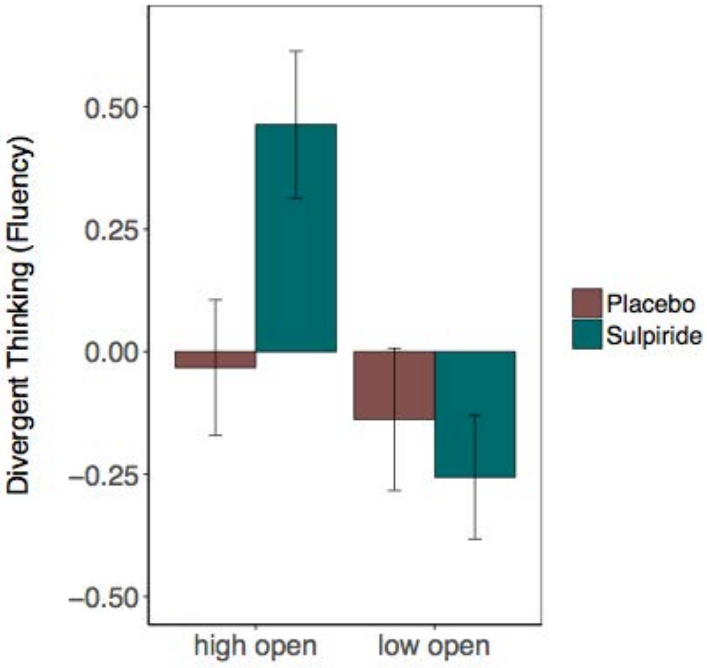


Figure 7. Mean divergent thinking scores separated by openness to experience and substance groups. Participants were assigned to high and low open groups by median split. Divergent thinking scores were z-transformed across the whole sample. Error bars depict standard errors of the mean (SEM).

2.3 Study 3: Are individual differences in openness and implicit sequence learning modulated by dopamine?

The third study was conducted to assess the influence of dopamine activity on the relationship between openness and implicit learning. Implicit learning has been described as information acquisition that does not require intention or conscious awareness of what is learned (Cleeremans, Destrebecqz, & Boyer, 1998). Since spontaneous pattern detection has been theoretically associated with trait characteristics of openness (DeYoung, 2010) it has been hypothesized that highly open people are more likely to behaviorally adapt to incidental stimulus patterns (Kaufman et al. 2010). An empirical

test of this idea has been reported by Kaufman et al., (2010) who found openness positively correlated with implicit sequence learning (Kaufman et al. 2010). However, a recent study that was published during our ongoing data collection failed to replicate this finding (Sobkow, Traczyk, Kaufman, & Nosal, 2018). Thus, trait levels of openness have been theoretically connected to implicit learning, but empirical evidence is ambiguous at present. Given the empirically underpinned involvement of dopamine in implicit learning (e.g., Uddén, Folia, & Petersson, 2010; Kumari, Corr, Mulligan, Cotter, Checkley, & Gray, 1997) and the theorized involvement of dopamine in openness to experience (DeYoung, 2013), we expected the effect of a pharmacological dopamine manipulation on implicit learning to interact with trait levels of openness.

To measure implicit learning, we used the same probabilistic serial reaction time task that has been reported by Kaufman et al. (2010) and Sobkow et al. (2018). Participants performed a simple reaction time paradigm (see Figure 8). Without their knowledge, the consecutive stimulus locations were probabilistically determined by two sequences that generated either probable or improbable stimulus locations. Implicit learning was inferred from relatively faster reaction times to probable stimuli.

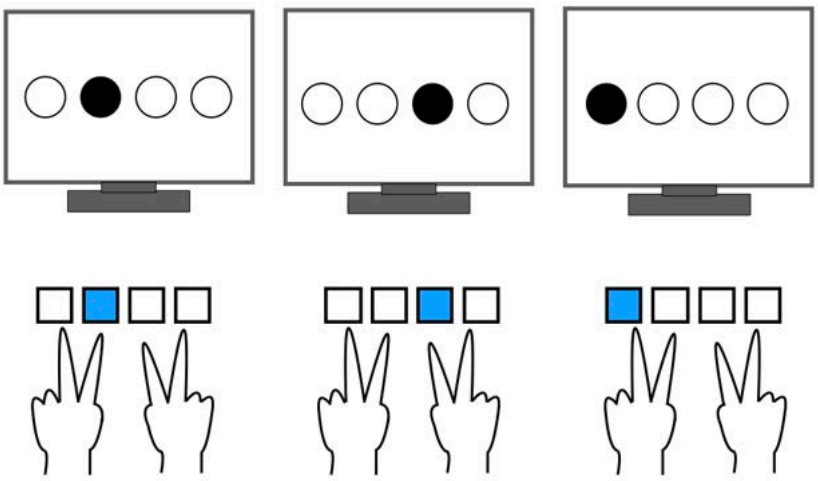


Figure 8. Illustration of the probabilistic serial reaction time task. A black dot appeared at one of four possible locations arranged horizontally on the computer screen. Participants were instructed to respond as quickly and accurately as possible by pressing the corresponding parallel key on the computer keyboard.

The task was performed in the same placebo-controlled between-subjects design as described in Study 2. We hypothesized that manipulating dopamine activity alters the relationship between self-reported openness and implicit learning. Contrary to our predictions, openness was not significantly associated with implicit learning in the placebo group and the hypothesized interaction with substance failed to reach statistical significance. Thus, the hypothesized effect of the dopamine manipulation was not confirmed. Furthermore, the association between openness and implicit learning did not reach significance when meta-analyzing the effects across our data and the two published studies that used the same task. The null findings may partly be attributed to psychometric issues of the implicit learning task. As illustrated in Figure 9, the expected reaction time differences between probable and improbable trails were not evident at all four stimulus

locations. Since the reaction time differences were aggregated across the four stimulus conditions, the absence of an effect in two of four conditions decreased the reliability of the outcome.

In summary, the third study was an initial test of the assumption that dopamine modulates the association between openness and implicit sequence learning. However, the data did neither replicate the initial findings nor confirmed a modulation by dopamine. Due to substantial reliability restrictions, the task in its current form is not considered suitable to investigate individual differences in implicit learning and should be revised before using it in future research.

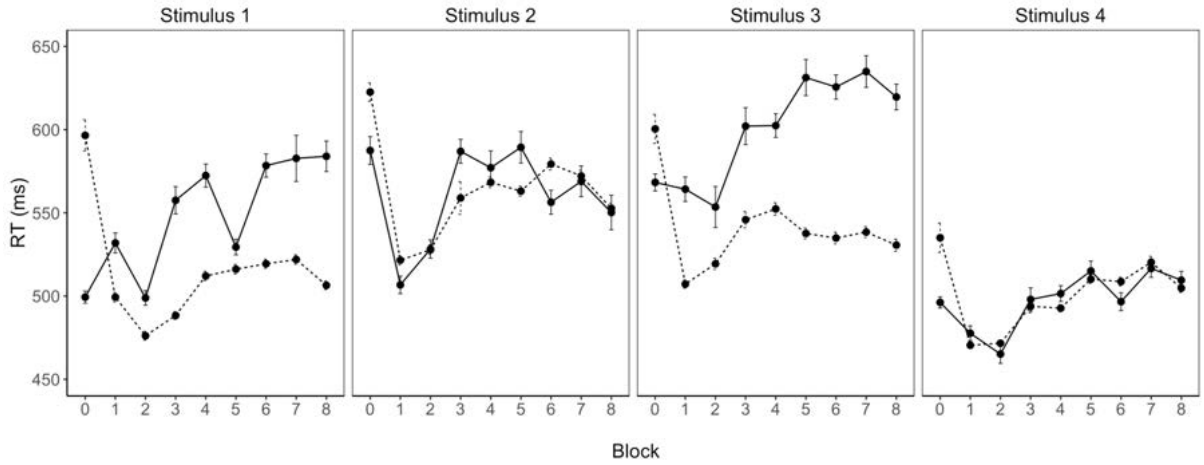


Figure 9. Reaction time differences obtained from the probabilistic serial reaction time task. Probable trials are illustrated with dashed lines and improbable trials with solid lines. Stimulus 1, 2, 3, and 4 denote the four stimulus locations. Block 0 = practice block. Error bars depict standard errors of the mean.

3 General discussion

Understanding the origins of relatively stable patterns in experiencing emotions, cognitive styles, and behavior enlarges our perspectives on individual differences in human personality. The complexity of personality characteristics implies a variety of underlying mechanisms that are involved in explaining trait manifestations. Among biological factors, neuromodulating agents have been suggested to influence brain functions that explain individual differences in emotional-motivational and behavioral tendencies. Contributing to the overall framework, the aim of this dissertation was to investigate the neurobiological basis of individual differences in openness to experience. The hypotheses were built on the theoretical framework by DeYoung (2013) who connected cognitive exploration to trait levels of openness to experience and the neuromodulator dopamine, respectively. The findings presented here contribute novel evidence to the idea that openness to experience partly origins from individual differences in dopaminergic neurotransmission.

3.1 Implications of the present findings

The present findings bear implications for existing theories and future research on the neurobiological basis of openness to experience. The results of the first study support the hypothesis of an incentive value of information and suggest that individual differences in uncertainty-related states might be explained by trait levels of openness. The results further support previous EEG and fMRI findings and encourage future research on individual differences in uncertainty-related states and curious anticipation. The second study most directly supported the overall hypothesis of openness to experience being related to dopamine function. For the first time, it was shown that the administration of a dopaminergic drug altered the association between openness to experience and divergent

thinking. These findings were in line with previous research, suggesting that novelty seeking partly explains the effects of a pharmacological dopamine manipulation on creative ideation (Gvirts et al., 2017). The third study was based on the theoretical link between openness and correlational pattern detection and the empirical link with implicit sequence learning (DeYoung, 2015). However, the results neither supported the initial findings by Kaufman et al. (2010) nor the presumed dopamine modulation. In summary, evidence for the initial hypotheses was found in two of three studies.

3.2 Limitations and methodological considerations

The present research calls attention to methodological considerations that are relevant for improving individual differences research in the future. General methodological arguments as well as specific considerations that arise when investigating behavioral and neurophysiological correlates of personality are discussed along with suggestions for improvement and future directions.

Although published results in personality research mostly yield small to moderate effect sizes (Gignac & Szodorai, 2016), the reported samples are often too small to ensure sufficient statistical power and thus increase the probability of missed effects, false positives, and low replicability. For instance, fMRI correlates of divergent thinking that were mostly obtained from less than thirty participants failed to replicate in large samples (Takeuchi & Kawashima, 2019). Because many EEG studies have similar power limitations, replications in sufficiently sized samples are now necessary to verify the claims that were made on the basis of underpowered studies. In the present research, power analyses were calculated assuming moderate effects ($r = .3$). Although the resulting sample sizes increased the probability of finding the hypothesized effects, the true effect size might still be smaller than expected. Within the placebo group in the second and third

study (n = 98), we could have detected an effect of at least .24 with 80% power. However, the correlation between openness and divergent thinking has been recently estimated at r = .201 (Puryear et al., 2017a). Therefore, even established effects in personality research are probably smaller than commonly assumed and have to be tested in sufficiently sized samples. Effects that do not have strong empirical support should be pre-tested in appropriate samples before conducting resource-intensive neuroscientific studies. To overcome power limitations, cooperative data collection has been suggested as one possible solution to deal with the limited resources of individual researchers (e.g., Wacker, 2017).

When investigating individual differences either in self-reports, task performance or physiological variables, the outcome is considered a relatively stable trait that varies between individuals. Consequently, between-subject variability as well as reliability are necessary requirements to measure individual differences in each outcome. In the present studies, reliability was limited in state levels of frontal asymmetry and implicit learning scores. In both measures, one possible source for reliability restrictions might have been the use of difference scores. That is, the subtraction of two correlated measures lowers the reliability of the resulting difference below the reliability of the individual components (Cronbach & Furby, 1970; Hedge, Powell, & Sumner, 2018). However, difference scores already reduce between-subject variance through subtraction from an individual baseline (e.g., reaction times in a control condition). Therefore, using a within-subject factor with two levels (e.g., sequential, random) does not necessarily overcome the reliability restrictions created by difference scores (Hedge et al., 2018). Using preferably reliable variables to compute difference scores might thus be the best way to ensure sufficient reliability. Regardless of the causes, it is important to compute reliability estimates of each outcome and, if necessary, to consider alternative measures and

analyses. In frontal asymmetry research, using the mean of a cluster of electrodes (e.g., F2/1, F4/3, F7/8) instead of data from only one pair of electrodes (e.g., F4/F3) might be advisable, especially, when using short recording periods.

Ideally, the results of personality research generalize to a broad population and, on the other hand, replicate previous findings. Since we recruited a typical student sample in the first study, the generalizability was somewhat limited, but the sample was comparable to most published studies. In the second and third study, the inclusion criteria were restricted to male gender and only 8% of the participants were psychology students. Thus, the sample differed not only from the general population but also from usually reported samples (i.e., predominantly female psychology students). As a consequence, the sampling bias might have contributed to the unexpected zero correlation within the placebo group. For instance, higher correlations between creative ideation and openness to experiences were reported in psychology student samples (Puryear et al., 2017a). Rather than gender, intelligence has to be considered a possible moderator of the association between divergent thinking and openness to experience. Specifically, openness to experience has been shown more predictive of creative ideation within the higher range of intelligence (Jauk, Benedek, Dunst, & Neubauer, 2013). Because almost half of the published studies employed psychology students (Puryear et al., 2017a), the association between openness and divergent thinking might be overestimated when compared to the general population. Overall, sampling biases have to be taken into account when generalizing findings as well as replicating previous results.

3.3 Future directions

Personality neuroscience is a progressing field with increasing research activity. However, our understanding of the biological basis of personality traits is still in early

stages. Besides developing novel theories, it is thus important to extend the already existing ideas and empirically test current theoretical assumptions.

In his theoretical framework, DeYoung (2013) proposed separable dopaminergic mechanisms that might explain trait characteristics of openness to experience and extraversion, respectively. The assumptions were built on Bromberg-Martin et al.'s (2010) theory of valence and salience coding dopaminergic neurons. He further presumed that extraversion connects to reward processing within a mesolimbic dopaminergic pathway and openness to salience processing within a mesocortical pathway (DeYoung et al., 2005). A direct test of these assumptions in human research, however, is hardly feasible or ethically acceptable. Indirect evidence can be obtained with imaging techniques or pharmacological interventions. In our first pharmacological study, extraversion did not explain variance in the observed interaction with openness to experience, suggesting the findings were not explained by shared variance with extraversion. Because this finding does only allow preliminary conclusions about the specificity of the effects of openness to experience, the approach should be followed up in future research to address the question of separable mechanisms in openness and extraversion, respectively.

Overall, pharmacological manipulations in healthy participants are a valuable approach to investigate the neurobiological basis of personality. As opposed to observational methods, the experimental variation of neurotransmitter activity allows to investigate behavioral or self-reported outcomes in response to centrally-acting substances. However, the intervention does not target specific networks or brain areas and thus limits the conclusions to unspecific effects. Future research should address the specificity of the effects of dopamine with varying dosages of sulpiride as well as other dopaminergic agents (e.g., methylphenidate, haloperidol) or substances (e.g., serotonin

re-uptake inhibitors). Because, to my knowledge, sulpiride has not yet been employed in any published study on creative thinking, I was not able to make specific predictions on how a dosage of 200mg affected divergent thinking. Furthermore, it has to be considered that the same dosage probably has differential effects on individual participants. To increase the accuracy of the results, it would be useful to statistically control for individual substance effects. This could be achieved either by measuring blood levels or using indirect indicators of dopamine activity (e.g., eyeblink rate).

Further steps towards a comprehensive understanding of personality should include more research on behavioral correlates of personality traits. Behavioral outcomes are necessary to investigate changes in response to pharmacological manipulations or neuroscientific techniques (e.g., fMRI, EEG). While associations of openness to experience with intelligence and creative ideation have been well established (e.g., Harris, 2004; Puryear et al., 2017a), attentional phenomena or apophenia have received preliminary support (e.g., Blain et al., 2019). More research is needed to identify correlations between personality traits and established cognitive tasks as well as developing novel paradigms. In the first study, we developed a novel task that can be useful to study the neurobiological basis of perceptual curiosity. However, the relationship between self-reported curiosity and uncertainty was not correlated with openness. Thus, further research is necessary to determine whether behavioral correlates of openness can be obtained with the newly developed task.

Furthermore, specific confounds have to be considered when investigating individual differences in cognitive phenomena and motivational states. Because intelligence explains variance in many performance measures as well as in openness to experience (e.g., Harris, 2004), intelligence should be controlled statistically when investigating behavioral correlates. Moreover, motivational aspects that result from the

experimental context might systematically affect the study of individual differences in emotional-motivational states. Experimental studies often require uniform conditions and many similar trials conducted in laboratory settings that contain little environmental stimulation. Probably, EEG laboratory environments do not optimally engage highly open or extraverted individuals. As an alternative to traditional laboratory studies, portable EEG devices should be considered to conduct research in more natural settings. Either approach, however, usually requires a compromise between internal and external validity. Overall, the study of individual differences adds a lot of complexity to cognitive sciences and generates the challenge to develop a well-functioning study design. Although the process takes time and effort, the results will ultimately contribute to our current understanding of the biological basis of personality.

References

Adcock, R. A., Thangavel, A., Whitfield-Gabrieli, S., Knutson, B., & Gabrieli, J. D. E. (2006). Reward-motivated learning: mesolimbic activation precedes memory formation. *Neuron, 50(3),* 507-517.

Akbari Chermahini, S. & Hommel, B. (2010). The (b)link between creativity and dopamine: Spontaneous eye blink rates predict and dissociate divergent and convergent thinking. *Cognition, 115,* 458-465.

Antinori, A. Carter, O. L. & Smillie, L. D. (2017). Seeing it both ways: Openness to experience and binocular rivalry suppression. *Journal of Research in Personality, 68*, 15-22.

Blain, S., Longenecker, J., Grazioplene, R. G., Klimes-Dougan, B., & DeYoung, C. G. Apophenia as the Disposition to False Positives: A Unifying Framework for Positive Symptoms across the Openness-Psychoticism Spectrum. doi: 10.31234/osf.io/d9wkc

Bromberg-Martin, E. S., Matsumoto, M., & Hikosaka, O. (2010). Dopamine in motivational control: rewarding, aversive, and alerting. *Neuron, 68(5),* 815-834.

Cleeremans, A, Destrebecqz, A. & Boyer, M. Implicit learning: news from the front. *Trends in Cognitive Sciences, 2(10)*, 406-416.

Cloninger, C. R. (1987). A Systematic Method for Clinical Description and Classification of Personality Variants. *Archives of General Psychiatry, 44,* 573-588

Coan, J. A., & Allen, J. J. (2004). Frontal EEG asymmetry as a moderator and mediator of emotion. *Biological Psychology, 67(1),* 7-50.

Costa, P. T., & McCrae, R. R. (1992). Four ways five factors are basic. *Personality and Individual Differences, 13(6),* 653-665.

Cronbach, L. J., & Furby, L. (1970). How we should measure" change": Or should we? *Psychological Bulletin, 74*(1), 68.

Davidson, R. J. (1992). Anterior Cerebral Asymmetry and the Nature of Emotion. *Brain and cognition, 20,* 125-151.

Davidson, R. J. (2003). Affective neuroscience and psychophysiology: Toward a synthesis. *Psychophysiology, 40(5),* 655-665.

De Manzano, Ö., Cervenka, S., Karabanov, A., Farde, L., & Ullén, F. (2010). Thinking outside a less intact box: thalamic dopamine D2 receptor densities are negatively related to psychometric creativity in healthy individuals. *PLoS One, 5,* e10670.

Depue, R. A., & Collins, P. F. (1999). Neurobiology of the structure of personality: Dopamine, facilitation of incentive motivation, and extraversion. *Behavioral and Brain Sciences, 22(3),* 491-517.

Depue, R. A., Luciana, M., Arbisi, P., Collins, P., & Leon, A. (1994). Dopamine and the Structure of Personality: Relation of Agonist-Induced Dopamine Activity to Positive Emotionality. *Journal of personality and social psychology, 67(3),* 485-498.

Depue, R. A. (1995). Neurobiological factors in personality and depression. *European Journal of Personality, 9(5),* 413-439.

DeYoung, C. G. (2010). Personality Neuroscience and the Biology of Traits. *Social and Personality Psychology Compass, 4(12),* 1165-1180.

DeYoung, C. G. (2013). The neuromodulator of exploration: A unifying theory of the role of dopamine in personality. *Frontiers in Human Neuroscience*, *7*, 1- 26.

DeYoung, C. G. (2015). Cybernetic big five theory. *Journal of Research in Personality*, *56*, 33-58.

DeYoung, C. G., Peterson, J. B., & Higgins, D. M. (2005). Sources of openness/intellect: Cognitive and neuropsychological correlates of the fifth factor of personality. *Journal of Personality*, *73(4)*, 825-858.

DeYoung, C. G., Gray, J. R. (2009). Personality neuroscience: explaining individual differences in affect, behaviour and cognition. In Corr, P. J., & Matthews, G. (Eds.). *The Cambridge handbook of personality psychology* (pp. 323–346). New York: Cambridge University Press.

Digman, J. M. (1990). Personality structure: emergence of the Five-Factor model. *Annual review of psychology*, *41*, 417-440.

Digman, J. M. (1997). Higher-order factors of the Big Five. *Journal of personality and social psychology*, *73*(6), 1246.

Eysenck, H. J. (1964). The principles and methods of personality description, classification and diagnosis. *The British Journal of Psychology, 55*(3), 284.

Eysenck, H. J. (1967). The Biological Basis of Personality. Charles C. Thomas. Springfield: Illinois.

Eysenck, H. J., & Eysenck, S. B. G. (1969). The structure and measurement of personality. London: Routledge & Kegan Paul.

Faust-Socher, A., Kenett, Y. N., Cohen, O. S., Hassin-Baer, S., & Inzelberg, R. (2014). Enhanced creative thinking under dopaminergic therapy in Parkinson disease. *Annals of Neurology, 75*(6), 935-942.

Gignac, G. E. & Szodorai, E. T., (2016). Effect size guidelines for individual differences researchers. *Personality and Individual Differences, 102*, 74-78.

Gray, J. A. (1970). The psychophysiological basis of introversion-extraversion. *Behaviour Research and Therapy, 8(3)*, 124-139.

Gray, J. A. (1987). Perspectives on anxiety and impulsivity: A commentary. *Journal of*

Research in Personality, 21(4), 493-509.

Gruber, M. J., Gelman, B. D., & Ranganath, C. (2014). States of curiosity modulate hippocampus-dependent learning via the dopaminergic circuit. Neuron, 84(2), 486-496.

Gvirts, H. Z., Mayseless, N., Segev, A., Lewis, D. Y., Feffer, K., Barnea, Y., ... & Shamay-Tsoory, S. G. (2017). Novelty-seeking trait predicts the effect of methylphenidate on creativity. *Journal of Psychopharmacology, 31,* 599-605.

Harmon-Jones, E. (2003). Clarifying the emotive functions of asymmetrical frontal cortical activity. *Psychophysiology, 40(6),* 838-848.

Harmon-Jones, E. & Allen J. J. (1998). Anger and Frontal Brain Activity: EEG Asymmetry Consistent With Approach Motivation Despite Negative Affective Valence. *Journal of Personality and Social Psychology, 74(5),* 1310-1316.

Harris, J. A. (2004). Measured intelligence, achievement, openness to experience, and creativity. *Personality and Individual Differences, 36(4),* 913-929.

Hedge, C., Powell, G., & Sumner, P. (2018). The reliability paradox: Why robust cognitive tasks do not produce reliable individual differences. *Behavior Research Methods*, *50*(3), 1166-1186.

Jäger, A. O., Süß, H.-M., & Beauducel, A. (1997). Berliner Intelligenzstruktur-Test. Göttingen: Hogrefe.

Jauk, E., Benedek, M., Dunst, B., & Neubauer A. C. (2013). The relationship between intelligence and creativity: New support for the threshold hypothesis by means of empirical breakpoint detection. *Intelligence, 41(4)*, 212-221.

Kang, M. J., Hsu, M., Krajbich, I. M., Loewenstein, G., McClure, S. M., Wang, J. T. & Camerer, C. F. (2009). The wick in the candle of learning. Epistemic curiosity

activates reward circuitry and enhances memory. *Psychological Science, 20(8),* 963-973.

Katz, A. C., Sarapas, C., Bishop, J. R., Patel, S. R., & Shankman, S. A. (2015). The Mediating Effect of Prefrontal Asymmetry on the Relationship between the COMT Val158 Met SNP and Trait Consummatory Positive Affect. Cognition & Emotion, 29(5), 229-262.

Kaufman, S. B., DeYoung, C. G., Gray, J. R., Jiménez, L., Brown, J., & Mackintosh, N. (2010). Implicit learning as an ability. *Cognition, 116(3),* 321-340.

Kreitz, C., Schnuerch, R., Gibbons, H., & Memmert, D. (2015). Some see it, some don't: Exploring the relation between inattentional blindness and personality factors. *PlosOne, 10*(5), 1-16.

Kumari, V., Gray, J. A., Corr, P. J., Mulligan, O. F., Cotter, P. A., & Checkley, S. A. (1997). Effects of acute administration of d-amphetamine and haloperidol on procedural learning in man. *Psychopharmacology*, *129*(3), 271-276.

Lhommée, E., Batir, A., Quesada, J. L., Arduin, C., Fraix, V. Seigneuret, E., … & Krack, P. (2014). Dopamine and the biology of creativity: Lessons from Parkinson's disease. *Frontiers in Neurology, 5,* 1-11. doi: 10.3389/fneur.2014.00055

Mauri, M. C., Bravin, S., Bitetto, A., Rudelli, R., Invernizzi, G. (1996). A risk-benefit assessment of sulpiride in the treatment of schizophrenia. *Drug Safety, 14 (5)*, 288-298.

McCrae, R. R. (1993). Openness to Experience as a Basic Dimension of Personality. *Imagination, Cognition and Personality, 13(1),* 39-55.

McCrae, R. R., & Costa P. T. (1997). Personality trait structure as a human universal. *American Psychologist, 52(5),* 509.

Miller, A., & Tomarken, A. J. (2001). Task-dependent changes in frontal brain asymmetry: effects of incentive cues, outcome expectancies, and motor responses. *Psychophysiology, 38(3),* 500-511.

Molochnikov, I., & Cohen, D. (2014). Hemispheric differences in the mesostriatal dopaminergic system. *Frontiers in Systems Neuroscience, 8,* 1-14.

Mueller, E. M., Burgdorf, C., Chavanon, M. L., Schweiger, D., Wacker, J., & Stemmler, G. (2014). Dopamine modulates frontomedial failure processing of agentic introverts versus extraverts in incentive contexts. *Cognitive, Affective, & Behavioral Neuroscience, 14(2),* 756-768.

Passamonti, L., Terracciano, A., Riccelli, R., Donzuso, G., Cerasa, A., Vaccaro, M. G., Novellino, F., Fera, F. & Quattrone, A. (2015). Increased functional connectivity within mesocortical networks in open people. *Neuroimage, 104,* 301-309.

Peterson, J. B., Carson, S. (2000). Latent Inhibition and Openness to Experience in a high-achieving student population. *Personality and Individual Differences, 28(2),* 323-332.

Peterson, J. B., Smith, K. W., Carson, S. (2002). Openness and extraversion are associated with reduced latent inhibition: Replication and commentary. *Personality and Individual Differences, 33(7),* 1137-1147.

Puryear, J. S., Kettler, T., & Rinn, A. N. (2017a). Relationships of personality to differential conceptions of creativity: a systematic review. *Psychology of Aesthetics, Creativity, and the Arts, 11,* 59-68.

Rademacher, L., Krach, S., Kohls, G., Irmak, A. Gründer, G., & Spreckelmeyer, K. N. (2010). Dissociation of neural networks for anticipation and consumption of monetary and social rewards. *NeuroImage, 49*(4), 3276-3285.

Sanchez-Roige, S., Gray, J. C., McKillop, J., Chen, C. H., & Palmer, A. A. (2018). The genetics of human personality. *Genes, Brain and Behavior, 17*(3), 1-13.

Schultz, W., Dayan, P, & Montague, P. R. (1997). A neural substrate of prediction and reward. *Science, 275,* 1593-1599.

Simon, J. J., Walther, S., Fiebach, C. J., Friederich, H. C., Stippich, C., Weisbrod, M., Kaiser, S. (2010). Neural reward processing is modulated by approach- and avoidance-related personality traits. *NeuroImage, 49(2),* 1868-1874.

Sobkow, A., Traczyk, J., Kaufman, S. B., & Nosal, C. (2018). The structure of intuitive abilities and their relationships with intelligence and Openness to Experience. *Intelligence*, *67*, 1-10.

Sobotka, S. S., Davidson, R. J., & Senulis, J. A. (1992). Anterior brain electrical asymmetries in response to reward and punishment. *Electroencephalography and clinical neurophysiology, 83,* 236-247.

Swerdlow, N. R., Stephany, N., Wasserman, L. C., Talledo, J., Sharp, R., & Auerbach, P. P. (2003). Dopamine agonists disrupt visual latent inhibition in normal males using a within-subject paradigm. *Psychopharmacology, 169,* 314-320. doi: 10.1007/s00213-002-1325-6

Takeuchi, Tomita, H., Taki, Y., Kikuchi, Y., Ono, C., Yu, Z., … & Kawashima, R. (2015). Cognitive and neural correlates of the 5-repeat allele of the dopamine D4 receptor gene in a population lacking the 7-repeat allele. *NeuroImage, 110,* 124-135.

Takeuchi, H. & Kawashima, R. (2019). Implications of large-sample neuroimaging studies of creativity measured by divergent thinking. *Current Opinion in Behavioral Sciences, 27*, 139-145.

Tomer, R., Goldstein, R. Z., Wang, G.-J., Wong, C., Nora, D. (2008). Incentive motivation is associated with striatal dopamine asymmetry. *Biological Psychology, 77(1),* 98-101.

Tomer, R., Slagter, H. A., Christian, B. T., Fox, A. S., King, C. R., Murali, D., Gluck, M. A., Davidson, R. J. (2014). Love to win or hate to lose? Asymmetry of dopamine D2 receptor binding predicts sensitivity to reward vs. punishment. *Journal of Cognitive Neuroscience, 26(5),* 1-10.

Uddén, J., Folia, V., & Magnus Petersson, K. (2010). The neuropharmacology of implicit learning. *Current neuropharmacology*, *8*(4), 367-381.

Vukasović, T. & Bratko, D. (2015). Heritability of personality: A meta-analysis of behavior genetic studies. *Psychological Bulletin, 141*(4), 769-785.

Wacker, J. (2017). Increasing the reproducibility of science through close cooperation and forking path analysis. *Frontiers in Psychology, 8*, 8-11.

Wacker, J. (2018). Effects of positive emotion, extraversion, and dopamine on cognitive stability-flexibility and frontal EEG asymmetry. *Psychophysiology, 55*(1), e12727.

Wacker, J., Chavanon, M. L., Stemmler, G. (2006). Resting EEG signatures of agentic extraversion: New results and meta-analytic integration. *Journal of Research in Personality, 44(2),* 167-179.

Wacker, J., Mueller, E. M., Pizzagalli, D. A., Hennig, J., Stemmler, G. (2013). Dopamine-d2-receptor blockade reverses the association between trait approach motivation and frontal asymmetry in an approach-motivation context. *Psychological Science, 24(4),* 489-97.

Wacker, J., & Smillie, L. D. (2015). Trait extraversion and dopamine function. *Social and Personality Psychology Compass, 9(6),* 225–238.

Weiner, I., Shadach, E., Tarrasch, R., Kidron, R., & Feldon, J. (1996). The latent inhibition model of schizophrenia: Further validation using the atypical neuroleptic, clozapine. *Biological Psychiatry, 40(9),* 834-843.

Weiner, I., & Feldon, J. (1987). Facilitation of latent inhibition by haloperidol in rats. *Psychopharmacology, 91(2),* 248-253.

Wilson, K. E., Lowe, Matthew X., Ruppel, J., Pratt, J., Ferber, S. (2016). The scope of no return: Openness predicts the spatial distribution of inhibition of return. *Attention, Perception, and Psychophysics, 78*(1), 209-217.

Wu, C. C., Samanez-Larkin, G. R., Katovich, K., Knutson, B. (2014). Affective traits link to reliable neural markers of incentive anticipation. *NeuroImage, 84,* 279-289.

Zinser, M. C., Fiore, M. C., Davidson, R. J., & Baker, T. B. (1999). Manipulating Smoking Motivation: Impact on an Electrophysiological Index of Approach Motivation. *Journal of Abnormal Psychology 108(2),* 240-254.

Appendix A

Käckenmester, W., Kroencke, L., & Wacker, J. (2018). Frontal asymmetry predicts the incentive value of perceptual information. *International Journal of Psychophysiology (134)*, 22-29.

International Journal of Psychophysiology 134 (2018) 22–29

Contents lists available at ScienceDirect

International Journal of Psychophysiology

journal homepage: www.elsevier.com/locate/ijpsycho

Frontal asymmetry predicts the incentive value of perceptual information☆

Wiebke Käckenmester, Lara Kroencke, Jan Wacker*

Faculty of Psychology and Human Movement Science, Institute for Psychology, Universität Hamburg, Germany

ARTICLE INFO

Keywords:
Frontal asymmetry
Motivation
Reward
Openness
Curiosity

ABSTRACT

Information has been suggested to convey incentive value mediated by dopaminergic systems similar to those implicated in extrinsic reward. Although the reward characteristics of information have received preliminary support by behavioral and fMRI findings, EEG correlates and individual differences have not yet been examined. In the current study, a novel perceptual paradigm was developed to probe the associations between anticipation of perceptual information and frontal electroencephalographic alpha asymmetry, i.e., a marker of approach motivation. Assuming individual differences in engaging with perceptual information, trait openness was examined as a moderator of the associations. One hundred and twenty participants viewed partly visible photos that were gradually uncovered. After they indicated state levels of confidence and curiosity, the photos were fully disclosed. During anticipation of the fully disclosed stimuli, left-lateralized asymmetry linearly increased with curiosity. Moreover, a curvilinear relationship between confidence and left-lateralized asymmetry emerged, suggesting enhanced motivational activation during medium levels of uncertainty. The curvilinear relationship was moderated by trait openness, indicating individual differences in the responsiveness to perceptual uncertainty. In summary, our findings provide novel empirical evidence for the incentive motivational value of information.

1. Introduction

Even in the absence of primary incentives, humans voluntarily engage in information acquisition. The desire for exploration motivates various activities, such as puzzle solving, encountering unfamiliar environments, or browsing the internet. Essentially, curiosity has been conceived of as an approach-oriented motivational state that is triggered by uncertainty (Berlyne, 1966; Kashdan and Silvia, 2009). While high levels of uncertainty or unpredictability usually cause fear and withdrawal (Hirsh et al., 2012), moderate levels of uncertainty trigger curiosity and exploration (DeYoung, 2013). From behavioral and neurophysiological findings, DeYoung (2013) concluded that the possibility to gain information is inherently rewarding. Consequently, it has been argued that information and primary rewards, e.g., food or money, are similarly incentivizing (DeYoung, 2013; Kang et al., 2009). For instance, people are willing to expend scarce resources in order to obtain answers that they are curious about (Kang et al., 2009; Loewenstein, 1994), supporting the idea that information conveys incentive value. On a neurobiological level, dopaminergic midbrain neurons have been shown to encode both reward and information prediction (Bromberg-Martin and Hikosaka, 2009; Bromberg-Martin and Hikosaka, 2011). Moreover, state curiosity has been associated with activation of regions with dense dopaminergic inputs like the nucleus caudatus (Kang et al., 2009), nucleus accumbens, and the midbrain (Gruber et al., 2014), regions similar to those implicated in monetary reward anticipation (Adcock et al., 2006; Rademacher et al., 2010; Simon et al., 2010). Accordingly, evidence suggests that anticipation of both extrinsic reinforcers and information activate dopaminergic reward networks (Gruber et al., 2014; Kang et al., 2009).

1.1. Individual differences in curiosity

From an individual differences perspective, the tendency for being curious has been described as a key characteristic of the Big Five domain openness to experience (Costa and McCrae, 1992). High trait levels of openness to experience have been associated with broader interests, wider attentional focus and inherent interest in perceptual stimuli (McCrae, 1994; McCrae, 2007; Peterson and Carson, 2000). Moreover, open people prefer complex stimulus patterns over simple ones (Silvia et al., 2009) and appraise ambiguity as interesting rather

☆ This research was supported by a stipend of the Winzig Stiftung to the first author. The sponsor was not involved in the current research at any point. The authors have no conflicts of interest to disclose.

* Corresponding author at: Faculty of Psychology and Human Movement Science, Institute for Psychology, Universität Hamburg, 5 Von-Melle-Park, Hamburg, DE 20146, Germany.
E-mail address: jan.wacker@uni-hamburg.de (J. Wacker).

https://doi.org/10.1016/j.ijpsycho.2018.10.002
Received 9 August 2018; Received in revised form 24 September 2018; Accepted 2 October 2018
Available online 06 October 2018

than aversive (Furnham and Marks, 2013). The broad Openness domain comprises intellect, a trait referring to engagement with abstract information, e.g., scientific insights or philosophical ideas, and openness, a trait referring to engagement with aesthetic and perceptual materials, e.g., visual art, poetry, or the aesthetic aspects of nature (DeYoung, 2010; Fayn et al., 2015). Given a preference for perceptual information, unusual or ambiguous stimulus patterns are supposed to be particularly interesting for highly open individuals.

1.2. Frontal asymmetry as an index of approach motivation

Conceiving of curiosity as an approach-oriented motivational state (Berlyne, 1966; Kashdan and Silvia, 2009; Loewenstein, 1994), we intend to capture its neurophysiological correlates with frontal EEG alpha asymmetry, an established index of approach motivation. Frontal asymmetry has been suggested to index motivational approach versus withdrawal (Davidson, 1992, 1993) or behavioral activation versus inhibition (Wacker et al., 2003; Wacker et al., 2010). In support of these suggestions, left-lateralized activation has been connected to states of reward anticipation, i.e., expecting monetary wins in a gambling task (Gorka et al., 2015; Lieberman et al., 2016; Miller and Tomarken, 2001; Nelson et al., 2017; Sobotka et al., 1992; but see Katz et al., 2015). Compared with monetary losses or neutral outcomes, reward-associated increases in frontal alpha asymmetry have been interpreted in terms of approach-directed motivation. Based on the connection between curiosity and approach motivation, we hypothesize that the index extends to state levels of curiosity.

1.3. The present study

The present study was designed to investigate EEG correlates of state curiosity within a newly developed perceptual paradigm. With the aim of creating an incentive motivational context, the task generates and resolves perceptual uncertainty. Specifically, details of photos are partially uncovered and thus create ambiguous visual percepts. Participants watch the continuously increasing part of the photo and try to identify the depicted object. After they indicate confidence in having identified the object and state levels of curiosity, the photo's content is fully revealed. Anticipating the fully revealed stimulus, frontal alpha asymmetry is analyzed as a function of self-reported curiosity and confidence. In line with previous studies using trivia questions, confidence ratings serve as an index of uncertainty (Kang et al., 2009). Importantly, the two consecutive stimuli are presented congruently such that the ambiguous and the fully revealed stimulus depict the same object. Thus, uncertainty will be created and subsequently dissolved within each trial. To test for the specificity of the effect in frontal asymmetry, we additionally designed a control condition with incongruent stimulus sequences. Therein, the two consecutive stimuli are non-equivalent such that the ambiguous stimulus and the fully revealed stimulus display different objects. Thus, uncertainty will be created but not dissolved in the control condition. If the effects of curiosity and confidence on frontal asymmetry were driven entirely by the anticipation of seeing the full picture (i.e., getting the desired information) one would not expect analogous effects for the incongruent control condition. However, if the effects were driven by the desire to get the information quite independently of the anticipation of actually getting it, one would expect similar effects for the control condition.

To our knowledge, EEG correlates of curiosity and its associations with trait openness have not yet been investigated in previous studies. All data obtained within the newly developed task is presented here for the first time.

1.4. Hypotheses

In previous studies, medium levels of self-reported confidence have been associated with highest states of curiosity, resulting in an inverted u-shaped relationship (Kang et al., 2009; Litman et al., 2005). Accordingly, we predicted an inverted u-shaped relationship between self-reports of confidence and curiosity. Assuming that frontal asymmetry may index the approach tendencies inherent in curiosity we also expected (1) an analogous inverted u-shaped relationship between confidence and frontal asymmetry as well as (2) a positive linear association between state curiosity and frontal asymmetry. As opposed to the incongruent condition, the presumed correlations with frontal asymmetry were expected to emerge in the congruent condition only. Furthermore, the hypothesized relationships were expected to be moderated by self-reports of openness. Since the hypotheses on openness have to be considered exploratory, we refrain from predicting specific directions of the moderating influences.

2. Methods

2.1. Participants

In order to collect a sample of 120 usable datasets, a total of 127 right-handed healthy volunteers participated in the EEG study. They received twenty-five euros ($27) or course credits in exchange for their participation. During the data collection, we lost data of three participants due to technical malfunctions. Following the data analyses, four participants had to be excluded due to missing data or insufficient data quality. The remaining 120 participants (90% university students, 36% male) ranged in age from 18 to 35 years ($M = 24.75$, $SD = 4$). Handedness was assessed using a short form of the Edinburgh Handedness Inventory (Veale, 2014). Following the authors' recommendations, laterality quotients ranging from 60 to 100 were classified as right-handedness (Veale, 2014). Participants who fulfilled this criterion and did not report any psychiatric or neurological disorders were invited to the laboratory study. The study was conducted in accordance with the Declaration of Helsinki and in keeping with the ethical guidelines of the German Psychological Society (DGPs). Written informed consent was obtained.

2.2. Experimental task and stimuli

The experimental task was programmed using the software Presentation (Neurobehavioral Systems, Berkeley, USA, Version 17.1). All participants completed the congruent condition. Because the study was developed in successive steps, the incongruent control condition was introduced during the ongoing data collection, such that half of the total sample (N = 62) additionally completed the incongruent condition. Each condition comprised 50 randomized trials that were conducted in blocks. The blocks were presented in counterbalanced order.

The trial sequence of the main condition is illustrated in Fig. 1. The first stimulus consisted of two layers: Centrally located in the background, a photo (700 by 560 pixels) was covered by an opaque gray surface. In its center, the surface enclosed a circular aperture (30 pixels diameter). Each trial started with a white fixation cross (1500 milliseconds). Subsequently, the partly covered photo was presented: Over the course of 5000 milliseconds, the circular aperture increased pixel by pixel until it reached a diameter of 190 pixels. Thus, 7% of the photo in the background were progressively uncovered. Participants were instructed to watch the enlarging visible part of the partly covered photo and try to identify the depicted object (e.g., apple, cat, or cube). Afterwards, they indicated how confident they were of having identified the object. Then, they typed in their guess and rated their level of curiosity. Following a variable inter-stimulus interval, a 1500 milliseconds fixation cross was presented. Subsequently, the same photo was presented without the opaque surface for 2500 milliseconds. Thus, the same object that was covered before was now fully visible. Each trial was concluded by self-reports of surprise. Inter-stimulus intervals preceding each fixation cross varied randomly between 500 and 1500 milliseconds. All quantitative ratings were displayed on visual

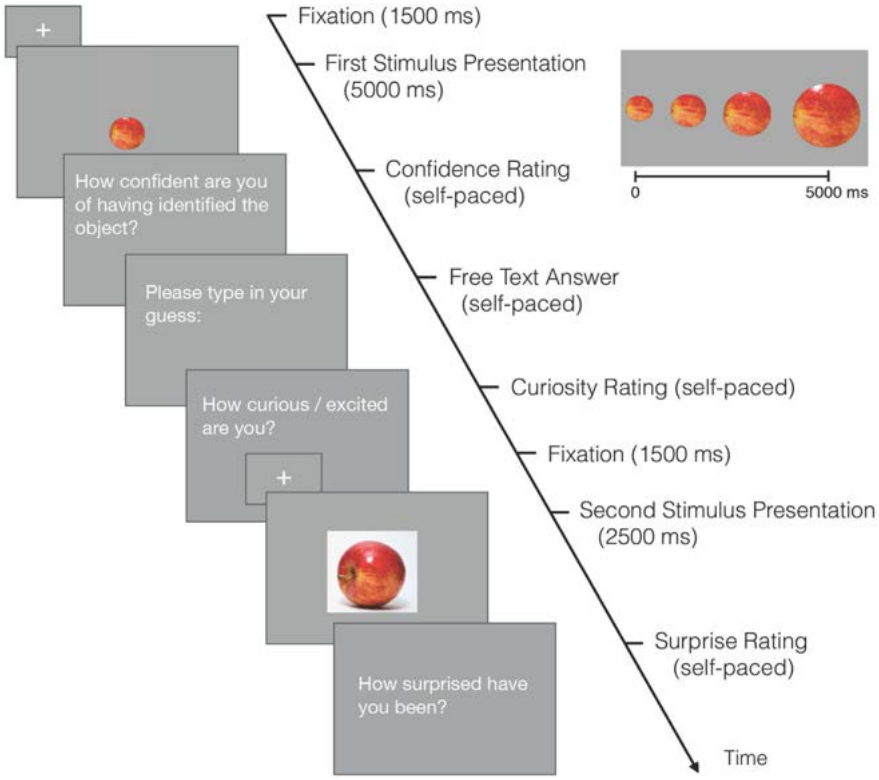


Fig. 1. Trial sequence of the congruent condition. The first stimulus presentation is illustrated in the upper right corner: Within the gray surface, a circular aperture increased continuously, gradually revealing the photo in the background. Following self-reported confidence, free text answer, and curiosity, the same photo was presented fully disclosed.

analogue scales with five labels and percent descriptions (0 to 100%). To obtain performance measures, two independent raters classified the free text answers into correct and incorrect responses. Deviating solutions were evaluated by a third person.

In addition to the main condition, a control condition was introduced. Here, the trial sequence was modified by incongruent sequences such that the partly covered photo and the fully disclosed photo depicted different objects. For example, the photo covered by the opaque gray surface would depict an apple and the fully disclosed photo within the same trial would depict a cube. Consequently, participants never saw the partly covered stimuli fully disclosed. The trial sequence and subjective ratings were the same as in the congruent condition. Prior to conducting the incongruent condition, participants were informed about the nature of the task, i.e., they were told that only incongruent stimuli were presented. By introducing this condition, we hoped to discriminate between anticipating wanted information and only wanting that information.

2.2.1. Stimulus selection and pre-testing

The task was developed and adjusted in consecutive pretests. In a first step, photos that depicted familiar, unambiguous, and emotionally neutral objects were searched from the internet. Only photos that were labeled for noncommercial reuse were considered. The selected stimuli depicted every-day objects, food, and animals. To avoid confounding effects of emotional arousal, we aimed for low arousing stimuli. In a second step, forty participants rated the selected photos for emotional valence and arousal using the Self-Assessment Manikin (SAM). SAM is an affective rating system in which graphic figures represent the values on the valence and arousal scales (Lang, 1980), and which is frequently used for the assessment of emotional stimuli in the context of experimental investigations. For comparison, we included 28 photos from the International Affective Picture System (IAPS, Lang et al., 1997). Fourteen IAPS stimuli with positive valence and high or low arousal ratings (e.g., skydiver, baby seal) were chosen, respectively. From our set of photos, stimuli with higher arousal ratings than at least one of the high arousal IAPS stimuli were excluded. Lastly, we pre-tested the remaining stimuli within the newly developed task to ensure that the final set comprised a broad range of confidence levels.

2.3. EEG data collection

In accordance with the international 10–20 system (Klem et al., 1999), the EEG was recorded from 64 electrode sites using the ActiveTwo system by BioSemi (Amsterdam, NL). All sites were online referenced to a Common Mode Sense (CMS) active electrode and a Driven Right Leg (DRL) passive electrode. EEG activity was recorded during the task as well as during a 5-minute eyes-open resting period while participants sat quietly and looked at a fixation cross. All pre-processing steps were performed using BrainVision Analyzer 2.1 (BrainProducts GmbH, Gilching, DE). The data was down-sampled to 512 Hz and high-pass filtered at 0.5 Hz. After visual rejection of large non-stereotyped artifacts, we applied extended infomax-independent component analysis (ICA) in order to identify artifacts caused by ocular activity. Channels that were not primarily relevant for the analyses and strongly contaminated with artifacts were replaced by a topographic interpolation algorithm. Data was then re-referenced to an average montage, and a detailed visual inspection was performed in order to exclude all trials with remaining artifacts. Seven percent of the EEG segments had to be rejected due to contamination with artifacts.

EEG frequency spectra were computed using Fast Fourier transforms (FFT). In preparation for FFT, the extracted task periods were segmented into 50% overlapping 1000 millisecond-intervals. All artifact-free epochs were submitted to a Fast Fourier transform, using a Hanning window. The total power density (μV^2/Hz) within the alpha frequency band (8–13 Hz) was extracted. For computation of frontal asymmetry indices, power density within the alpha frequency spectrum was log-transformed and subtracted at the homologous midfrontal electrodes F4–F3, following the recommendations by Allen et al. (2004). In order to compute Cronbach's alpha internal reliability, the five-minute resting EEG recordings were split into one-minute intervals. To compute internal reliability of the task recordings, each of the confidence and curiosity categories were split into odd and even trials,

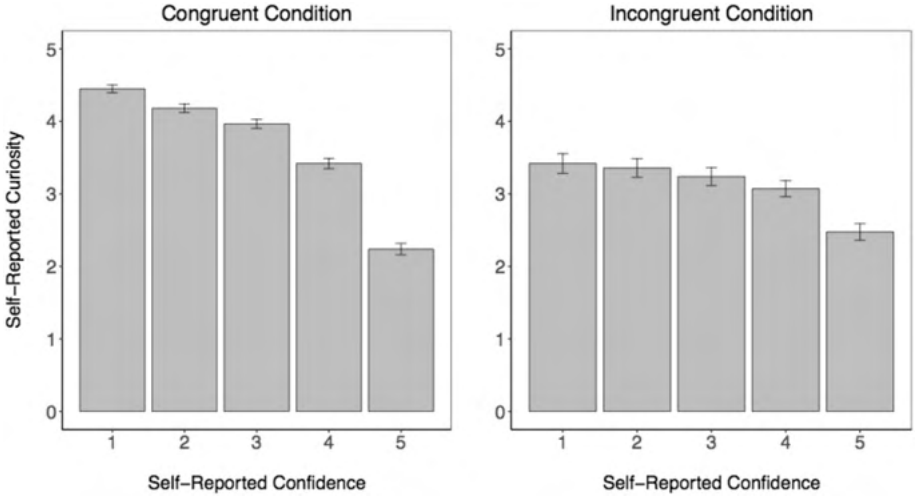


Fig. 2. Self-reported curiosity as a function of confidence in identifying the partly covered objects. The partly covered and the fully revealed stimuli depicted the same object (congruent condition, n = 120) or unrelated objects (incongruent condition, n = 62). Error bars depict standard errors of the mean (SEM).

respectively.

In previous studies, frontal asymmetry has been calculated within intervals of up to 11 s during event-related anticipation periods (Lieberman et al., 2016; Katz et al., 2015; Nelson et al., 2017). However, when presenting approach-related stimuli, Schöne et al. (2016) found significant event-related changes in frontal asymmetry only within 500 to 1000 milliseconds post-stimulus. Assuming that the motivational states, which we aim to target, are relatively brief, we specified anticipation periods of 1500 milliseconds prior to stimulus onset.

2.4. Statistical data analysis

To account for multiple correlated observations within participants, the main hypotheses were tested with generalized estimating equations (GEEs). Unlike traditional regression-based approaches, GEEs do not assume equal correlations across repeated measurements, thus allowing for correlated residuals and flexible correlation structures (Muth et al., 2016). Although GEEs yield similar results to linear mixed effects (LME) models, their results have been found less biased due to robust standard error estimation (Hubbard et al., 2010; Muth et al., 2016). All models were fitted with the geeglm function in R (R Core Team, 2012), version 3.2.1., using an exchangeable working correlation matrix. Since we were specifically interested in task-related changes in alpha asymmetry we included alpha asymmetry obtained during rest to control for individual differences in resting frequency patterns. To test for the regional specificity of the effects, all models predicting alpha asymmetry included a region factor contrasting frontal (F3/F4) with parietal (P3/P4) sites. Self-reported curiosity (Model 1) was predicted with confidence, squared confidence, condition (congruent, incongruent), openness, and the respective interactions. Task-related changes in alpha asymmetry (Model 2) were predicted with confidence, squared confidence, condition (congruent, incongruent), region (frontal, parietal), resting asymmetry, openness, and the respective interactions. In Model 3, task-related changes in alpha asymmetry were predicted with curiosity, condition, region, resting asymmetry, openness, and the respective interactions. According to the above stated hypotheses, we expect interactions between self-reports, condition, region, and openness. Significant interactions were tested post hoc in separate models. Because participants did not use the sections of the rating scale with equivalent frequency and because the number of aggregated trials influences the reliability of frontal asymmetry estimates, the number of trials per category was included as weight. Ratings and openness scores were z-transformed prior to the analysis. The R script we used for statistical analyses can be found on https://osf.io/6z5yp/ (Open Science Framework).

2.5. Personality assessment

We administered a German version of the Big Five Aspect-Scales, which were designed to measure two subdomains of each of the Big Five personality domains (DeYoung et al., 2007; German version by Paelecke & Mussel, in preparation). The openness scale (10 items) yielded a Cronbach's alpha internal-consistency of 0.79.

3. Results

3.1. Behavioral data

As predicted, self-reported confidence was curvilinearly associated with self-reported curiosity, $b = -0.359$, $X^2(1) = 37.18$, $p < .001$, such that highest states of curiosity were associated with medium levels of confidence. Additionally, a negative linear effect emerged, $b = -0.853$, $X^2(1) = 640.2$, $p < .001$. Thus, confidence ratings predicted linear as well as curvilinear trends in curiosity ratings. Openness, however, did not interact with either the linear relationship, $b = 0.0067$, $X^2(1) = 0.02$, $p = .88$, nor the curvilinear relationship, $b = -0.0358$, $X^2(1) = 1.38$, $p = .24$. Additionally, a main effect of condition emerged, $b = -0.613$, $X^2(1) = 21.65$, $p < .001$, suggesting overall higher states of curiosity within the congruent condition. Furthermore, condition interacted with the linear effect of confidence ($b = -0.613$, $X^2(1) = 21.65$, $p < .001$), indicating that the difference between conditions was particularly pronounced in low confidence trials. Although the curvilinear trend in confidence was diminished in the incongruent condition, the interaction with condition did not reach significance, $b = 0.103$, $X^2(1) = 3.42$, $p = .065$. The correlations between self-reports are illustrated in Fig. 2.

As intended when constructing the task, about half of the presented objects were identified correctly (M = 55.5%, SD = 9.7%). Confidence ratings were positively correlated with task performance, $r = 0.7$, such that participants were more likely to answer correctly when they were certain of having identified the depicted objects. Moreover, task performance was not associated with openness scores, $r = 0.09$, $p = .3$. Therefore, we assume that any effects of openness are not influenced by individual differences in task performance.

3.2. EEG alpha asymmetry

Within the five-minute resting recordings, frontal alpha asymmetry

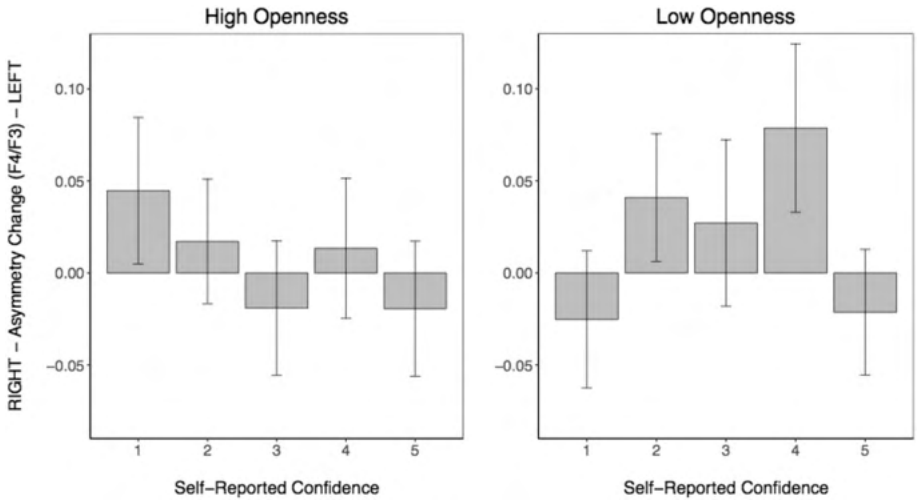


Fig. 3. Task-related changes in frontal alpha asymmetry (F3/F4) as a function of self-reported confidence and trait openness. Frontal asymmetry was calculated during anticipation periods within the congruent condition, i.e., 1500 milliseconds prior to the onset of the fully disclosed stimuli. To graphically illustrate the interaction with openness, participants were assigned to high and low open groups by median split. The error bars depict standard errors of the mean (SEM).

(F3/F4) yielded an internal consistency of 0.95. As a function of the task recordings, the reliability estimates ranged from 0.46 to 0.68 within confidence categories and from 0.38 to 0.67 within curiosity categories. Resting asymmetry scores (F3/F4) were unrelated to self-reports of openness, $r = 0.03$, $p = .7$.

3.2.1. Task-related asymmetry changes

Task-related changes in alpha asymmetry were calculated during anticipation periods. Predicting alpha asymmetry with confidence ratings (Model 2), a significant Confidence^2 X Region interaction emerged, $b = 0.076$, $\chi^2(1) = 9.87$, $p = .0017$. As hypothesized, follow up analyses revealed an inverted u-shaped relationship at frontal sites (F3/F4), $b = -0.029$, $\chi^2(1) = 5.43$, $p = .02$, indicating that left-lateralized frontal activation was highest during medium states of confidence. Furthermore, the curvilinear trend significantly interacted with openness, $b = 0.031$, $\chi^2(1) = 6.15$, $p = .013$, such that the curvilinear relationship was evident in less open individuals while highly open individuals demonstrated a rather negative linear relationship (see Fig. 3). For comparison with related personality traits, we tested whether Intellect and Extraversion yielded the same moderating effect as Openness. Both Intellect, $b = -0.012$, $\chi^2(1) = 0.66$, $p = .42$, and Extraversion, $b = -0.00075$, $\chi^2(1) = 0.00$, $p = .95$, did not interact with the curvilinear effect in confidence. Finally, we tested the specificity of the effects when comparing the congruent with the incongruent condition. However, the interaction Confidence^2 X Region X Condition just failed to reach significance, $b = -0.075$, $\chi^2(1) = 3.61$, $p = .057$. Thus, the effects of self-reported confidence and trait openness did not significantly differ between conditions.

Predicting alpha asymmetry with curiosity ratings (Model 3), a significant Curiosity X Region X Condition interaction emerged, $b = 0.135$, $\chi^2(1) = 4.79$, $p = .029$. Follow up analyses revealed a linear increase in frontal alpha asymmetry with curiosity, $b = 0.02$, $\chi^2(1) = 4.64$, $p = .031$, such that left-lateralized activation was highest when participants were most curious (see Fig. 4). Furthermore, condition significantly interacted with curiosity at parietal sites, $b = 0.099$, $\chi^2(1) = 11.63$, $p = .0065$, but not at frontal sites, $b = -0.033$, $\chi^2(1) = 2.63$, $p = .105$. The interaction at parietal electrodes was due to a decrease in alpha asymmetry within the congruent condition. The topographical distributions of the effects are displayed in Fig. 5. Openness did not yield significant interactions with curiosity, region, or condition, $\chi^2(1) < 0.62$, $p > .43$.

In sum, self-reported confidence and self-reported curiosity predicted task-related changes in frontal alpha asymmetry. As expected, left-lateralized frontal activation increased with state curiosity and the curvilinear association with confidence was moderated by trait openness. When testing the regional specificity, we found reversed effects of confidence and curiosity at parietal sites. Contrary to our hypotheses, the frontal effects of confidence and curiosity were not specific to the congruent condition.

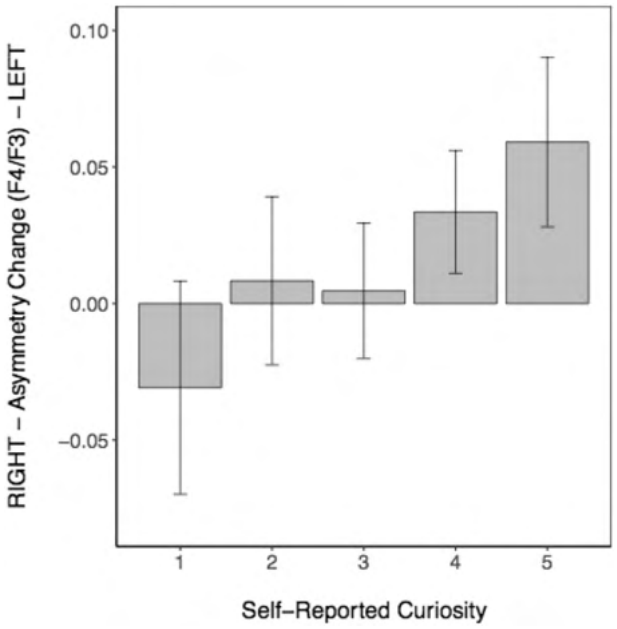


Fig. 4. Task-related changes in frontal alpha asymmetry (F3/F4) as a function of self-reported curiosity. Frontal asymmetry was calculated during anticipation periods, i.e., 1500 milliseconds prior to the onset of the fully disclosed stimuli. Error bars depict standard errors of the mean (SEM).

4. Discussion

We examined the incentive value of perceptual information with frontal alpha asymmetry. A novel paradigm was designed to elicit and subsequently resolve varying levels of uncertainty during visual object recognition. Photos of everyday objects were partly uncovered and subsequently fully revealed. As an index of approach motivation, frontal alpha asymmetry was measured during anticipation periods. We found that relative left-frontal activation was positively related to self-reported curiosity. Moreover, medium levels of confidence in identifying the presented objects was associated with highest states of left-lateralized activation. This curvilinear relationship was moderated by trait levels of openness. In highly open individuals, enhanced left-frontal activation was associated with lowest states of confidence. Less

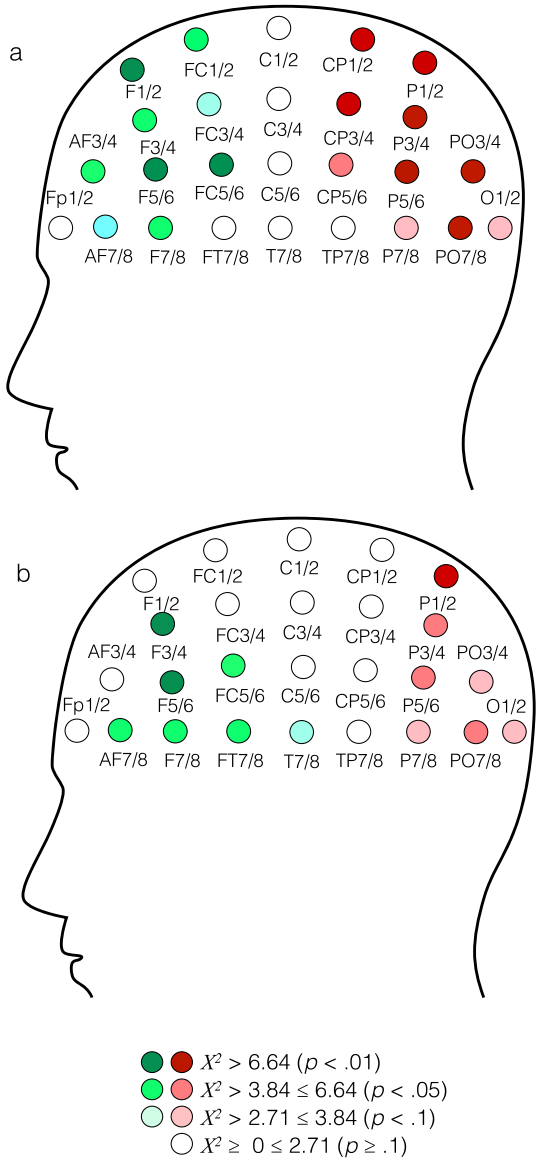


Fig. 5. Scalp topography of the asymmetry effects during anticipation periods (congruent condition). χ^2 values were derived from generalized estimating equations (GEEs) predicting alpha asymmetry with (a) curiosity ratings (linear relationship) and (b) squared confidence ratings (inverted u-shaped relationship). The hypothesized effects are plotted in green, reversed effects are plotted in red. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

open individuals, however, showed highest states of left-lateralized activation during medium and high states of confidence.

4.1. Frontal asymmetry and motivational states

Event-related changes in left-lateralized activation have previously been connected to monetary reward anticipation (Gorka et al., 2015; Lieberman et al., 2016; Miller and Tomarken, 2001; Nelson et al., 2017; Sobotka et al., 1992). During the expectation of perceptual information, we found analogous associations in the absence of external reward. Thus, our findings provide further evidence for an incentive value of information. In fMRI studies, state curiosity has been associated with dopaminergic reward networks (Gruber et al., 2014; Kang et al., 2009). Jepma et al. (2012) found the anterior cingulate cortex and anterior insular cortex activated when presenting ambiguous visual stimuli. However, they presented congruent and incongruent trials in random order. Thus, participants were not able to anticipate whether context-relevant information would be revealed or denied. The task might therefore have induced uncertainty about the outcomes rather than anticipation of context-relevant information. Presenting congruent stimuli as opposed to incongruent stimuli was associated with enhanced activation of the striatum (Jepma et al., 2012), indicating that reductions in uncertainty activated regions implicated in reward processing.

In order to ascribe the left-frontal activation observed in the present study to an inherent reward value of information, one needs to rule out the possibility that changes in asymmetry were merely due to the expectation of positive or negative feedback. When conducting the congruent condition, participants might have felt not only curious, but also anxious to see whether their answer was correct or not. Because the correctness of participant's guesses was closely related to subjective confidence, Kang et al. (2009) statistically controlled for the influence of confidence on curiosity ratings. Irrespective of confounding influences of confidence, they found curiosity related to striatal activation. In our study, curiosity was positively associated with frontal asymmetry but negatively associated with self-reported confidence. Consequently, low confidence was related to more left-lateralized asymmetry even though participants were more likely to receive negative feedback. For the same reason, we assume that left-lateralized asymmetry indicated anticipation of salient information rather than positive feedback. Note that we cannot rule out the possibility that some participants felt anxious during the anticipation periods since we did not measure anxiety-related states. In future studies, state and trait levels of anxiety should be included to examine the specificity of the effects reported here and to expand the empirical evidence on frontal asymmetry as an indicator of emotional-motivational states in conjunction with personality traits.

As a result of testing the regional specificity of the effects, we found reversed patterns of alpha asymmetry at parietal sites (P3/P4), such that curiosity and medium levels of confidence were associated with increased right-lateralized activation. Thus, the effects at parietal electrodes were contrary to the effects at frontal electrodes. Relative right parietal activity has been previously connected to physiological arousal (Heller, 1990; Nitschke et al., 1999; Wacker et al., 2003; Wacker et al., 2008; Wacker et al., 2010), for instance, during the imagination of emotionally arousing scenarios (Wacker et al., 2003; Wacker et al., 2008). In our task, right-lateralized activation might have been caused by perceptual uncertainty. However, a connection between perceptual uncertainty, alpha asymmetry, and physiological arousal cannot be verified within the current study. In future work, physiological indicators like skin conductance or heart rate could be used to investigate the relationship between physiological arousal and EEG alpha asymmetry during states of reward anticipation and information anticipation.

In addition to the main task, we conducted a control condition in which the fully disclosed stimuli were presented incongruently, i.e., did not match the partly covered photos. If the effects of curiosity and confidence on frontal asymmetry were driven by the anticipation of getting desired information one would expect the hypothesized effects within the congruent condition only. However, if the effects were driven by a more general desire to receive any kind of information, one would expect similar effects for the incongruent condition. Because in the present study the contrast between congruent and incongruent condition just failed to reach statistical significance, future work is needed to decide between these two possibilities as the lack of significance may also be due to insufficient statistical power.

4.2. Self-reports and the perceptual task

The behavioral data revealed that highest levels of curiosity were associated with low to medium levels of uncertainty. These results are partly in line with previous studies reporting inverted u-shaped associations (Kang et al., 2009; Litman et al., 2005). Since we presented partly covered photos, our task differed in several respects from the

trivia questions used in previous studies. When answering trivia questions, confidence levels might partly stem from interests in specific fields (e.g., sports or history). Given a lack of interest, low confidence levels are more likely be accompanied by low levels of curiosity. Assuming that curiosity in perceptual materials is less dependent on specific domains, even low confidence trials might evoke high levels of curiosity. Secondly, our low confidence stimuli might have contained comparatively high amounts of information. To evoke lower levels of perceptual ambiguity, we could have presented plain black or white stimuli. However, uncertainty and curiosity would probably still increase due to the continuous stimulus presentations. Finally, it has to be considered that self-reports of emotional states often evoke demand effects and stereotypic response patterns (Davidson, 2004; Larsen and Fredrickson, 1999). Stereotypic responses eventually lead to enhanced linear correlations among self-reports. The curvilinear association, however, might have been less influenced by conscious evaluations, which was supported by the curvilinear relationship between confidence and frontal asymmetry. Especially when investigating emotional-motivational states, self-reports might be usefully complemented by neurophysiological measurements.

4.3. Individual differences

The broad personality domain openness to experience comprises trait curiosity and the tendency to engage in information acquisition (Costa and McCrae, 1992; DeYoung, 2010). Since the openness aspect has been characterized by perceptual sensibility (DeYoung, 2010), open people should be particularly responsive to perceptual information. Therefore, we investigated individual differences in trait openness as a moderator of the association between perceptual uncertainty and frontal asymmetry. Our findings suggest that highly open people are more responsive to the rewarding aspects of uncertainty, as indicated by increased left-lateralized activation during low levels of confidence. Less open people, however, demonstrated highest levels of motivational activation when they were more confident, i.e., less uncertain. Since confidence ratings were positively associated with task performance, low open individuals might have been rather motivated by the expectation of positive feedback. Highly open individuals, on the contrary, might have been motivated by the expectation of information itself. Although the current findings concerning openness should be considered preliminary, they suggest a promising new approach for further investigations of the neurophysiological underpinnings of individual differences in uncertainty-related motivational states.

4.4. Conclusions

Our findings obtained with frontal EEG asymmetry provide further evidence for an incentive motivational value of information. The newly developed paradigm proved to be useful in an event-related EEG setting. The task could be used in future studies, for instance, to more directly investigate the mediating role of dopamine in motivational states. Finally, we present preliminary support for the idea that trait openness is associated with individual differences in approach motivation associated with the incentive value of information.

References

Adcock, R.A., Thangavel, A., Whitfield-Gabrieli, S., Knutson, B., Gabrieli, J.D.E., 2006. Reward-motivated learning: mesolimbic activation precedes memory formation. Neuron 50 (3), 507–517. https://doi.org/10.1016/j.neuron.2006.03.036.

Allen, J.J., Coan, J.A., Nazarian, M., 2004. Issues and assumptions on the road from raw signals to metrics of frontal EEG asymmetry in emotion. Biol. Psychol. 67 (1), 183–218. https://doi.org/10.1016/j.biopsycho.2004.03.007.

Berlyne, D.E., 1966. Curiosity and exploration. Science 153 (3731), 25–33.

Bromberg-Martin, E.S., Hikosaka, O., 2009. Midbrain dopamine neurons signal preference for advance information about upcoming rewards. Neuron 63 (1), 119–126. https://doi.org/10.1016/j.neuron.2009.06.009.

Bromberg-Martin, E.S., Hikosaka, O., 2011. Lateral habenula neurons signal errors in the prediction of reward information. Nat. Neurosci. 14 (9), 1209–1216. https://doi.org/10.1038/nn.2902.

R Core Team, 2012. R: a language and environment for statistical computing. In: R Foundation of Statistical Computing, Vienna, Austria, URL. http://www.R-project.org/.

Costa, P.T., McCrae, R.R., 1992. Four ways five factors are basic. Personal. Individ. Differ. 13 (6), 653–665.

Davidson, R.J., 1992. Anterior cerebral asymmetry and the nature of emotion. Brain Cogn. 20, 125–151. https://doi.org/10.1016/0278-2626(92)90065-T.

Davidson, R.J., 1993. Parsing affective space: perspectives from neuropsychology and psychophysiology. Neuropsychology 7 (4), 464.

Davidson, R.J., 2004. What does the prefrontal cortex "do" in affect: perspectives on frontal EEG asymmetry research. Biol. Psychol. 67 (1), 219–234. https://doi.org/10.1016/j.biopsycho.2004.03.008.

DeYoung, C.G., 2010. Personality neuroscience and the biology of traits. Soc. Personal. Psychol. Compass 4 (12), 1165–1180. https://doi.org/10.1111/j.1751-9004.2010.00327.

DeYoung, C.G., 2013. The neuromodulator of exploration: a unifying theory of the role of dopamine in personality. Front. Hum. Neurosci. 7, 1–26. https://doi.org/10.3389/fnhum.2013.00762.

DeYoung, C.G., Quilty, L.C., Peterson, J.B., 2007. Between facets and domains: 10 aspects of the Big Five. J. Pers. Soc. Psychol. 93 (5), 880. https://doi.org/10.1037/0022-3514.93.5.880.

Fayn, K., MacCann, C., Tiliopoulos, N., Silvia, P.J., 2015. Aesthetic emotions and aesthetic people: openness predicts sensitivity to novelty in the experiences of interest and pleasure. Front. Psychol. 6. https://doi.org/10.3389/fpsyg.2015.01877.

Furnham, A., Marks, J., 2013. Tolerance of ambiguity: a review of the recent literature. Psychology 4 (09), 717–728.

Gorka, S.M., Phan, K.L., Shankman, S.A., 2015. Convergence of EEG and fMRI measures of reward anticipation. Biol. Psychol. 112, 12–19. https://doi.org/10.1016/j.biopsycho.2015.09.007.

Gruber, M.J., Gelman, B.D., Ranganath, C., 2014. States of curiosity modulate hippocampus-dependent learning via the dopaminergic circuit. Neuron 84 (2), 486–496. https://doi.org/10.1016/j.neuron.2014.08.060.

Heller, W., 1990. The neuropsychology of emotion: Developmental patterns and implications for psychopathology. In: Stein, N.L., Leventhal, B., Trabasso, T. (Eds.), Psychological and biological approaches to emotion. Erlbaum, Hillsdale, NJ, pp. 167–211.

Hirsh, J.B., Mar, R.A., Peterson, J.B., 2012. Psychological entropy: a framework for understanding uncertainty-related anxiety. Psychol. Rev. 119 (2), 304.

Hubbard, A.E., Ahern, J., Fleischer, N.L., Van der Laan, M., Lippman, S.A., Jewell, N., Bruckner, T., Satariano, W.A., 2010. To GEE or not to GEE: comparing population average and mixed models for estimating the associations between neighborhood risk factors and health. Epidemiology 21 (4), 467–474.

Jepma, M., Verdonschot, R.G., Van Steenbergen, H., Rombouts, S.A., Nieuwenhuis, S., 2012. Neural mechanisms underlying the induction and relief of perceptual curiosity. Front. Behav. Neurosci. 6, 1–9. https://doi.org/10.3389/fnbeh.2012.00005.

Kang, M.J., Hsu, M., Krajbich, I.M., Loewenstein, G., McClure, S.M., Wang, J.T., Camerer, C.F., 2009. The wick in the candle of learning. Epistemic curiosity activates reward circuitry and enhances memory. Psychol. Sci. 20 (8), 963–973. https://doi.org/10.1111/j.1467-9280.2009.02402.x.

Kashdan, T.B., Silvia, P.J., 2009. Curiosity and interest: the benefits of thriving on novelty and challenge. In: Oxford Handbook of Positive Psychology. 2. pp. 367–374.

Katz, A.C., Sarapas, C., Bishop, J.R., Patel, S.R., Shankman, S.A., 2015. The mediating effect of prefrontal asymmetry on the relationship between the COMT Val158 met SNP and trait consummatory positive affect. Cognit. Emot. 29 (5), 229–262. https://doi.org/10.1080/02699931.2014.951030.

Klem, G.H., Lüders, H.O., Jasper, H.H., Elger, C., 1999. The ten-twenty electrode system of the International Federation. Electroencephalogr. Clin. Neurophysiol. 52 (3), 3–6.

Lang, P.J., 1980. Self-assessment Manikin. The Center for Research in Psychophysiology, University of Florida, Gainesville, FL.

Lang, P.J., Bradley, M.M., Cuthbert, B.N., 1997. International Affective Picture System (IAPS): Technical Manual and Affective Ratings. NIMH Center for the Study of Emotion and Attention, pp. 39–58.

Larsen, R.J., Fredrickson, B.L., 1999. Measurement issues in emotion research. In: Kahneman, D., Diener, E., Schwarz, N. (Eds.), Well-being: The Foundations of Hedonic Psychology. Russell Sage Foundation, New York.

Lieberman, L., Liu, H., Huggins, A.A., Katz, A.C., Zvolensky, M.J., Shankman, S.A., 2016. Comparing the validity of informant and self-reports of personality using laboratory indices of emotional responding as criterion variables. Psychophysiology 53 (9), 1386–1397. https://doi.org/10.1111/psyp.12680.

Litman, J.A., Hutchins, T., Russon, R., 2005. Epistemic curiosity, feeling-of-knowing and exploratory behaviour. Cognit. Emot. 19 (4), 559–582. https://doi.org/10.1080/02699930441000427.

Loewenstein, G., 1994. The psychology of curiosity: a review and reinterpretation. Psychol. Bull. 116, 75–98.

McCrae, R.R., 1994. Openness to experience: expanding the boundaries of Factor V. Eur. J. Personal. 8 (4), 251–272.

McCrae, R.R., 2007. Aesthetic chills as a universal marker of openness to experience. Motiv. Emot. 31 (1), 5–11.

Miller, A., Tomarken, A.J., 2001. Task-dependent changes in frontal brain asymmetry: effects of incentive cues, outcome expectancies, and motor responses. Psychophysiology 38 (3), 500–511. https://doi.org/10.1111/1469-8986.3830500.

Muth, C., Bales, K.L., Hinde, K., Maninger, N., Mendoza, S.P., Ferrer, E., 2016. Alternative models for small samples in psychological research: applying linear mixed effects models and generalized estimating equations to repeated measures data. Educ.

Psychol. Meas. 76 (1), 64–87. https://doi.org/10.1177/0013164415580432.
Nelson, B.D., Kessel, E.M., Klein, D.N., Shankman, S.A., 2017. Depression symptom dimensions and asymmetrical frontal cortical activity while anticipating reward. Psychophysiology 1–14. https://doi.org/10.1111/psyp.12892.
Nitschke, J.B., Heller, W., Palmieri, P.A., Miller, G.A., 1999. Contrasting patterns of brain activity in anxious apprehension and anxious arousal. Psychophysiology 36, 628–637.
Paelecke, M., Mussel, P., 2018. Reliabilität und Validität einer deutschsprachigen Fassung der Big Five Aspect Scales (BFAS). (in preparation).
Peterson, J.B., Carson, S., 2000. Latent inhibition and openness to experience in a high-achieving student population. Personal. Individ. Differ. 28 (2), 323–332. https://doi.org/10.1016/S0191-8869(99)00101-4.
Rademacher, L., Krach, S., Kohls, G., Irmak, A., Gründer, G., Spreckelmeyer, K.N., 2010. Dissociation of neural networks for anticipation and consumption of monetary and social rewards. NeuroImage 49 (4), 3276–3285. https://doi.org/10.1016/j.neuroimage.2009.10.089.
Schöne, B., Schomberg, J., Gruber, T., Quirin, M., 2016. Event-related frontal alpha asymmetries: electrophysiological correlates of approach motivation. Exp. Brain Res. 234 (2), 559–567. https://doi.org/10.1007/s00221-015-4483-6.
Silvia, P.J., Henson, R.A., Templin, J.L., 2009. Are the sources of interest the same for everyone? Using multilevel mixture models to explore individual differences in appraisal structures. Cognit. Emot. 23 (7), 1389–1406.
Simon, J.J., Walther, S., Fiebach, C.J., Friederich, H.C., Stippich, C., Weisbrod, M., Kaiser, S., 2010. Neural reward processing is modulated by approach- and avoidance-related personality traits. NeuroImage 49 (2), 1868–1874. https://doi.org/10.1016/j.neuroimage.2009.09.016.
Sobotka, S.S., Davidson, R.J., Senulis, J.A., 1992. Anterior brain electrical asymmetries in response to reward and punishment. Electroencephalogr. Clin. Neurophysiol. 83, 236–247.
Veale, J.F., 2014. Edinburgh Handedness Inventory - Short Form: a revised version based on confirmatory factor analysis. Brain Cogn. 19 (2), 164–177. https://doi.org/10.1080/1357650X.2013.783045.
Wacker, J., Heldmann, M., Stemmler, G., 2003. Separating emotion and motivational direction in fear and anger: effects on frontal asymmetry. Emotion 3 (2), 167. https://doi.org/10.1037/1528-3542.3.2.167.
Wacker, J., Chavanon, M.L., Leue, A., Stemmler, G., 2008. Is running away right? The behavioral activation-behavioral inhibition model of anterior asymmetry. Emotion 8, 232–249.
Wacker, J., Chavanon, M.L., Leue, A., Stemmler, G., 2010. Trait BIS predicts alpha asymmetry and P300 in a Go/No-Go task. Eur. J. Personal. 24 (2), 85–105. https://doi.org/10.1002/per.740.

Appendix B

Käckenmester, W., Bott, A., & Wacker J. (2019). Openness to experience predicts dopamine effects on divergent thinking. *Personality Neuroscience*, *2*(3), 1-7. doi: 10.1017/pen.2019.3

Personality Neuroscience

cambridge.org/pen

Openness to experience predicts dopamine effects on divergent thinking

Wiebke Käckenmester, Antonia Bott and Jan Wacker

Institute for Psychology, Universität Hamburg, Hamburg, DE Germany

Empirical Paper

Cite this article: Käckenmester W, Bott A, and Wacker J. (2019) Openness to experience predicts dopamine effects on divergent thinking. *Personality Neuroscience*. Vol **2:** e3, 1–7. doi: 10.1017/pen.2019.3

Received: 20 February 2019
Revised: 5 June 2019
Accepted: 18 June 2019

Key words:
openness to experience; dopamine; divergent thinking

Author for correspondence:
Wiebke Käckenmester,
Email: wiebke.kaeckenmester@t-online.de

Abstract

Individual differences in trait levels of openness to experience and creativity have been theoretically linked to dopamine function. However, empirical evidence for this assumption is scarce, especially for causal connections. The present study aims to directly assess the influence of dopamine activity on the established association between openness to experience and divergent thinking (i.e., an index of creativity). We hypothesized that manipulating dopamine activity alters the relationship between self-reported openness to experience and ideational fluency and flexibility. In a placebo-controlled between-subjects design, 193 healthy male volunteers completed four divergent thinking tasks after they received either the dopamine-receptor blocker sulpiride (200 mg) or a placebo. The data revealed an interaction such that openness to experience was more positively associated with divergent thinking in the dopamine blocker group ($r = 0.304$) than in the placebo group ($r = -0.002$). Specifically, highly open individuals in the dopamine blocker group reached the highest divergent thinking scores. Thus, sulpiride administration selectively affected divergent thinking as a function of trait levels of openness to experience. Although somewhat limited by the unexpected absence of the association between openness to experience and divergent thinking in the placebo group, the present study provides novel evidence for an association between dopamine activity and both openness to experience and divergent thinking.

Openness to experiences has been prominently described as "the breadth, depth, and permeability of consciousness" (McCrae & Costa, 1997, p. 826). Open people notice and appreciate novel, complex, and unusual information in a variety of everyday experiences (DeYoung, Quilty, Peterson, & Gray, 2014; McCrae, 1994). Conceptually and empirically, individual differences in openness to experience have been closely related to creativity. Some have even proposed creativity as an alternative label for the fifth factor of personality (Johnson, 1994; Saucier, 1992); others viewed creativity as a central characteristic of openness to experience, including the ability to make remote and unusual associations (Costa & McCrae, 1992). Still others regard openness to experience as a psychological factor that promotes the acquisition of cognitive creative potential and facilitates everyday creative activities (Jauk, 2019). Empirically, openness to experience has been positively associated with self-reported creative activities (Batey, Chamorro-Premuzic, & Furnham, 2010; Jauk, Benedek, & Neubauer, 2014; Wolfradt & Pretz, 2001), creative achievements (Feist, 1998; Kaufman et al., 2015; King, Walker, & Broyles, 1996), and performance in creative thinking tasks, such as remote consequences and divergent thinking (e.g., Jauk et al., 2014; McCrae, 1987). The association between openness to experience and divergent thinking has been frequently studied and empirically well established (Puryear, Kettler, & Rinn, 2017). Requiring the ability to generate numerous, various, and original ideas for a given scenario, usually either in the verbal domain (e.g., list various uses for a brick; Guilford, 1967) or in the figural domain (e.g., draw objects that complete given lines; Torrance, 1972), divergent thinking has been viewed as one of the most essential cognitive prerequisites of creativity (Guilford, 1957).

1. The dopaminergic basis of openness to experience and creativity

Recent years have seen an increase in work on the neurobiological basis of openness to experience and creativity (for a brief recent review, see Jauk, 2019), at least partly inspired by a series of reviews and theoretical articles by Colin DeYoung and colleagues (e.g., DeYoung, 2013, 2014; DeYoung, Peterson & Higgins, 2005): DeYoung et al. (2005) initially suggested that openness to experience is based on individual differences in cognitive exploration, which in turn partly results from individual differences in dopaminergic neurotransmission. Similar assumptions have been made for the closely related creativity dimension (DeYoung, 2013).

The following observations provide initial indirect support for these ideas: First, openness to experience (Peterson & Carson, 2002; Peterson, Smith, & Carson, 2002) and creative achievement (Carson, Higgins, & Peterson, 2003) have been reported to negatively correlate with latent inhibition, a low-level cognitive phenomenon relevant for shielding formerly ignored

CAMBRIDGE UNIVERSITY PRESS

information from further processing (i.e., arguably an indicator of "permeability of consciousness") and sensitive to dopaminergic drugs (Swerdlow et al. 2003; Weiner & Feldon, 1987; Weiner, Shadach, Tarrasch, Kidron, & Feldon, 1996). Second, openness to experience has been shown to correlate with increased functional connectivity within dopamine-rich mesocortical networks (Passamonti et al., 2015). Third, divergent thinking has been associated with decreased dopamine D2 receptor density in a very small sample of $n = 14$ (de Manzano, Cervenka, Karabanov, Farde, & Ullén, 2010) and with increased mean diffusivity in dopamine-rich brain regions (Takeuchi et al., 2015). Fourth, creative thinking has been associated with eye blink rate (i.e., an indicator of dopamine activity; Akbari Chermahini & Hommel, 2010). Finally, it has been demonstrated that Parkinson's disease patients increasingly engaged in creative activities with the introduction of dopaminergic medication and reduced these activities after dose reductions (Lhommée et al., 2014). When treated with dopamine-increasing medication, Parkinson's disease patients have further demonstrated enhanced divergent thinking performance compared with non-medicated healthy controls (Faust-Socher, Kenett, Cohen, Hassin-Baer, & Inzelberg, 2014).

Although these converging findings are encouraging, more direct evidence from pharmacological studies targeting dopamine activity in larger samples is needed. To our knowledge, only one published study has addressed connections between dopamine, creativity, and personality traits using a pharmacological approach in healthy participants: In a small sample ($n = 33$), Gvirts and colleagues (2017) reported diminished verbal divergent thinking under the dopamine reuptake inhibitor methylphenidate (20 mg) versus placebo only in participants high in novelty seeking (i.e., a trait moderately associated with both openness to experience and divergent thinking; Goclowska, Ritter, Elliot, & Baas, 2018). Whether analogous modulating effects of dopamine can be demonstrated for openness to experience remains to be tested.

2. The present study

The present study provides an initial direct test of the hypothesis that openness to experience modulates the effects of a pharmacological manipulation of dopamine on measures of divergent thinking. Groups of healthy males received either the dopamine receptor blocker sulpiride or a placebo prior to performing four divergent thinking tasks. Openness to experience was measured beforehand and independently of the pharmacological manipulation. The main prediction of an interaction between openness to experience and substance group (sulpiride vs. placebo) was based on the general observation that traits thought to be associated with individual differences in dopamine typically modulate the effects of pharmacological manipulations of dopamine on variables associated with the trait in question. Although this pattern remains to be demonstrated for openness to experience, it has already been documented quite consistently for extraversion, that is, a trait likewise hypothesized to be associated with brain dopamine (Depue & Collins, 1999; Wacker & Smillie, 2015). While openness to experience is thought to be based on individual differences in cognitive exploration resulting from dopaminergic variability in a mesocortical pathway underlying salience processing, extraversion is thought to be based on individual differences in behavioral exploration resulting from dopaminergic variability in a mesolimbic pathway underlying reward processing (DeYoung et al., 2005). Supporting the later suggestion, extraversion has been connected to individual differences in electroencephalogram (EEG) and functional magnetic resonance imaging indicators of reward processing (Müller et al. 2014; Wu, Samanez-Larkin, Katovich, Knutson, 2014) and responsivity to dopaminergic drugs (Depue, Luciana, Arbisi, Collins, Leon, 1994; Depue, 1995). Furthermore, pharmacological manipulations have been shown to alter the association between extraversion and EEG correlates of reward processing (Mueller et al. 2014; Wacker, Mueller, Pizzagalli, Hennig, Stemmler, 2013). Because openness to experience and extraversion are typically moderately correlated and systemic pharmacological manipulations cannot specifically target either the mesocortical or the mesolimbic dopamine system, potential effects of extraversion were statistically controlled in the current study. The same presumption holds for intelligence, which has been regularly found to be moderately correlated with both divergent thinking and openness to experience (Ashton, Lee, Vernon, Jang, 2000; Austin, Deary, & Gibson, 1997; Benedek, Jauk, Sommer, Arendasy, & Neubauer, 2014; Harris, 2004; McCrae, 1993; Nussbaum & Silvia, 2011).

3. Methods

3.1 Participants

A total of 210 healthy male volunteers participated in the present experiment. The study was part of a larger research project investigating the effects of dopamine on behavioral measures. Participants were recruited on social media platforms, job fair websites, and on campus. They provided written informed consent and received monetary compensation (€70) or course credit for their 6-h involvement in the research project. The study was approved by the Ethics Committee of the German Society for Psychology. Accordingly, the authors assert that all procedures contributing to this work comply with the ethical standards of the relevant national and institutional committees on human experimentation and with the Helsinki Declaration of 1975, as revised in 2008. Inclusion criteria were male gender, right-handedness, physical and mental health, and age between 18 and 35 years. The sample was restricted to male participants to control for sex-specific differences that might interfere with substance effects (e.g., due to the female hormonal cycle). In a pretesting session, the absence of psychiatric disorders was verified using a standardized clinical interview (Mini-DIPS; Margraf, 1994). Indications of psychiatric disorders as well as hypertension (blood pressure higher than 140/90) led to exclusion. Further self-reported exclusion criteria were the intake of any prescription medication or illegal drugs during the last 3 months, and habitual smoking of more than 10 cigarettes per week. In total, 17 participants were excluded from this study because they reported a first language other than German ($n = 10$), refused to comply with task instructions ($n = 2$), were not able to swallow the capsule ($n = 2$), arrived too late for medication intake ($n = 1$), had already eaten on the study day ($n = 1$), and did not complete the personality questionnaire due to technical failure ($n = 1$). The final sample reported here consisted of 193 males (mean age = 25.8, $SD = 3.9$; $n = 95$ in the sulpiride group and $n = 98$ in the placebo group). Of them, 76% were university students (7.7% psychology students). As intended, statistical power was therefore >0.80 to detect correlations of $\rho = 0.30$ ($\alpha = 0.05$) within each of the two substance groups.

3.2 Materials and tasks

3.2.1 Pharmacological manipulation

In a placebo-controlled, double-blind between-subjects design, participants orally ingested either 200 mg sulpiride or a placebo. Both substances were delivered in capsules matched for weight

https://doi.org/10.1017/pen.2019.3

and color to assure double-blindness to participants' experimental conditions. Sulpiride is classified as substituted benzamide that predominantly acts as selective D2-receptor antagonist (Mauri, Bravin, Bitetto, Rudelli, & Invernizzi, 1996). While showing high affinity to both pre- and postsynaptic D2 receptors (Missale, Nash, Robinson, Jaber, & Caron, 1998), the substance appears to lack significant effects on other receptor types (e.g., histaminergic, cholinergic, serotonergic, adrenergic, or γ-aminobutyric acid, and D1-type receptors). Its absorption from the gastrointestinal tract is slow and even reduced by concomitant food intake, with reported peak serum levels ranging from 1 to 6 h after oral intake and average elimination half-life ranging from 3 to 10 h (Mauri et al., 1996). In higher dosages (e.g., 800–1000 mg/day), sulpiride causes antipsychotic effects, probably by equally blocking both pre- and postsynaptic receptors. In lower dosages (e.g., 50–150 mg/day), however, sulpiride exhibits a mild stimulant effect that is used for treating symptoms of depression (Mauri et al., 1996; Uchida et al., 2005). This paradoxical effect was hypothesized to be due to prevalent blockage of presynaptic autoreceptors leading to enhanced dopamine neurotransmission (Kuroki, Meltzer, & Ichikawa, 1999). In previous studies with healthy participants, single doses of sulpiride have been well tolerated, and participants were usually not able to guess whether they received sulpiride or placebo (Chavanon, Wacker, & Stemmler, 2013; Wacker, 2018; Wacker et al. 2013).

3.2.2 Divergent thinking assessment

Participants completed four paper-and-pencil tasks obtained from the inventiveness scale from the Berlin Intelligence Structure Test (BIS-4; Jäger, Süß, & Beauducel, 1997): The verbal subtests *possible uses* (list as many alternate uses for a cushion as possible; AM) and *specific traits* (enumerate distinct characteristics and skills a good salesman should not have; EF) as well as the two figural-spatial subtests *symbol completion* (draw various real-life objects by completing a single figural element; ZF) and *object design* (compose real-life objects out of given figural elements; OJ). Each task was time-limited, and all instructions were read out aloud by one experimenter to assure standardized instruction times. In line with the manual's instructions, the tasks were scored for ideational fluency (number of valid solutions) and ideational flexibility (number of categorically different valid solutions) by two independent raters.

3.2.3 Personality assessment

To assess participants' trait level of openness to experience, we administered a German version of the third edition of the NEO Personality Inventory (NEO-PI-3; revised version of the NEO-PI-R by Costa & McCrae, 2010). The five domains are assessed with 48 items each, resulting in a total of 240 items (Costa & McCrae, 2010).

3.2.4 Intelligence assessment

In order to control for individual differences in cognitive ability, we estimated participants' fluid and crystallized intelligence by administering six computer-based subtests from the Intelligence Structure Battery (INSBAT; Arendasy et al., 2012). The INSBAT provides an adaptive intelligence measurement with all subtests showing conformity to the Rasch model (Frey & Moshagen, 2015). Fluid intelligence was assessed with the subtests *numeric-inductive thinking (number series)*, *figural-inductive thinking (matrices)*, and *verbal-deductive thinking (verbal reasoning)*. Crystallized intelligence was measured using the subtests *common knowledge*, *verbal fluency*, and *word meaning* (Arendasy et al., 2012). Due to the adaptive nature of the test, the overall processing time varied between participants ($M = 56$ min, $SD = 10.6$ min).

3.3 Procedure

In a pretesting session, participants' eligibility for participation was verified and self-report measures were assessed. Participants were then invited to the main experimental session in groups of four. Each experimental session started at 9:30 AM in the morning and was supervised by two out of five female experimenters. When arriving at the laboratory, participants were randomly assigned to a single cabin. After ingesting the capsule, they received a light standardized breakfast and subsequently completed six subtests of the intelligence structure battery (INSBAT), on average finishing within 1.2 h ($SD = 0.2$) and thus well before sulpiride typically reaches its maximum plasma level (after $M = 2.3$ h, $SD = 0.37$, according to Caley & Weber, 1995). About 1.4 h after medication intake ($SD = 0.21$), assessments of divergent thinking ability with four paper–pencil tasks began and lasted for around 15 min. Afterwards, seven more tasks were completed to assess implicit learning, working memory, effort expenditure, information preference, and behavior in a group discussion. The results will be reported elsewhere. In the end, participants were debriefed about their experimental condition, thanked, and compensated.

3.4 Statistical data analysis

As recommended by the authors of the test, the divergent thinking tasks were independently scored by two trained raters (Jäger et al., 1997). For five participants, who refrained from labeling their answers in one of the figural subtasks albeit conforming to the other tasks' instructions, we estimated their scores by imputing the mean values across the three valid scores of each participant. Mean scores were then calculated by averaging fluency and flexibility scores across the four subtasks and then centering across the whole sample. Openness to experience scores were averaged across the 48-item openness to experience scale from the NEO-PI-3. To predict divergent thinking ability from participants' openness scores, Substance, and the Openness × Substance interaction, linear regression analyses were computed. To control for potential effects of related traits, fluid intelligence, crystallized intelligence, and extraversion were entered as covariates into the multiple regression models. All continuous predictor variables were z-transformed within Substance groups. Furthermore, post-hoc analyses were conducted to compare performance levels of participants high versus low in openness between Substance groups. For this purpose, the sample was separated into high and low open participants by median split. Statistical analyses were implemented with R, version 3.4.3 (R Core Team, 2012). The main hypotheses and analyses were preregistered at the Open Science Framework on August 9, 2017, after the collection of 70 data sets and before accessing any of the data included in the current analyses (https://osf.io/mv4xs/register/5771ca429ad5a1020de2872e). The results of the other tasks addressed in the preregistration were part of the larger project investigating the effects of dopamine on behavioral measures and will be reported elsewhere.

3.5 Blindness to the psychopharmacological treatment

The majority of participants (78%) indicated in a forced-choice item as part of the post-experimental questionnaire that they assumed having received placebo. The two substance groups did

https://doi.org/10.1017/pen.2019.3

not differ in the percentage of participants who guessed that they had taken the drug (sulpiride group: 21.1%, placebo group: 22.7%), $\chi^2(1) = 0.1, p = 0.76$. Importantly, the percentage of correct guesses was independent from substance group guess (48% correct sulpiride guesses and 50% correct placebo guesses), $\chi^2(1) = 0.07$, $p = 0.79$. Furthermore, participant's subjective confidence in whether they had taken sulpiride was not related to the correctness of their guess ($\chi^2(3) = 0.96$, $p = 0.81$). Overall, we assume that participants were not able to guess their experimental condition above chance.

4 Results

4.1 Preliminary analyses

Prior to testing the main hypotheses, we examined potential trait differences between groups that might bias the hypothesized outcomes. The placebo group did not differ from the sulpiride group in age ($t(181.9) = -0.85$, $p = 0.34$), weight ($t(190.5) = -0.04$, $p = 0.97$), fluid intelligence ($t(186.4) = -1.50$, $p = 0.14$), crystallized intelligence ($t(187.4) = 0.46$, $p = 0.65$), or openness to experience ($t(184.5) = 0.27$, $p = 0.79$). Thus, we assume that any substance effects were not confounded with relevant trait differences between groups. The inter-rater reliability of the divergent thinking scores ranged from 0.87 to 0.98 (flexibility) and 0.96 to 1.0 (fluency), indicating high to perfect agreement among raters. Treating the four tasks as items, Cronbach's alpha internal consistency was considerably higher for fluency ($\alpha = 0.72$) than for flexibility ($\alpha = 0.61$). Furthermore, fluency and flexibility scores were highly correlated, $r = 0.86$. Because flexibility contained highly redundant and less reliable information, we decided to focus the analyses on fluency scores. However, in line with the preregistered analysis plan all main analyses are also reported for flexibility. The openness to experiences scale yielded an internal consistency of $\alpha = 0.87$. Mean openness scores in our sample ($M = 122.6$, $SD = 17.6$) were very similar to the mean of the norm sample reported in the NEO-PI-R manual for males of a similar age ($M = 122.7$, $SD = 19.3$). The aggregated openness scores were normally distributed and did not contain any outliers (i.e., more than three standard deviations from the mean). In divergent thinking, however, three participants reached fluency and flexibility scores more than three standard deviations above the mean. Since we did not specify the removal of outliers prior to analyzing the data (see preregistration link in the methods section), the data were analyzed as they are. However, additional analyses were performed without the outliers to ensure that the effects were not driven by extreme values.

4.2 Divergent thinking performance

Predicting fluency with openness to experience and substance group, a significant Openness × Substance interaction emerged ($b = 0.31$, $t(189) = 2.19$, $p = 0.029$). Follow-up analyses revealed a positive correlation between fluency and openness to experience within the sulpiride group ($r(93) = 0.304$, $p = 0.0027$), and a near zero correlation within the placebo group ($r(96) = -0.002$, $p = 0.98$; see Figure 1). The data did not reveal any main effects of either openness ($b = -0.001$, $t(189) = -0.016$, $p = 0.99$) or substance group ($b = 0.166$, $t(189) = 1.18$, $p = 0.24$). When conducting the analyses without outliers, the interaction remained significant ($b = 0.34$, $t(187) = 2.66$, $p = 0.0086$). Furthermore, the Openness × Substance interaction was also significant for flexibility, $b = 0.29$, $t(189) = 2.05$, $p = 0.041$ (without outliers: $b = 0.32$,

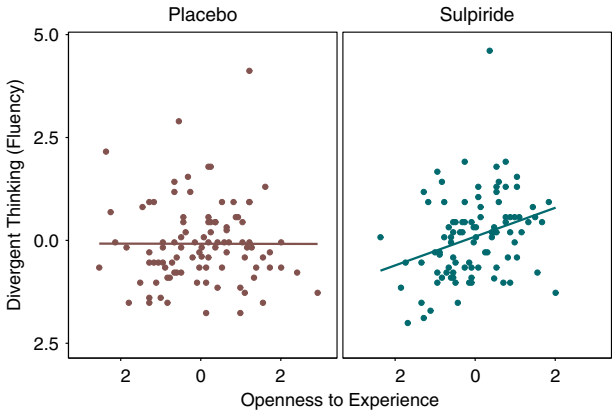


Figure 1. Relationship between openness to experience and divergent thinking in each substance group. Fluency scores (i.e., number of valid solutions) were z-standardized across the whole sample. Openness to experience scores were z-standardized within each experimental group.

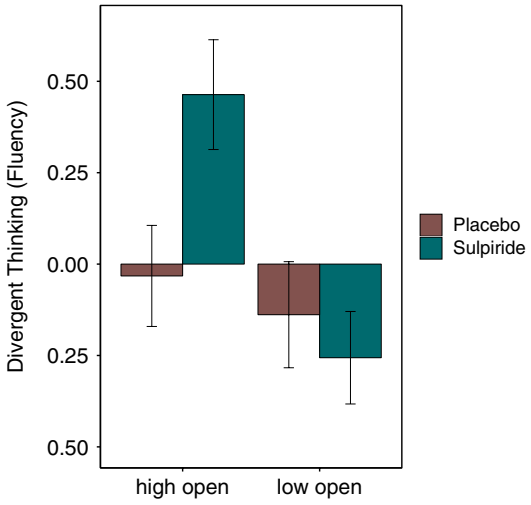


Figure 2. Mean divergent thinking scores separated by openness to experience and substance groups. Participants were assigned to high and low open groups by median split. Divergent thinking scores were z-standardized across the whole sample. Error bars depict standard errors of the mean (*SEM*).

$t(186) = 2.47$, $p = 0.014$). To examine the effects of sulpiride on mean performance levels, we compared the scores of participants high versus low in openness between substance groups. As illustrated in Figure 2, the highest scores were reached by highly open participants within the sulpiride group. Specifically, highly open participants reached significantly higher fluency scores within the sulpiride group than within the placebo group, $t(92.8) = 2.43$, $p = 0.017$ (without outliers: $t(91.6) = 2.92$, $p = 0.0044$). Less open participants did not show any significant differences as a function of substance group, $t(91) = 0.61$, $p = 0.54$ (without outliers: $t(91) = 0.61$, $p = 0.54$).

To examine the specificity of the effects to openness to experience, we additionally tested a regression model with Openness, Substance, Fluid Intelligence, Crystallized Intelligence, Openness × Substance, Fluid Intelligence × Substance, and Crystallized Intelligence × Substance. Neither fluid nor crystallized intelligence significantly interacted with substance group ($b \leq 0.21$, $t(185) \leq 1.44$, $p \geq 0.15$) and the Openness × Substance interaction remained significant, $b = 0.31$, $t(185) = 2.13$, $p = 0.035$ (without

https://doi.org/10.1017/pen.2019.3

outliers: $b = 0.34$, $t(183) = 2.64$, $p = 0.009$), indicating that the hypothesized effects were not driven by intelligence. In the total sample, openness to experience was unrelated to fluid intelligence ($r = 0.055$, $t(191) = 0.76$, $p = 0.45$) and positively correlated with crystallized intelligence ($r(191) = 0.14$, $p = 0.045$). Since openness was also positively associated with extraversion ($r(191) = 0.25$, $p = 0.0005$), we tested possible effects of extraversion in a separate model including Openness, Extraversion, Substance, Openness × Substance, and Extraversion × Substance. When extraversion was included as a predictor, the Openness × Substance interaction just failed to reach statistical significance in the analysis including the outliers, $b = 0.28$, $t(187) = 1.9$, $p = 0.059$ (without outliers: $b = 0.31$, $t(185) = 2.36$, $p = 0.019$). However, the effect observed for openness was not driven by extraversion as indicated by the nonsignificant Extraversion × Substance interaction ($b = 0.16$, $t(189) = 1.13$, $p = 0.26$).

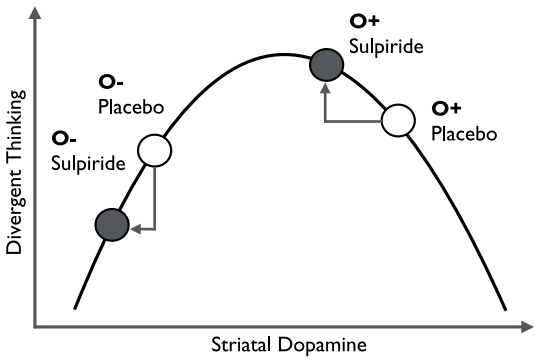


Figure 3. Interpretation of the current results based on the model suggested by Boot et al. (2017) linking striatal dopamine and divergent thinking via an inverted U-shaped function. O− = low trait levels of openness to experience; O+ = high trait levels of openness to experience.

5. Discussion

In the present study, we examined the effects of a pharmacological manipulation of dopamine on divergent thinking and its association with openness to experience. The dopamine receptor blocker sulpiride was administered in a placebo-controlled between-subjects design in a sample of healthy males. As expected, the dopamine manipulation moderated the relationship between openness to experience and divergent thinking. Specifically, we observed a positive correlation in the sulpiride group and a near zero correlation in the placebo group. Furthermore, highly open participants reached higher scores under sulpiride versus placebo, whereas less open individuals did not show significant differences between substance groups.

These observations are broadly consistent with the hypothesis that trait variation in openness to experience partly stems from individual differences in dopamine activity (DeYoung, 2013; DeYoung et al., 2005): Matching the empirically underpinned involvement of dopamine in creative potential (e.g., de Manzano et al., 2010; Lhommée et al., 2014) and the theorized involvement of dopamine in openness to experience (DeYoung, 2013), we expected and found that the effect of the dopaminergic agent sulpiride on divergent thinking interacts with individual differences in trait levels of openness to experience.

According to a framework integrating creative cognition with dopaminergic modulation of fronto-striatal dopamine networks (Akbari Chermahini & Hommel, 2012; Boot, Baas, van Gaal, & De Dreu, 2017), the manipulation of striatal dopamine neurotransmission via dopaminergic substances might lead to opposing effects in healthy individuals with low versus high baseline levels of dopamine due to an inverted U-shaped relationship between striatal dopamine levels and divergent thinking. Supposing that certain personality traits are linked to differences in baseline dopamine activity, this idea implies a dependence of pharmacological dopamine effects on the personality traits in question. Supporting this claim, our results suggest that sulpiride enhanced divergent thinking only in highly open individuals, while performance levels of less open individuals were not significantly affected by the sulpiride administration. Assuming that sulpiride (200 mg) had mostly antagonistic effects in the current study, it would be conceivable that pharmacological reductions in dopamine activity caused only highly open individuals to reach an optimal striatal dopamine level, whereas less open individuals were pushed down the ascending limb of Boot et al.'s (2017) inverted U (see Figure 3). Using the indirect dopamine agonist methylphenidate in a similar design, Gvirts et al. (2017) found verbal divergent thinking (numerically) diminished in participants scoring highly on novelty seeking (i.e., a trait positively correlated to openness; Goclowska et al., 2018), but (numerically) increased in participants scoring low in novelty seeking resulting in a drug-induced cancellation of the positive association between novelty seeking and divergent thinking present under placebo. Assuming that novelty seeking, like openness, is associated with elevated levels of dopamine, methylphenidate may have pushed individuals high in novelty seeking just beyond the optimal dopamine level, whereas it moved individuals low in novelty seeking to a point just before the optimal dopamine level in the study by Gvirts et al. (2017).

While the model proposed by Boot et al. (2017) may thus potentially explain both the current findings and the earlier results by Gvirts et al. (2017), it should be noted that proposed interpretation relies on the assumption that sulpiride (200 mg) primarily acted as an *antagonist* in the present study, whereas some of Wacker's earlier pharmacological work on extraversion was more compatible with a predominantly presynaptic effects on autoreceptors and, thus, an *agonistic* postsynaptic effect (e.g., Wacker et al., 2006, 2013). In addition, the interpretation proposed in Figure 3 leaves open the puzzling question, why the current study did not replicate the well-established association between openness to experience and divergent thinking under placebo conditions (Puryear et al., 2017). Possibly contextual factors of the present investigation like the group setting, the intelligence tests preceding the divergent thinking tasks, or the presence of two opposite-sex experimenters may have led to state increases in dopamine levels that pushed the high openness beyond the optimal level of Boot et al.'s (2017) inverted U, thereby canceling out the otherwise existing openness-related differences in divergent thinking. Of course, this suggestion remains speculative until directly tested by future work.

In order to determine the specificity of the observed effects, we also tested for potential effects of intelligence and extraversion (i.e., dimensions likewise associated with brain dopamine, e.g., Grazioplene et al., 2015; Wacker & Smillie, 2015). Although openness was positively related to both crystallized intelligence and extraversion, its interaction with Substance remained virtually unchanged after statistically controlling for either extraversion or fluid and crystallized cognitive ability. The findings are in line with the previous research, suggesting that openness to experience explains a unique proportion of variance in divergent thinking even when controlling for intelligence (Benedek et al. 2014;

https://doi.org/10.1017/pen.2019.3

Silvia, 2008). They are also in line with the assumption of separable dopaminergic bases for openness and extraversion.

Ideally, future research could provide a stringent test of the model depicted in Figure 3 by comparing dopamine blockage and activation induced by varying dosages of dopaminergic agents including (but not limited to) sulpiride and methylphenidate. Additional substance groups (e.g., serotonin reuptake inhibitors) should also be examined to probe the specificity of the effects of dopamine, as opposed to other neurotransmitters. Moreover, the concurrent assessment of at least somewhat more direct indicators of dopamine (i.e., eyeblink rate) could help validate the presumed effects of dopaminergic substances and dosages. Finally, future work may also address the limitation of the current study resulting from our sample restriction to male participants. Although gender has not been identified as a correlate of divergent thinking (Baer & Kaufman, 2011), it remains to be tested whether the present results replicate in other populations.

6. Conclusions

Taken together, the current findings provide partial support for a modulating role of individual differences in dopaminergic neurotransmission in both openness to experience and divergent thinking. Future studies should employ even larger and more diverse samples to investigate dose–response relationships using several dopaminergic and non-dopaminergic agents and measuring eyeblink rate (or other indicators of dopamine level) in addition to divergent thinking.

Due to the data protection statement included in the informed consent of this study, data cannot be made publicly available. However, data will be shared with research collaborators upon request.

Author ORCIDs. Wiebke Käckenmester 0000-0002-6052-7192

Conflicts of interest. The authors have no conflicts of interest to disclose.

References

Akbari Chermahini, S. A., & Hommel, B. (2010). The (b)link between creativity and dopamine: Spontaneous eye blink rates predict and dissociate divergent and convergent thinking. *Cognition*, *115*, 458–465. https://doi.org/10.1016/j.cognition.2010.03.007

Akbari Chermahini, S. A., & Hommel, B. (2012). More creative through positive mood? Not everyone! *Frontiers in Human Neuroscience*, *6*, 1–7. https://doi.org/10.3389/fnhum.2012.00319

Arendasy, M., Hornke, L. F., Sommer, M., Wagner-Menghin, M., Gittler, G., Häusler, J., & Wenzl, B. M. (2012). *Intelligenz-Struktur-Batterie–INSBAT*. Mödling: Schuhfried.

Ashton, M. C., Lee, K., Vernon, P. A., & Jang, K. L. (2000). Fluid intelligence, crystallized intelligence, and the openness/intellect factor. *Journal of Research in Personality*, *34*, 198–207. https://doi.org/10.1006/jrpe.1999.2276

Austin, E. J., Deary, I. J., & Gibson, G. J. (1997). Relationships between ability and personality: Three hypotheses tested. *Intelligence*, *25*, 49–70. http://dx.doi.org/10.1016/S0160-2896(97)90007-6

Baer, J., & Kaufman, J. C. (2011). Gender differences in creativity. *Journal of Creative Behavior*, *42*, 75–105. https://doi.org/10.1002/j.2162-6057.2008.tb01289.x

Batey, M., Chamorro-Premuzic, T., & Furnham, A. (2010). Individual differences in ideational behavior: Can the big five and psychometric intelligence predict creativity scores? *Creativity Research Journal*, *22*, 90–97. https://doi.org/10.1080/10400410903579627

Benedek, M., Jauk, E., Sommer, M., Arendasy, M., & Neubauer, A. C. (2014). Intelligence, creativity, and cognitive control: The common and differential involvement of executive functions in intelligence and creativity. *Intelligence*, *46*, 73–83. https://doi.org/10.1016/j.intell.2014.05.007

Boot, N., Baas, M., van Gaal, S., Cools, R., & De Dreu, C. K. (2017). Creative cognition and dopaminergic modulation of fronto-striatal networks: Integrative review and research agenda. *Neuroscience & Biobehavioral Reviews*, *78*, 13–23. https://dx.doi.org/10.1016/j.neubiorev.2017.04.007

Caley, C. F., & Weber, S. S. (1995). Sulpiride: An antipsychotic with selective dopaminergic antagonist properties. *Annals of Pharmacotherapy*, *29*, 152–160. https://doi.org/10.1177/106002809502900210

Carson, S. H., Higgins, D. M., & Peterson, J. B. (2003). Decreased latent inhibition is associated with increased creative achievement in high-functioning individuals. *Journal of Personality and Social Psychology*, *85*, 499–506. https://doi.org/10.1037/0022-3514.85.3.499

Chavanon, M. L., Wacker, J., & Stemmler, G. (2013). Paradoxical dopaminergic drug effects in extraversion: Dose- and time-dependent effects of sulpiride on EEG theta activity. *Frontiers in Human Neuroscience*, *7*, 117. https://doi.org/10.3389/fnhum.2013.00117

Costa, P. T., & McCrae, R. R. (1992). Four ways five factors are basic. *Personality and Individual Differences*, *13*, 653–665. https://doi.org/10.1016/0191-8869(92)90236-I

Costa, P. T., & McCrae, R. R. (2010). *The NEO Personality Inventory: 3*. Odessa, FL: Psychological assessment resources.

De Manzano, Ö., Cervenka, S., Karabanov, A., Farde, L., & Ullén, F. (2010). Thinking outside a less intact box: Thalamic dopamine D2 receptor densities are negatively related to psychometric creativity in healthy individuals. *PLoS One*, *5*, e10670. https://doi.org/10.1371/journal.pone.0010670

Depue, R. A. (1995). Neurobiological factors in personality and depression. *European Journal of Personality*, *9*, 413–439. http://dx.doi.org/10.1002/per.2410090509

Depue, R. A., & Collins, P. F. (1999). Neurobiology of the structure of personality: Dopamine, facilitation of incentive motivation, and extraversion. *Behavioral and Brain Sciences*, *22*, 491–569. http://dx.doi.org/10.1017/S0140525X99002046

Depue, R. A., Luciana, M., Arbisi, P., Collins, P., & Leon, A. (1994). Dopamine and the structure of personality: Relation of agonist-induced dopamine activity to positive emotionality. *Journal of Personality and Social Psychology*, *67*, 485–498. http://dx.doi.org/10.1037/0022-3514.67.3.485

DeYoung, C. G. (2013). The neuromodulator of exploration: A unifying theory of the role of dopamine in personality. *Frontiers in Human Neuroscience*, *7*, 1–26. https://doi.org/10.3389/fnhum.2013.00762

DeYoung, C. G. (2014). Openness/Intellect: A dimension of personality reflecting cognitive exploration. In M. L. Cooper & R. J. Larsen (Eds.), *APA handbook of personality and social psychology: Personality processes and individual differences* (Vol. 4, pp. 369–399). Washington, DC: American Psychological Association.

DeYoung, C. G., Peterson, J. B., & Higgins, D. M. (2005). Sources of openness/intellect: Cognitive and neuropsychological correlates of the fifth factor of personality. *Journal of Personality*, *73*, 825–858. https://doi.org/10.1111/j.1467-6494.2005.00330.x

DeYoung, C. G., Quilty, L. C., Peterson, J. B., & Gray, J. R. (2014). Openness to experience, intellect, and cognitive ability. *Journal of Personality Assessment*, *96*, 46–52. https://doi.org/10.1080/00223891.2013.806327

Faust-Socher, A., Kenett, Y. N., Cohen, O. S., Hassin-Baer, S., & Inzelberg, R. (2014). Enhanced creative thinking under dopaminergic therapy in Parkinson disease. *Annals of Neurology*, *75*, 935–942. https://doi.org/10.1002/ana.24181

Feist, G. J. (1998). A meta-analysis of personality in scientific and artistic creativity. *Personality and Social Psychology Review*, *2*, 290–309. https://doi.org/10.1207/s15327957pspr0204_5

Frey, A., & Moshagen, M. (2015). TBS-TK rezension: Intelligenz-Struktur-Batterie (INSBAT). *Psychologische Rundschau*, *66*, 86–88. https://doi.org/10.1026/0033-3042/a000237

Goclowska, M. A., Ritter, S. M., Elliot, A. J., & Baas, M. (2018). Novelty seeking is linked to openness and extraversion, and can lead to greater creative performance. *Journal of Personality*, *87*, 252–266. https://doi.org/10.1111/jopy.12387

Grazioplene, R. G., Ryman, S. G., Gray, J. R., Rustichini, A., Jung, R. E., & DeYoung, C. G. (2015). Subcortical intelligence: Caudate volume predicts

IQ in healthy adults. *Human Brain Mapping*, *36*, 1407–1416. https://doi.org/10.1002/hbm.22710

Guilford, J. P. (1957). Creative abilities in the arts. *Psychological Review*, *64*, 110–118. http://dx.doi.org/10.1037/h0048280

Guilford, J. P. (1967). *The nature of human intelligence*. New York: McGraw-Hill

Gvirts, H. Z., Mayseless, N., Segev, A., Lewis, D. Y., Feffer, K., Barnea, Y., . . . & Shamay-Tsoory, S. G. (2017). Novelty-seeking trait predicts the effect of methylphenidate on creativity. *Journal of Psychopharmacology*, *31*, 599–605. https://doi.org/10.1177/0269881116667703

Harris, J. A. (2004). Measured intelligence, achievement, openness to experience, and creativity. *Personality and Individual Differences*, *36*, 913–929. https://doi.org/10.1016/S0191-8869(03)00161-2

Jäger, A. O., Süß, H. M., & Beauducel, A. (1997). *BIS-TEST Berliner Intelligenzstruktur- Test–Form 4*. Göttingen: Hogrefe.

Jauk, E. (2019). A bio-psycho-behavioral model of creativity. *Current Opinion in Behavioral Sciences*, *27*, 1–6. https://doi.org/10.1016/j.cobeha.2018.08.012

Jauk, E., Benedek, M., & Neubauer, A. C. (2014). The road to creative achievement: A latent variable model of ability and personality predictors. *European Journal of Personality*, *28*, 95–105. https://doi.org/10.1002/per.1941

Johnson, J. A. (1994). Clarification of Factor Five with the help of the AB5C Model. *European Journal of Personality*, *8*, 311–334. https://doi.org/10.1002/per.2410080408

Kaufman, S. B., Quilty, L. C., Grazioplene, R. G., Hirsh, J. B., Gray, J. R., Peterson, J. B., & DeYoung, C. G. (2015). Openness to experience and intellect differentially predict creative achievement in the arts and sciences. *Journal of Personality*, *84*, 248–258. https://doi.org/10.1111/jopy.12156

King, L. A., Walker, L. M., & Broyles, S. J. (1996). Creativity and the five-factor model. *Journal of Research in Personality*, *30*, 189–203. https://doi.org/10.1006/jrpe.1996.0013

Kuroki, T., Meltzer, H. Y., & Ichikawa, J. (1999). Effects of antipsychotic drugs on extracellular dopamine levels in rat medial prefrontal cortex and nucleus accumbens. *Journal of Pharmacology and Experimental Therapeutics*, *288*, 774–781.

Lhommée, E., Batir, A., Quesada, J. L., Arduin, C., Fraix, V., Seigneuret, E., . . . & Krack, P. (2014). Dopamine and the biology of creativity: Lessons from Parkinson's disease. *Frontiers in Neurology*, *5*, 1–11. https://doi.org/10.3389/fneur.2014.00055

Margraf, J. (1994). *Diagnostisches Kurz-Interview bei psychischen Störungen, Mini-DIPS*. Berlin, Heidelberg: Springer Verlag.

Mauri, M. C., Bravin, S., Bitetto, A., Rudelli, R., & Invernizzi, G. (1996). A risk-benefit assessment of sulpiride in the treatment of schizophrenia. *Drug Safety*, *14*, 288–298. https://doi.org/10.2165/00002018-199614050-00003

McCrae, R. R. (1987). Creativity, divergent thinking, and openness to experience. *Journal of Personality and Social Psychology*, *52*, 1258–1265. http://dx.doi.org/10.1037/0022-3514.52.6.1258

McCrae, R. R. (1993). Openness to experience as a basic dimension of personality. *Imagination, Cognition, and Personality*, *13*, 39–55. http://dx.doi.org/10.2190/H8H6-QYKR-KEU8-GAQ0

McCrae, R. R. (1994). Openness to experience: Expanding the boundaries of Factor V. *European Journal of Personality*, *8*, 251–272. http://dx.doi.org/10.1002/per.2410080404

McCrae, R. R., & Costa, P. T. (1997). Conceptions and correlates of Openness to Experience. In R. Hogan, J. A. Johnson, & S. R. Briggs (Eds.), *Handbook of personality psychology* (pp. 825–847). Orlando, FL: Academic Press.

Missale, C., Nash, S. R., Robinson, S. W., Jaber, M., & Caron, M. G. (1998). Dopamine receptors: from structure to function. *Physiological Reviews*, *78*, 189–225. https://doi.org/10.1152/physrev.1998.78.1.189

Mueller, E. M., Burgdorf, C., Chavanon, M. L., Schweiger, D., Wacker, J., & Stemmler, G. (2014). Dopamine modulates frontomedial failure processing of agentic introverts versus extraverts in incentive contexts. *Cognitive, Affective, & Behavioral Neuroscience*, *14*, 756–768. https://doi.org/10.3758/s13415-013-0228-9

Nussbaum, E. C. & Silvia, P. J. (2011). Are intelligence and creativity really so different? Fluid intelligence, executive processes, and strategy use in divergent thinking. *Intelligence*, *39*, 36–45. https://doi.org/10.1016/j.intell.2010.11.002

Passamonti, L., Terracciano, A., Riccelli, R., Donzuso, G., Cerasa, A., Vaccaro, M. G., . . . Quattrone, A. (2015). Increased functional connectivity within mesocortical networks in open people. *Neuroimage*, *104*, 301–309. https://doi.org/10.1016/j.neuroimage.2014.09.017

Peterson, J. B., & Carson, S. (2000). Latent inhibition and openness to experience in a high-achieving student population. *Personality and Individual Differences*, *28*, 323–332. https://doi.org/10.1016/S0191-8869(99)00101-4

Peterson, J. B., Smith, K. W., & Carson, S. (2002). Openness and extraversion are associated with reduced latent inhibition: Replication and commentary. *Personality and Individual Differences*, *33*, 1137–1147. https://doi.org/10.1016/S0191-8869(02)00004-1

Puryear, J. S., Kettler, T., & Rinn, A. N. (2017). Relationships of personality to differential conceptions of creativity: A systematic review. *Psychology of Aesthetics, Creativity, and the Arts*, *11*, 59–68. http://dx.doi.org/10.1037/aca0000079

R Core Team. (2012). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation of Statistical Computing. Retrieved from http://www.R-project.org/

Saucier, G. (1992). Openness versus intellect: Much ado about nothing? *European Journal of Personality 6*, 381–386. https://doi.org/10.1002/per.2410060506

Silvia, P. J. (2008). Another look at creativity and intelligence: Exploring higher-order models and probable confounds. *Personality and Individual Differences*, *44*, 1012–1021. https://doi.org/10.1016/j.paid.2007.10.027

Swerdlow, N. R., Stephany, N., Wasserman, L. C., Talledo, J., Sharp, R., & Auerbach, P. P. (2003). Dopamine agonists disrupt visual latent inhibition in normal males using a within-subject paradigm. *Psychopharmacology*, *169*, 314–320. https://doi.org/10.1007/s00213-002-1325-6

Takeuchi, H., Taki, Y., Sekiguchi, A., Hashizume, H., Nouchi, R., Sassa, Y., . . . & Kawashima, R. (2015). Mean diffusivity of globus pallidus associated with verbal creativity measured by divergent thinking and creativity-related temperaments in young healthy adults. *Human Brain Mapping*, *36*, 1808–1827. https://doi.org/10.1002/hbm.22739

Torrance, E. P. (1972). Predictive validity of the Torrance Tests of Creative Thinking. *Journal of Creative Behavior*, *6*, 236–252. http://dx.doi.org/10.1002/j.2162-6057.1972.tb00936.x

Uchida, H., Takeuchi, H., Suzuki, T., Nomura, K., Watanabe, K., & Kashima, H. (2005). Combined treatment with sulpiride and paroxetine for accelerated response in patients with major depressive disorder. *Journal of Clinical Psychopharmacology*, *25*, 545–551. https://doi.org/10.1097/01.jcp.0000185425.00644.41

Wacker, J. (2018). Effects of positive emotion, extraversion, and dopamine on cognitive stability-flexibility and frontal EEG asymmetry. *Psychophysiology*, *55*, e12727. https://doi.org/10.1111/psyp.12727

Wacker, J., & Smillie, L. (2015). Trait extraversion and dopamine function. *Social and Personality Psychology Compass*, *9*, 225–238. https://doi.org/10.1111/spc3.12175

Wacker, J., Mueller, E. M., Pizzagalli, D. A., Hennig, J., Stemmler, G. (2013). Dopamine-D2 receptor blockade reverses the association between trait approach motivation and frontal asymmetry in an approach-motivation context. *Psychological Science*, *24*, 489–497. https://doi.org/10.1177/0956797612458935

Weiner, I., & Feldon, J. (1987). Facilitation of latent inhibition by haloperidol in rats. *Psychopharmacology*, *91*, 248–253. http://dx.doi.org/10.1007/BF00217073

Weiner, I., Shadach, E., Tarrasch, R., Kidron, R., & Feldon, J. (1996). The latent inhibition model of schizophrenia: Further validation using the atypical neuroleptic, clozapine. *Biological Psychiatry*, *40*, 834–843. http://dx.doi.org/10.1016/0006-3223(95)00573-0

Wolfradt, U. & Pretz, J. E. (2001). Individual differences in creativity: Personality, story writing, and hobbies. *European Journal of Personality*, *15*, 297–310. https://doi.org/10.1002/per.409

Wu, C. C., Samanez-Larkin, G. R., Katovich, K., Knutson, B. (2014). Affective traits link to reliable neural markers of incentive anticipation. *NeuroImage*, *84*, 279–289. https://doi.org/10.1016/j.neuroimage.2013.08.055

Appendix C

Käckenmester, W. & Wacker J. Are individual differences in openness and implicit sequence learning modulated by dopamine? Submitted to *Personality and Social Psychology Bulletin*.

Are Individual Differences in Openness and Implicit Sequence Learning Modulated by Dopamine?

Wiebke Käckenmester & Jan Wacker

Universität Hamburg

Author Note

Wiebke Käckenmester, Faculty of Psychology and Human Movement Science, Institute for Psychology, Universität Hamburg; Jan Wacker, Faculty of Psychology and Human Movement Science, Institute for Psychology, Universität Hamburg

Correspondence concerning this article should be addressed to Wiebke Käckenmester, Faculty of Psychology and Human Movement Science, Institute for Psychology, Universität Hamburg, 5 Von-Melle-Park, Hamburg, DE 20146, Tel.: +49 40 42838 5403, E-mail: wiebke.kaeckenmester@t-online.de

Abstract

The hypothesized link between dopamine and trait levels of openness has so far been supported by indirect evidence. We used implicit learning as a behavioral correlate of openness to directly investigate the effect of dopamine within a pharmacological design. 193 healthy male volunteers completed a probabilistic serial reaction time task after they received either the dopamine receptor blocker sulpiride (200mg) or a placebo. Contrary to our predictions, openness was not significantly associated with implicit learning in the placebo group and the hypothesized change of this association in the dopamine blocker group likewise failed to reach statistical significance. These null findings may partly be attributed to previously unknown psychometric issues with the implicit learning task.

Keywords: Implicit Learning, Openness, Dopamine, Implicit cognition

1 Introduction

Implicit learning broadly describes learning without awareness (Cleeremans, Destrebecqz, & Boyer, 1998). More precisely, implicit information acquisition characterizes learning processes that do not require intention or conscious awareness of what is learned. Implicit learning paradigms generate incidental experiences with associated stimuli that participants behaviorally adapt to despite usually not being able to report the underlying principle. The serial reaction time task (SRTT) is a commonly used paradigm that infers visuomotor learning from reaction time differences to random versus sequential stimuli (Robertson, 2007). As opposed to cognitive tasks that require higher cognitive processing, implicit information acquisition has been characterized as a complex form of priming (Cleeremans et al., 1998). Based on rather small empirical associations with intelligence measures, implicit learning has been dissociated from explicit cognitive abilities (Danner, Hagemann, Schankin, Hager, & Funke, 2011; Gebauer & Mackintosh, 2007; Kaufman, DeYoung, Gray, Jiménez, Brown, & Mackintosh, 2010; Reber, Walkenfeld, & Hernstadt, 1991). Instead, Kaufman et al. (2010) found implicit sequence learning more strongly correlated with self-reported intuition and openness. Individual differences in openness refer to engagement with perceptual information and the ability to detect and utilize patterns of sensory information (DeYoung, Quilty, & Peterson, 2007). A second aspect of the broader openness to experience domain has been labeled intellect and refers to engagement with abstract information (e.g., scientific insights or philosophical ideas; DeYoung et al. 2007). Finding intellect more strongly correlated with intelligence and openness with implicit learning, Kaufman et al. (2010) argued for a dissociation between openness and intellect in predicting implicit and explicit cognitive abilities. However, a recent study that was published during our ongoing data collection failed to replicate the association between openness and implicit sequence learning (Sobkow, Traczyk, Kaufman, & Nosal, 2018). Thus, trait levels of openness have been theoretically

connected to implicit learning, but empirical evidence is ambiguous at present.

1.1 The dopaminergic basis of openness and implicit learning

The midbrain dopamine system has been critically implicated in feedback-related associative learning (Graybiel, 1995, 1998; Shohamy, Myers, Kalanithi, & Gluck, 2008). Implicit stimulus-response learning has been connected to dopaminergic networks between frontal regions and the basal ganglia (Uddén, Folia, & Petersson, 2010). In healthy participants, performance in implicit sequence learning has been found to be reduced after the administration of Haloperidol (i.e., a dopamine antagonist) in contrast with d-amphetamine (i.e., an indirect dopamine agonist) (Kumari, Corr, Mulligan, Cotter, Checkley, & Gray, 1997). The suppressing effects of Haloperidol on implicit learning have been confirmed in schizophrenic patients who did not show deficits under Olanzapine (Paquet, Soucy, Stip, Lévesque, Elie, & Bédard, 2004; Stevens, Schwarz, Schwarz, Ruf, Kolter, & Czekalla, 2002). The authors concluded that Haloperidol-related deficits might result from striatal D2 receptor blockage (Paquet et al., 2004). In contrast, Levodopa (i.e., a dopamine precursor) has been connected to enhanced performance in feedback-based artificial grammar learning in healthy participants (De Vries, Ulte, Zwitserlood, Szymanski, & Knecht, 2010). Furthermore, sequential learning has been shown to provoke endogenous dopamine release (although in a very small sample, Badgaiyan, Fischman, & Alpert, 2007). In sum, dopaminergic neurotransmission has been generally implicated in stimulus-response learning and particularly in implicit sequence learning.

So far, individual differences in openness to experience have been indirectly connected to dopamine function. Based on cognitive functions related to both openness and dopamine, DeYoung, Peterson & Higgins (2005) suggested that individual differences in openness to experience partly result from dopaminergic neurotransmission. Supporting the assumption, Peterson and colleagues (Peterson & Carson, 2000; Peterson, Smith, & Carson, 2002) found

openness to experience negatively correlated with latent inhibition, a low-level cognitive phenomenon relevant for shielding formerly ignored information from further processing that has been shown sensitive to dopaminergic drugs (Swerdlow, Stephany, Wasserman, Talledo, Sharp, & Auerbach, 2003; Weiner & Feldon, 1987; Weiner, Shadach, Tarrasch, Kidron, & Feldon, 1996). Moreover, openness to experience has been associated with functional connectivity within dopamine-rich mesocortical networks (Passamonti et al., 2015). Although these findings indirectly support the initial hypothesis, more direct evidence is needed to connect trait characteristics of openness to dopamine function.

1.2 The present study

In the present study, a pharmacological manipulation of dopamine was used to test the hypothesis that dopamine modulates the association between openness and implicit sequence learning. Two groups of healthy males received either the dopamine receptor blocker sulpiride or a placebo prior to performing a probabilistic serial reaction time task. We hypothesized that manipulating dopamine activity alters the relationship between openness and implicit learning. Accordingly, we expected an interaction between self-reports of openness and substance group (sulpiride, placebo). Because openness, intellect, and intelligence are typically correlated (Ashton, Lee, Vernon, Jang, 2000; Austin, Deary, & Gibson, 1997; Harris, 2004), the effects of fluid intelligence and self-reported intellect were assessed in secondary analyses.

2 Methods

2.1 Participants

Two hundred and ten healthy male volunteers participated in the present study as part of a larger research project investigating the effects of dopamine on behavioral measures. Participants were recruited on social media platforms, job fair websites, and on campus. They

provided written informed consent and received monetary compensation (€70) or course credit for their six-hour involvement in the study. The research project was approved by the Ethics Committee of the German Society for Psychology. Inclusion criteria were male gender, right-handedness, physical and mental health, and age between 18 and 35 years. The sample was restricted to male participants to control for sex specific differences that might interfere with substance effects (e.g., due to the female hormonal cycle). Psychiatric disorders were assessed in a pretesting session using a standardized clinical interview (Mini-DIPS; Margraf, 1994) and led to exclusion as well as hypertension (blood pressure higher than 140/90). Further self-reported exclusion criteria were the intake of any prescription medication or illegal drugs during the last three months, and habitual smoking of more than 10 cigarettes per week. In total, 17 participants were excluded from this study because they reported a first language other than German (n = 10), refused to comply with task instructions (n = 2), were not able to swallow the capsule (n = 2), arrived too late for medication intake (n = 1), had already eaten on the study day (n = 1), and did not complete the personality questionnaire due to technical failure (n = 1). The final sample reported here consisted of *n* = 193 males (mean age = 25.8, *SD* = 3.9, *n* = 95 in the sulpiride group and *n* = 98 in the placebo group). Seventy-six percent of them were university students (7.7% psychology students). As intended, statistical power was >.80 to detect correlations of rho = .30 (alpha = .05) within each of the two experimental groups.

2.2 Materials and tasks

Pharmacological manipulation. In a placebo-controlled, double-blind between-subjects design, participants orally ingested either 200 mg sulpiride or a placebo. Both substances were delivered in capsules matched for weight and color to assure double-blindness to participants' experimental conditions. Sulpiride is classified as substituted benzamide that predominantly acts as selective D2-receptor antagonist (Mauri, Bravin,

Bitetto, Rudelli, & Invernizzi, 1996). While showing high affinity to both pre- and postsynaptic D2 receptors (Missale, Nash, Robinson, Jaber, & Caron, 1998), the substance appears to lack significant effects on other receptor types (e.g., histaminergic, cholinergic, serotonergic, adrenergic, or γ-aminobutyric acid, and D1-type receptors). Its absorption from the gastrointestinal tract is slow and even reduced by concomitant food intake, with reported peak serum levels ranging from 1 to 6 hours after oral intake and average elimination half-life ranging from 3 to 10 hours (Mauri et al., 1996). In higher dosages (e.g., 800 to 1000 mg/day), sulpiride causes antipsychotic effects, probably by equally blocking both pre- and postsynaptic receptors. In lower dosages (e.g., 50 to 150 mg/day), however, sulpiride exhibits a mild stimulant effect that is used for treating symptoms of depression (Mauri et al., 1996; Uchida et al., 2005). This paradoxical effect was hypothesized to be due to prevalent blockage of presynaptic autoreceptors leading to enhanced dopamine neurotransmission (Kuroki, Meltzer, & Ichikawa, 1999). In previous studies with healthy participants, single doses of sulpiride have been well tolerated and participants were usually not able to guess whether they received sulpiride or placebo (Wacker, Mueller, Pizzagalli, Hennig, & Stemmler, 2013; Chavanon, Wacker, & Stemmler, 2013; Wacker, 2018).

Implicit sequence learning. Implicit learning was assessed using a probabilistic serial reaction time task (SRT; Destrebecqz & Cleeremans, 2001; Kaufman et al., 2010). Participants were instructed to perform a simple four-choice reaction time paradigm: A black dot appeared at one of four possible locations arranged horizontally on a computer screen. The stimulus locations (1-4) corresponded to parallel keys on the computer keyboard (c, v, b, and n). When a dot appeared on the screen, the appropriate response button had to be pressed. The correct button press ended the trial and the next stimulus appeared. Participants were instructed to respond as quickly and accurately as possible. Without their knowing, the stimulus locations followed a probabilistic rule according to which the targets were chosen

from two sequences with varying probability. Following a second-order conditional, each stimulus was probabilistically determined by its two predecessors. For example, after the target appeared at locations 2 and 4, location 3 followed with 85% probability. Thus, each trial represented either a probable stimulus location (in 85% of the trials) or an improbable stimulus location (in 15% of the trials). Note that the design did not include a first-order conditional (i.e., the immediate successor was equally likely to be one of the remaining locations). After a training block in which both sequences appeared with equal probabilities, eight task blocks were performed with each 120 trials.

Personality assessment. Openness was assessed using the openness scale from the Big Five Aspect Scales that measures each of the Big Five domains with two 10-item scales, respectively (BFAS, DeYoung et al., 2007). Additionally, the broad openness to experience domain was assessed using the NEO Personality Inventory (NEO-PI-3; Costa & McCrae, 2010) that measures six facets of openness to experience (fantasy, feelings, aesthetics, ideas, actions, and values) with a total of 48 items. Note that four of the six facets (fantasy, feelings, aesthetics, and actions) have been classified as markers of openness, while the ideas facet has been more strongly associated with intellect (DeYoung et al., 2007). Intellect was further assessed using a 24-item Intellect Scale (Mussel, 2013).

Intelligence assessment. We estimated participants' fluid intelligence by administering three computer-based subtests from the Intelligence Structure Battery (INSBAT; Arendasy et al., 2012). The INSBAT provides an adaptive intelligence measurement with all subtests showing conformity to the Rasch model (Frey & Moshagen, 2015). Fluid intelligence was assessed with the subtests numeric-inductive thinking (number series), figural-inductive thinking (Raven's matrices) and verbal-deductive thinking (verbal reasoning) (Arendasy et al., 2012). Additionally, three tasks measuring crystallized intelligence were conducted and will be reported elsewhere. Due to the adaptive test

construction, the overall duration of the intelligence assessment varied between participants (M = 56 minutes, SD = 10.6 minutes).

2.3 Procedure

Inclusion criteria and personality questionnaires were assessed in a pretesting session. Participants were then invited to the main experimental session in groups of four. Each experimental session started at 9:30 in the morning and was supervised by two out of five female experimenters. When arriving at the laboratory, participants were randomly assigned to a single cabin. After ingesting the capsule, they received a light standardized breakfast and subsequently completed six subtests of the intelligence structure battery (INSBAT) and four divergent thinking tasks. About 1.8 hours after the medication intake (SD = 0.21), the serial reaction time task was conducted. Afterwards, a battery of computer tasks was completed (results will be reported elsewhere). In the end, participants were debriefed about their experimental condition, thanked and compensated.

2.4 Statistical data analysis

For comparison with previous findings, all pre-processing steps were applied as described by Kaufman et al. (2010). Accordingly, trials with incorrect responses and reaction times more than three standard deviations above the mean were excluded. Subsequently, binary implicit learning scores were calculated for each participant based on reaction time differences between probable and improbable trials. Namely, larger differences relatively to the effect of the whole sample were coded as 1 while differences smaller than the sample effect were coded as 0. Following Kaufman et al.'s (2010) procedure, the binary coding was applied from block 3 to 8 and the scores were summed up across these six blocks. To predict the binary learning scores with Openness, Substance, and the Openness × Substance interaction, linear regression analyses were computed. Openness scores were z-transformed within each of the experimental groups.

Furthermore, we used linear mixed effects models to predict the raw data (reaction times) with Probability (probable, improbable), Openness (continuous scores), Substance (placebo, sulpiride), and the respective interactions. Unlike traditional regression-based approaches, mixed models allow to calculate within and between subject effects on single-trial level and without reducing the data prior to the analysis. Accordingly, reaction times were entered without calculating difference scores or binary scores that inevitably cause information loss. A maximum likelihood estimation (ML) was applied using the lme function in R. Note that the hypotheses and analyses were pre-registered at the Open Science Framework on August 9 in 2017 after the collection of 70 data sets and before accessing any of the data included in the current analyses (https://osf.io/mv4xs/register/5771ca429ad5a1020de2872e). The results of the other task addressed in the pre-registration have been reported elsewhere (i.e., Käckenmester, Bott, & Wacker, 2019).

In addition to the pre-registered analysis plan, we conducted a meta-analysis using our data from the placebo group and the results of two published studies that used the same task and largely overlapping personality scales (Kaufman et al., 2010 and Sobkow et al. 2018). The analysis was motivated by recent findings by Sobkow et al. (2018) that were inconsistent with the results by Kaufman et al. (2010) on which our hypotheses were built. To ensure that all available studies were included, we searched the databases PsychInfo and Medline (PubMed) for the terms “implicit learning” or “probabilistic learning” or “serial reaction time” or “incidental learning” and “openness”. The literature search was updated on 15th of July in 2019, yielding 11 results in PubMed and 9 results in PsychInfo. Other than Kaufman et al. (2010) and Sobkow et al. (2018), none of the publications reported correlations between measures of openness and the same version of the probabilistic serial reaction time task. We used the rma function of the metafor package in R to calculate overall effect sizes for

Openness, Intellect, and Fluid Intelligence. The total sample was N = 451 (k = 3). As recommended by DeYoung et al. (2007), the BFAS openness subscale and the NEO-PI-3 facets fantasy, feelings, aesthetics, and actions were coded as Openness. The intellect subscale from the BFAS, the intellect scale by Mussel (2013), and the ideas facet of the NEO-PI-3 were coded as Intellect. Raven's advanced progressive matrices, mental rotation, verbal reasoning (verbal analogies, verbal deductive thinking), and numeric inductive thinking (number series) were used as indicators of fluid intelligence.

3 Results

3.1 Preliminary analyses

First, all trials with incorrect responses (3.5%) and reaction times more than three standard deviations from the mean (1.7%) were removed. Reliability estimates of the implicit learning scores were calculated across the six blocks that were later used for the main analyses. Cronbach's alpha of the raw difference scores did not reach an acceptable level (α = .37). When using the binary coding method, internal consistency increased to α = .54. Although these values are similar to those reported by Kaufman et al. (2010), they are clearly unsatisfactory and prompted us to examine the task more closely. Doing so we found that the implicit learning effect was not evident at all stimulus locations. As illustrated in Figure 2, the hypothesized effects were present at stimulus locations 1 and 3, ambiguous at location 2, and absent at location 4. To verify these observations, we used the lme function in R to predict the observed reaction times with Probability (probable, improbable), Stimulus (1,2,3,4), and the Stimulus X Probability interaction. Besides the hypothesized main effect of Probability (b = -34.4, t(130998) = -14.9, p < .001), an unexpected main effect of Stimulus (b = -8.96, t(130998) = -11.07, p < .001), and an unexpected Stimulus X Probability interaction emerged, b = 5.36, t(130998)= 6.14, p < .001. Thus, the main effect of Probability

substantially differed between the four stimulus locations (1,2,3, and 4). Specifically, significant Probability effects only emerged at stimulus 3 (b = -53.8, t(32427) = -25.2, p < .001) and stimulus 1 (b = -32.9, t(33608) = -17.7, p < .001) and were not found at stimulus 2 (b = 0.6, t(32322) = 0.3, p = .76) and stimulus 4 (b = -1.31, t(32061) = -.82, p = .41). Accordingly, reliability estimates of the difference scores were highest for stimulus 3 (α = .89), lower for stimulus 1 (α = .56), below an acceptable level for stimulus 2 (α = .25) and practically zero for stimulus 4 (α = .093; see Figure 1 for the average reaction time differences). Examining possible programming errors, we did not find any mistakes in the execution of the probabilistic construction as described by Kaufman et al. (2010). Given the size of the observed effects of stimulus location, it seems reasonable to assume inherent problems with the task construction. Furthermore, we found a programming error in the practice block that probably caused unintended reaction time differences during the practice trials (see Figure 1, block 0). Instead of an alternating order, the sequences 1 and 2 were presented in the order 1-2-2-1 such that sequence 2 occurred in direct succession. As a result, reaction times within sequence 2 were significantly shorter (b = 36.9, t(8727) = 16.16, p < .001). Since the expected probability effect was still observed in the first task block, it seems unlikely that the analyses trials (block 3 to 8) were systematically affected by the practice difference. Still, systematic practice effects might have unknown consequences that we cannot rule out at this point.

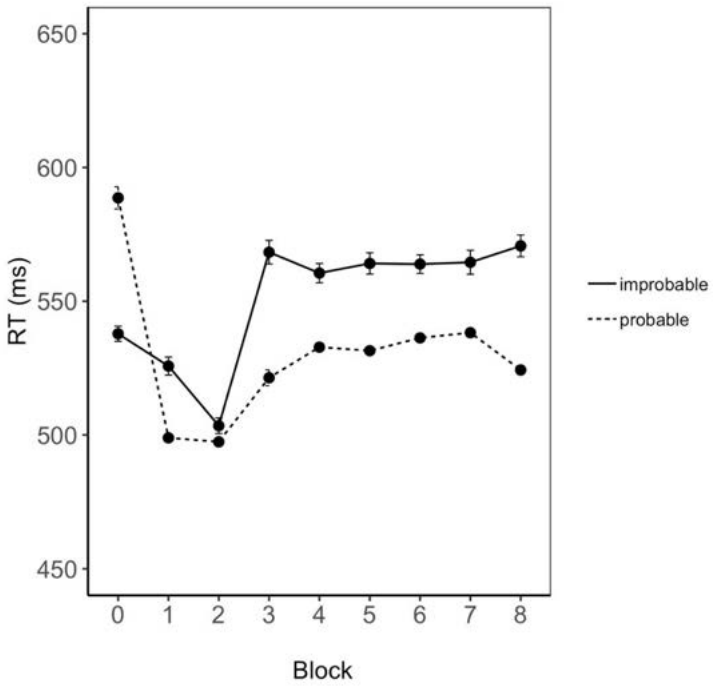


Figure 1. Mean reaction times in probable and improbable trials across all stimulus locations. Error bars depict standard errors of the mean.

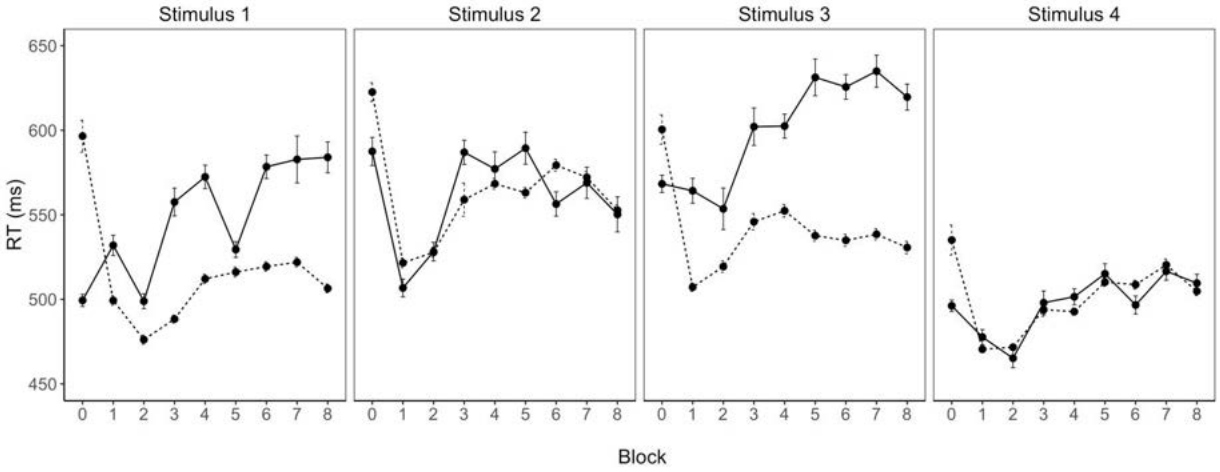


Figure 2. Mean reaction times in probable and improbable trials at stimulus locations 1-4. Probable trials are illustrated with dashed lines, improbable trials with solid lines. Error bars depict standard errors of the mean.

3.2 Blindness to the psychopharmacological treatment

The majority of participants (78%) indicated in a forced-choice item as part of the post-experimental questionnaire that they assumed to have received the placebo. The two substance groups did not differ in the percentage of participants who guessed that they had taken the dopamine blocker (sulpiride group: 21.1%, placebo group: 22.7%), $\chi^2(1) = 0.1$, $p = .76$. Importantly, the percentage of correct guesses was independent from guessed substance group (48% correct sulpiride guesses and 50% correct placebo guesses), $\chi^2(1) = 0.07$, $p = .79$. Furthermore, participant's subjective confidence in whether they had taken sulpiride was not related to the correctness of their guess ($\chi^2(3) = 0.96$, $p = .81$). Overall, we assume that participants were not able to guess their experimental condition above chance.

3.3 Main analyses

Predicting implicit learning based on the binary coding method with Openness and Substance (placebo, sulpiride), the expected Openness x Substance interaction failed to reach statistical significance, $b = -0.25$, $t(189) = 1.75$, $p = .082$. Neither Openness nor Substance showed a main effect on implicit learning ($b = 0.145$, $t(189) = 1.43$, $p = .15$, and $b = -0.03$, $t(189) = -0.21$, $p = .83$, respectively). Within the placebo group, the expected correlation between openness and implicit learning was not significantly different from zero, $r(96) = .148$, $p = .15$. Furthermore, none of the NEO facets displayed significant interactions with Substance ($b < 0.18$ $t(189) < 1.21$, $p > .23$). Additionally, linear mixed effects models were used to predict reaction times with Probability (probable, improbable), Substance (sulpiride, placebo), and Openness (continuous scores). A main effect of Probability confirmed that participants reacted faster to probable than to improbable trials ($b = -21$, $t(130996) = -12.4$, $p < .0001$). In line with the results reported above, the Probability x Substance x Openness interaction just failed to reach statistical significance, $b = 20.4$, $t(130996) = 1.66$, $p = .096$. Significant Probability x Substance x Openness interactions emerged for the NEO facets

Feelings (b = 24.6, t(130996) = 2, p = .043) and Actions (b = 33.03, t(130996) = 2.75, p = .006). In sum, the predicted interaction between Openness and Substance failed to reach statistical significance in both analyses and Openness was not significantly associated with implicit learning in the placebo group. The NEO Openness facets yielded two out of four significant results using the mixed model approach and no significant results using the multiple regression approach.

Finally, we conducted a meta-analysis across our data and two published studies that used the same task (k = 3, N = 451). Implicit learning was not significantly correlated with Openness, r = .073 [-.05, .199], Z = 1.13, p = .26. Small but significant correlations were observed for Intellect, r = .12 [.03, .21], Z = 2.55, p = .01, and Fluid Intelligence, r = .17 [.08, .26], Z = 3.58, p = .0003.

4 Discussion

In the present study, we examined the effects of a pharmacological dopamine manipulation on the association between implicit sequence learning and trait levels of openness. The dopamine receptor blocker sulpiride was administered in a placebo-controlled between subjects design in a sample of healthy males. Contrary to our predictions, the interaction with substance failed to reach statistical significance. Thus, correlations between openness and implicit learning did not differ between substance groups. Moreover, the predicted positive association in the placebo group was too small to reach significance. A meta-analysis of two published studies and our data confirmed previously reported associations between implicit learning and both intellect and fluid intelligence, but not openness.

4.1 Association of implicit learning with openness

The ability to spontaneously detect stimulus patterns has been theoretically associated with trait characteristics of openness (DeYoung, 2010). In line with this assumption, openness has been associated with implicit sequence learning (Kaufman et al. 2010). Contrary to these predictions, openness and implicit sequence learning were not significantly correlated in our placebo group. Therefore, our findings did not confirm the results by Kaufman et al. (2010) but are rather in line with subsequent findings by Sobkow et al. (2018), who did not find significant correlations either using the same task. Because our likewise non-significant meta-analysis combining all available data on the openness-implicit learning association had higher power (> .95) to detect an effect of moderate size (r = .20), the effect (if existent) is likely smaller than anticipated. However, in line with previous results (Danner et al., 2011; Sobkow et al., 2018), the meta-analytical findings support a positive association between implicit learning and fluid intelligence.

4.2 Dopaminergic basis of implicit learning and openness

Given the empirically underpinned involvement of dopamine in implicit learning (e.g., Uddén, Folia, & Petersson, 2010) and the theorized involvement of dopamine in openness to experience (DeYoung, 2013), we expected the effect of the dopaminergic agent sulpiride on implicit learning to interact with trait levels of openness. If the positive association between openness and implicit learning is indeed rather weak as suggested by our meta-analysis, detecting changes in this association likely also requires even larger samples to achieve sufficient statistical power.

Previous studies found pharmacological effects on implicit learning using Haloperidol versus d-amphetamine (Kumari, Corr, Mulligan, Cotter, Checkley, & Gray, 1997) as well as Levodopa (De Vries, Ulte, Zwitserlood, Szymanski, & Knecht, 2010). Using sulpiride (200 mg), an overall substance effect on implicit learning did not emerge in the present study. Since we used a different substance and a different task, the findings cannot be compared

directly. Future research may probe the specificity of the effect to certain dopaminergic agents in sufficiently large samples .

4.3 Limitations

Besides the sample size considerations already alluded to above another critical limitation lies in the low reliability of implicit learning tasks including the one used in this study. Implicit sequence learning as well as artificial grammar learning tasks usually lack reliability, especially when compared to explicit measures (Gebauer & MackIntosh; Danner et al., 2011; Kaufman et al., 2010; Sobkow et al., 2018). Using modified versions of the same task, Buchner and colleagues (Buchner & Wippich, 2000; Buchner & Brandt, 2003) demonstrated that the reliability of implicit tasks systematically falls below the reliability of equivalent explicit paradigms. They assumed this might partly be due to a greater variety of processes that are used to perform implicit tasks (Buchner & Wippich, 2000). Nevertheless, systematic differences in reliability can artificially cause dissociations between explicit and implicit measures (Chapman & Chapman, 1978). Moreover, correlations with between-subject variables (i.e., intelligence, openness) might be underestimated due to insufficient reliability. A second source of reliability constraints arises from the use of difference scores. Although difference scores are popular in many fields (e.g., clinical pre-post comparisons or event-related potentials), their use has long been criticized for a lack of reliability (Cronbach & Furby, 1970). Besides, the subtraction procedure reduces information that might be particularly relevant when investigating individual differences (Meyer, Lerner, de los Reyes, Laird, & Hajcak, 2017), for instance, to answer the question whether intelligence is associated with faster reactions to probable trials or slower reactions to improbable trials. As an alternative to traditional regression models, more complex analyses like linear mixed effects models provide the opportunity to predict the raw data (e.g., reaction times) with continuous between-subject measures (e.g., openness, intelligence) and within-subject

conditions (e.g., sequential versus random). Analyzing the raw data instead of difference scores might help to reduce reliability restrictions and information loss. A further limitation of our study resides in the decision to only investigate male participants.

4.4 Conclusions

In summary, the present study provides an initial test of the assumption that dopamine modulates the association between openness and implicit sequence learning. However, the association between openness and implicit learning was found to be very small and could not be confirmed when aggregating the effects across three studies that used the same task. In addition, we did not find the expected modulating effect of dopamine on this association. Due to substantial reliability restrictions of the task measure, personality correlates of implicit abilities and their associations with dopamine activity need to be tested with more reliable measures of implicit learning in future studies.

The authors have no conflicts of interest to disclose.

References

Arendasy, M., Hornke, L. F., Sommer, M., Wagner-Menghin, M., Gittler, G., Häusler, J., & Wenzl, B. M. (2012). Intelligenz-Struktur-Batterie–INSBAT. Mödling: Schuhfried.

Ashton, M. C., Lee, K., Vernon, P. A., Jang, K. L. (2000). Fluid intelligence, crystallized intelligence, and the openness/intellect factor. *Journal of Research in Personality, 34,* 198-207. https://doi.org/10.1006/jrpe.1999.2276

Austin, E. J., Deary, I. J., & Gibson, G. J. (1997). Relationships between ability and personality: three hypotheses tested. *Intelligence, 25,* 49-70. http://dx.doi.org/10.1016/S0160-2896(97)90007-6

Badgaiyan, R. D., Fischman, A. J., & Alpert, N. M. (2007). Striatal dopamine release in sequential learning. *Neuroimage*, *38*(3), 549-556.

Buchner, A., & Brandt, M. (2003). Further evidence for systematic reliability differences between explicit and implicit memory tests. *The Quarterly Journal of Experimental Psychology Section A*, *56*(2), 193-209.

Buchner, A., & Wippich, W. (2000). On the reliability of implicit and explicit memory measures. *Cognitive psychology*, *40*(3), 227-259.

Chapman, L. J., & Chapman, J. P. (1978). The measurement of differential deficit. *Journal of Psychiatric Research*, *14*(1-4), 303-311.

Chavanon, M. L., Wacker, J., & Stemmler, G. (2013). Paradoxical dopaminergic drug effects in extraversion: dose- and time-dependent effects of sulpiride on EEG theta activity. *Frontiers in Human Neuroscience*, *7*, 117. https://doi.org/10.3389/fnhum.2013.00117

Cleeremans, A., Destrebecqz, A., & Boyer, M. (1998). Implicit learning: News from the front. *Trends in cognitive sciences*, *2*(10), 406-416.

Costa, P. T., & McCrae, R. R. (2010). The NEO Personality Inventory: 3. Odessa, FL: Psychological assessment resources.

Cronbach, L. J., & Furby, L. (1970). How we should measure" change": Or should we?. *Psychological bulletin*, *74*(1), 68.

Danner, D., Hagemann, D., Schankin, A., Hager, M., & Funke, J. (2011). Beyond IQ: A latent state-trait analysis of general intelligence, dynamic decision making, and implicit learning. *Intelligence*, *39*(5), 323-334.

Destrebecqz, A., & Cleeremans, A. (2001). Can sequence learning be implicit? New evidence with the process dissociation procedure. *Psychonomic bulletin & review*, *8*(2), 343-350.

De Vries, M. H., Ulte, C., Zwitserlood, P., Szymanski, B., & Knecht, S. (2010). Increasing dopamine levels in the brain improves feedback-based procedural learning in healthy participants: an artificial-grammar-learning experiment. *Neuropsychologia*, *48*(11), 3193-3197.

DeYoung, C. G. (2010). Personality neuroscience and the biology of traits. *Social and Personality Psychology Compass*, *4*(12), 1165-1180.

DeYoung, C. G. (2013). The neuromodulator of exploration: A unifying theory of the role of dopamine in personality. *Frontiers in Human Neuroscience*, *7*, 1- 26. https://doi.org/10.3389/fnhum.2013.00762

DeYoung, C. G., Peterson, J. B., & Higgins, D. M. (2005). Sources of Openness/Intellect: Cognitive and neuropsychological correlates of the fifth factor of personality. *Journal of Personality, 73,* 825-858. https://doi.org/10.1111/j.1467-6494.2005.00330.x

DeYoung, C. G., Quilty, L. C., & Peterson, J. B. (2007). Between facets and domains: 10 aspects of the Big Five. *Journal of personality and social psychology*, *93*(5), 880.

Frey, A. & Moshagen, M. (2015). TBS-TK Rezension: Intelligenz-Struktur-Batterie (INSBAT)“. *Psychologische Rundschau, 66,* 86–88. https://doi.org/10.1026/0033-3042/a000237

Gebauer, G. F., & Mackintosh, N. J. (2007). Psychometric intelligence dissociates implicit and explicit learning. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *33*(1), 34.

Graybiel, A. M. (1995). Building action repertoires: memory and learning functions of the basal ganglia. *Current opinion in neurobiology*, *5*(6), 733-741.

Graybiel, A. M. (1998). The basal ganglia and chunking of action repertoires. *Neurobiology of learning and memory*, *70*(1-2), 119-136.

Harris, J. A. (2004). Measured intelligence, achievement, openness to experience, and creativity. *Personality and Individual Differences, 36,* 913-929. https://doi.org/10.1016/S0191-8869(03)00161-2

Käckenmester, W., Bott, A., & Wacker, J. (2019). Openness to experience predicts dopamine effects on divergent thinking. *Personality Neuroscience 2*(3), 1-7.

Kaufman, S. B., DeYoung, C. G., Gray, J. R., Jiménez, L., Brown, J., & Mackintosh, N. (2010). Implicit learning as an ability. *Cognition*, *116*(3), 321-340.

Kumari, V., Gray, J. A., Corr, P. J., Mulligan, O. F., Cotter, P. A., & Checkley, S. A. (1997). Effects of acute administration of d-amphetamine and haloperidol on procedural learning in man. *Psychopharmacology*, *129*(3), 271-276.

Kuroki, T., Meltzer, H. Y., & Ichikawa, J. (1999). Effects of antipsychotic drugs on extracellular dopamine levels in rat medial prefrontal cortex and nucleus accumbens. *Journal of Pharmacology and Experimental Therapeutics, 288,* 774-781.

Margraf, J. (1994). *Diagnostisches Kurz-Interview bei psychischen Störungen, Mini-DIPS*. Berlin, Heidelberg: Springer Verlag.

Mauri, M. C., Bravin, S., Bitetto, A., Rudelli, R., & Invernizzi, G. (1996). A risk-benefit assessment of sulpiride in the treatment of schizophrenia. *Drug Safety, 14*, 288-298. https://doi.org/10.2165/00002018-199614050-00003

Meyer, A., Lerner, M. D., De Los Reyes, A., Laird, R. D., & Hajcak, G. (2017). Considering ERP difference scores as individual difference measures: Issues with subtraction and alternative approaches. *Psychophysiology*, *54*(1), 114-122.

Missale, C., Nash, S. R., Robinson, S. W., Jaber, M., & Caron, M. G. (1998). Dopamine receptors: from structure to function. *Physiological reviews, 78,* 189-225. https://doi.org/10.1152/physrev.1998.78.1.189

Mussel, P. (2013). Intellect: A theoretical framework for personality traits related to intellectual achievements. *Journal of Personality and Social Psychology*, *104*(5), 885.

Paquet, F., Soucy, J. P., Stip, E., Levesque, M., Elie, A., & Bedard, M. A. (2004). Comparison between olanzapine and haloperidol on procedural learning and the relationship with striatal D2 receptor occupancy in schizophrenia. *The Journal of neuropsychiatry and clinical neurosciences*, *16*(1), 47-56.

Passamonti, L., Terracciano, A., Riccelli, R., Donzuso, G., Cerasa, A., Vaccaro, M. G., ... & Quattrone, A. (2015). Increased functional connectivity within mesocortical networks in open people. *Neuroimage, 104*, 301-309. https://doi.org/ 10.1016/j.neuroimage.2014.09.017

Peterson, J. B., & Carson, S. (2000). Latent Inhibition and Openness to Experience in a high-achieving student population. *Personality and Individual Differences, 28,* 323-332. https://doi.org/10.1016/S0191-8869(99)00101-4

Peterson, J. B., Smith, K. W., & Carson, S. (2002). Openness and extraversion are associated with reduced latent inhibition: Replication and commentary. *Personality and Individual Differences, 33,* 1137-1147. https://doi.org/10.1016/S0191-8869(02)00004-1

Reber, A. S., Walkenfeld, F. F., & Hernstadt, R. (1991). Implicit and explicit learning: Individual differences and IQ. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *17*(5), 888.

Robertson, E. M. (2007). The serial reaction time task: implicit motor skill learning?. *Journal of Neuroscience*, *27*(38), 10073-10075.

Shohamy, D., Myers, C. E., Kalanithi, J., & Gluck, M. A. (2008). Basal ganglia and dopamine contributions to probabilistic category learning. *Neuroscience & Biobehavioral Reviews*, *32*(2), 219-236.

Sobkow, A., Traczyk, J., Kaufman, S. B., & Nosal, C. (2018). The structure of intuitive abilities and their relationships with intelligence and Openness to Experience. *Intelligence*, *67*, 1-10.

Stevens, A., Schwarz, J., Schwarz, B., Ruf, I., Kolter, T., & Czekalla, J. (2002). Implicit and explicit learning in schizophrenics treated with olanzapine and with classic neuroleptics. *Psychopharmacology*, *160*(3), 299-306.

Swerdlow, N. R., Stephany, N., Wasserman, L. C., Talledo, J., Sharp, R., & Auerbach, P. P. (2003). Dopamine agonists disrupt visual latent inhibition in normal males using a within-subject paradigm. *Psychopharmacology, 169,* 314-320. https://doi.org/10.1007/s00213-002-1325-6

Uchida, H., Takeuchi, H., Suzuki, T., Nomura, K., Watanabe, K., & Kashima, H. (2005). Combined treatment with sulpiride and paroxetine for accelerated response in patients with major depressive disorder. *Journal of clinical psychopharmacology*, *25*, 545-551. https://doi.org/10.1097/01.jcp.0000185425.00644.41

Uddén, J., Folia, V., & Magnus Petersson, K. (2010). The neuropharmacology of implicit learning. *Current neuropharmacology*, *8*(4), 367-381.

Wacker, J., Mueller, E. M., Pizzagalli, D. A., Hennig, J., Stemmler, G. (2013). Dopamine-D2 receptor blockade reverses the association between trait approach motivation and frontal asymmetry in an approach-motivation context. *Psychological Science, 24,* 489-97. https://doi.org/10.1177/0956797612458935

Weiner, I. & Feldon, J. (1987). Facilitation of latent inhibition by haloperidol in rats. *Psychopharmacology, 91,* 248-253. http://dx.doi.org/10.1007/BF00217073

Weiner, I. Shadach, E., Tarrasch, R., Kidron, R., & Feldon, J. (1996). The latent inhibition model of schizophrenia: Further validation using the atypical neuroleptic, clozapine. *Biological Psychiatry, 40,* 834-843. http://dx.doi.org/10.1016/0006-3223(95)00573-0

Methods reporting

Original task instruction:

Sie sehen gleich vier nebeneinander liegende Quadrate in der Mitte des Bildschirms. In jeweils einem der Quadrate wird ein schwarzer Punkt erscheinen.

Ihre Aufgabe ist es, diejenige Taste auf der Tastatur zu drücken, die der Position des Punktes entspricht.

Bitte legen Sie dafür den Zeige- und Mittelfinger der linken und rechten Hand nebeneinander auf die Tasten „v“, „b“, „n“ und „m“.

Weiter mit Leertaste!

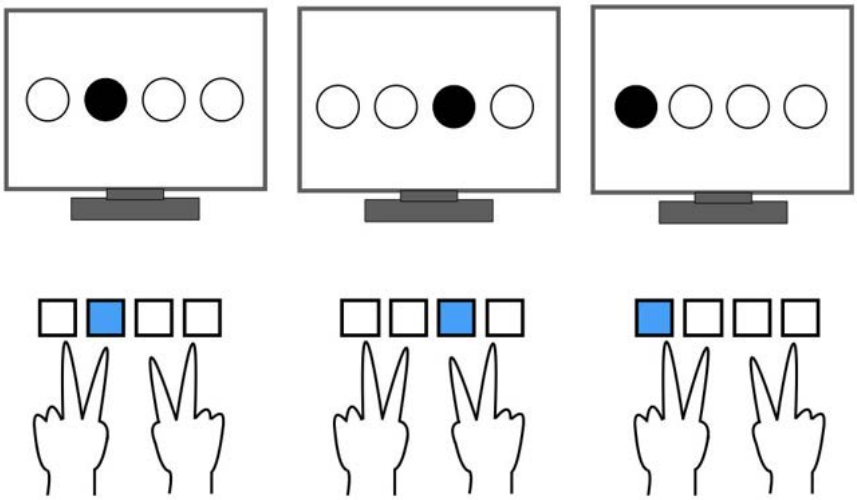
Lassen Sie die Finger während der Aufgabe nebeneinander auf den Tasten „v“ bis „m“ liegen.

Wenn der Punkt im ganz linken Quadrat erscheint, drücken Sie bitte „v“. Erscheint der Punkt im ganz rechten Quadrat erscheint, drücken Sie bitte „m“. Für die eher links benutzen Sie entsprechend „b“, für die eher rechts „n“.

Reagieren Sie so fehlerfrei und so schnell wie möglich!

Weiter mit Leertaste!

Illustration of the serial reaction time task (SRT)



A black dot appeared at one of four possible locations arranged horizontally on the computer screen. Participants were instructed to respond as quickly and accurately as possible by pressing the corresponding parallel key on the computer keyboard.

Universität Hamburg
DER FORSCHUNG | DER LEHRE | DER BILDUNG

FAKULTÄT
FÜR PSYCHOLOGIE UND
BEWEGUNGSWISSENSCHAFT
Institut für Bewegungswissenschaft
Institut für Psychologie

Eidesstattliche Erklärung nach *(bitte Zutreffendes ankreuzen)*

☐ **§ 7 (4) der Promotionsordnung des Instituts für Bewegungswissenschaft der Universität Hamburg vom 18.08.2010**

☐ **§ 9 (1c und 1d) der Promotionsordnung des Instituts für Psychologie der Universität Hamburg vom 20.08.2003**

Hiermit erkläre ich an Eides statt,

1. dass die von mir vorgelegte Dissertation nicht Gegenstand eines anderen Prüfungsverfahrens gewesen oder in einem solchen Verfahren als ungenügend beurteilt worden ist.
2. dass ich die von mir vorgelegte Dissertation selbst verfasst, keine anderen als die angegebenen Quellen und Hilfsmittel benutzt und keine kommerzielle Promotionsberatung in Anspruch genommen habe. Die wörtlich oder inhaltlich übernommenen Stellen habe ich als solche kenntlich gemacht.

_____ _____

Ort, Datum Unterschrift

Universität Hamburg
DER FORSCHUNG | DER LEHRE | DER BILDUNG

FAKULTÄT
FÜR PSYCHOLOGIE UND
BEWEGUNGSWISSENSCHAFT
Institut für Bewegungswissenschaft
Institut für Psychologie

Erklärung gemäß *(bitte Zutreffendes ankreuzen)*

☐ **§ 4 (1c) der Promotionsordnung des Instituts für Bewegungswissenschaft der Universität Hamburg vom 18.08.2010**

☐ **§ 5 (4d) der Promotionsordnung des Instituts für Psychologie der Universität Hamburg vom 20.08.2003**

Hiermit erkläre ich,

_____ (Vorname, Nachname),

dass ich mich an einer anderen Universität oder Fakultät noch keiner Doktorprüfung unterzogen oder mich um Zulassung zu einer Doktorprüfung bemüht habe.

_____ _____

Ort, Datum Unterschrift