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Original Research Article

Frontal alpha asymmetries and behavioral immune system: moderating role of behavioral inhibition system

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Abstract

Background and purpose: *Behavioral immune system is a cluster of psychological mechanisms enabling detection and avoidance of pathogens in one's immediate environment. Its presumed activation has been implicated in myriads of psychological phenomena, stemming from pathogen related disgust to more complex behaviors, such as mate choice and xenophobic cognitions. However, little is known about its biological underpinnings. The aim of this preliminary study was twofold: 1) to explore the role of another neuropsychological system governing avoidant motivations, the behavioral inhibition system, in pathogen-induced disgust and 2) to determine if frontal hemispheric asymmetries (a neural correlate of avoidant motivations) might serve as indicators of behavioral immune system activation.*

Materials and methods: *62 participants completed the Behavioral inhibition scale. Based on their z-scores, two extreme groups were formed: high (n=9) and low behavioral inhibition (n=9) group. After the baseline EEG recordings, participants were exposed to a set of neutral stimuli, followed by a set of pathogen disgust inducing stimuli. The frontal asymmetry (FAA) indexes (lnR-LnL) were calculated within both low (8-10 Hz) and high (11-13 Hz) alpha frequency bands on analogue pairs of frontal electrodes.*

Results: *There were no baseline FAA differences between groups. However, compared to low behavioral inhibition group, high behavioral inhibition group showed larger shifts in FAA on frontopolar locations while watching the pathogen related disgust-inducing stimuli, as compared to neutral photographs.*

Conclusions: *This pattern of FAA shifts suggests that high behavioral inhibition individuals attend to pathogen threat related cues more readily, i.e., have a more reactive behavioral immune system. With this preliminary study we are proposing a new line of research in order to determine if there is evidence of a calibrated response in terms of interplay between one's immune status and pathogen treat related neural reactivity.*

INTRODUCTION

Throughout its evolutionary history, humankind has constantly been exposed to various parasitic organisms. This caused tremendous selection pressures, resulting in a variety of physiological adaptations, i.e., immune system. The immune system is a highly sophisticated, versatile set of physiological defense mechanisms. Its adaptive value is beyond repute. However, like any adaptation – its benefits come along with costs *(1, 2)*. Efficient immunological response is metabolically costly, can be temporarily debilitating (due to fever, cytokine induced sickness behavior, etc.) and in some cases can even cause more permanent damage (when an overly aggressive immune response results in an autoimmune disease). But most of all, immunological defense is reactive: the pathogen has to enter the organism in order for the immune system to react. This is where the behavioral immune system enters into equation. If we had to describe its function with a proverb, it would be "Prevention is better than cure". This set of psychological mechanisms is proactive – it detects the possible presence of pathogens (i.e., contagious individuals and/or objects) in an organism's immediate environment and triggers avoidant and prophylactic behaviors. Thus, the two systems, the physiological immune system and the behavioral immune system, complement one another *(3–5)*.

How does the behavioral immune system work?

The concept of behavioral immune system has been extensively analyzed on perceptual level (detection of pathogen), affective-cognitive level (emotions and cognitions related to activation of behavioral immune system) and output (behavior) level. Pathogens are not necessarily accessible to our senses, but they tend to visibly change their host. In case of contaminated food, sometimes, the presence of other organisms is actually visible (e.g., flies, worms etc.), but even when it is not, we can spot a change in its color, taste and smell. In case of sick conspecifics, they may have skin lesions, rashes, swellings, they might vomit, have diarrhea, sneeze, cough etc. *(6)*. Recent research has shown that humans have the ability to detect even very subtle facial and olfactory cues of sickness in others just hours after experimental activation of their immune system, and that this olfactory–visual integration of sickness cues likely involves intraparietal sulcus (functionally connected to core areas of multisensory integration; *7, 8*)

These perceptual cues then activate specific emotional and cognitive responses. When it comes to emotions, disgust has been primarily implicated in behavioral immune system activation. The main feature of this emotion is repulsion, sometimes accompanied by a feeling of nausea and a strong desire to distance ourselves from the stimulus *(9, 10)*. Thus, many agree that the main function of disgust is to prevent one from ingesting potentially toxic substances and contracting disease in general *(5, 9, 11)*. In a classic example it has been shown that people, rather irrationally, refuse to eat chocolate pudding in the form of feces *(12)*. Driven largely by this emotional component, activation of behavioral immune system is for the most part unconscious and automatic. However, prophylactic behaviors activated by the behavioral immune system also include rational, conscious choices, such as vaccination or avoidance of public transportation during a flu season *(13)*. The later area of investigation saw a massive proliferation of studies recently, with the pandemic of COVID-19, confirming that variables related to the behavioral immune system (perceived infectability, germ aversion, disgust sensitivity) predicted various facets of human behavior during the pandemic – including adherence to epidemiological measures, willingness to vaccinate, illness-threat appraisal, social cognitions etc. *(14–20)*. Specifically, perceived vulnerability to disease was found to be associated with increased COVID-19 anxiety and greater need for behavioral change and social distancing *(16)*. On an individual level, germ-aversion was shown to be related with the willingness to implement COVID-19 preventative behaviors *(20)*, but more interestingly, the group level scores on germ aversion, disgust sensitivity and perceived infectability have risen significantly during the pandemic as compared to the pre-pandemic scores *(14)*, reflecting the context-related reactivity of the BIS.

Not surprisingly, a large part of disgust-inducing stimuli, such as feces, sweat, blood, sexual secretions, corpses, wounds, etc., comes from the human body (9). And thus, the unconscious processes described earlier can be triggered by the vicinity of other people. Not only do the cues of potential sickness have a high attention drawing potential, but they are also easily remembered *(21–23)*. The fact that certain disease-related but not contagious features (e.g., some skin conditions) can automatically activate unpleasant emotions, aversive thoughts, and behaviors (i.e., the behavioral immune system), corroborates this notion *(24)*.

In certain situations, these feelings motivate us to distance ourselves from other people. While reduction in contact with members of other groups reduces the likelihood of contracting infectious diseases, this threat detection system often overshoots. This overreaction has been extensively studied in the context of social evolutionary psychology: numerous studies investigated the effects of the behavioral immune system on various aspects of social cognition, such as ethnocentrism, conformism and conservative attitudes, prejudice, xenophobia political orientation, attitudes towards certain groups, but also sexual behavior and partner choice *(24–33)*.

Separating one avoidant motivational system from another

Humans are equipped with at least one other motivational system governing avoidant motivations – the behavioral inhibition system *(34)*. It has been described as a neuropsychological system that predicts an individual's response to anxiety-relevant cues in a given environment. This system is sensitive to cues of punishment, unpleasant consequences of an ongoing action, or generally negative events. Individuals differ in their responsiveness to cues of impending reward and/or punishment. These interindividual variations have since been described in detail within the Reinforcement sensitivity theory of personality *(35)*. The Reinforcement sensitivity theory differentiates further between two systems governing defensive behaviors: the fight-flight-freeze system and the behavioral inhibition system (the former governing active avoidance behaviors and the latter being activated by goal conflict, i.e., concurrent co-activation of both the fight-flight-freeze and behavioral approach systems; *(36)*. Much like in the case of the behavioral immune system, these avoidance motivational tendencies drive attention to social and environmental cues, influencing perception, cognition, and ultimately, behavior *(37)*. And also, like the behavioral immune system, these two systems have recently been shown to predict a significant proportion of variance of pandemic behaviors *(38)*. In fact, both theoretical frameworks have been applied simultaneously, in an attempt to explain conformity, warmth toward others and attitudes toward lockdown during the COVID-19 pandemic, contributing to the body of knowledge regarding motivations underlying public behavior during such crises *(39)*.

High activity of the behavioral inhibition system means a heightened sensitivity to non-reward, punishment, and novel experience. This higher level of sensitivity to these cues results in a natural avoidance of such environments in order to prevent negative experiences such as fear, anxiety, frustration, and sadness. Thus, one might be inclined to question the necessity of conceptualizing the behavioral immune system as a separate system, not just one facet of the more general, behavioral inhibition system. While it is true that both the behavioral inhibition system and behavioral immune system represent avoidance tendencies, the latter is more specific regarding the triggers of withdrawal motivations. Furthermore, the behavioral inhibition/activation systems are considered to be relatively stable, trait-like features, while the activation of behavioral immune system is usually conceptualized as domain specific, mostly elicited by pathogen threat related cues. If a certain motivational system has unique function and different biological underpinnings from another motivational system, two different systems can be postulated.

Even though motivational systems have drawn substantial theoretical interest, they are still underesearched area. For example, differences between self-protection and disease avoidance systems have been systematically demonstrated *(40)*. The two systems are fueled by different emotions (fear versus disgust), accompanied by different cognitive processes, and are regulated via different neurobiological mechanisms. Evolution has equipped humans with specific tools for facing specific forms of threats.

The physiological mechanism behind the behavioral inhibition system is believed to be the septohippocampal system and its monoaminergic afferents from the brainstem *(41)*. It was shown that the orbitofrontal cortex and precuneus gray matter volume correlates with individual differences in the behavioral inhibition system *(42)*. Activation-wise, one of the most often used neural markers of behavioral inhibition is the asymmetry in frontal cortical activation *(44, 45)*. Evidence from studies using measurements of frontal alpha asymmetry (FAA) suggests that increased activity in the left frontal cortical region of the brain reflects activation of approach motivation and activity in the right frontal cortex indicates activation of withdrawal motivation *(46, 47)*. Based on these theories and findings, a number of studies have examined both resting asymmetry in the frontal cortex as a predictor of motivations and affective response to stimuli, and context-dependent reactive asymmetries as indicators of motivational states. Specifically, prefrontal EEG alpha asymmetry (FAA) studies suggest that the left hemisphere is more involved in the processing of positive emotions and approach-related behaviors, whereas the right hemisphere is more involved in the processing of negative emotions and withdrawal behaviors *(43–47)*. Based on these findings, we opted to use FAAs as neural indicators of motivational states in the present study.

In search of a proximal mechanism

While the concept of behavioral immune system is theoretically conceptualized as an extended arm of the physiological immune system, there are only a handful of studies exploring the biological mechanisms underlying its activation. In general, evolutionary psychology has been criticized for rarely pursuing the search for the specific neural networks underlying postulated psychological adaptations. In the case of the behavioral immune system, it has been suggested that the research in this area should be integrated into broader fields of research from other disciplines, such as psychoneuroimmunology and psychoneuroendocrinology *(48, 49)*. The interplay between our immune, endocrine, and nervous systems, and our psychological makeup has been investigated for decades in these disciplines, though mostly through exploration of proximal mechanisms. Emerging integration of these fields is promising, as it has the potential to provide both proximal and ultimate (evolutionary) levels of causation *(50)*. So far, we have described studies investigating the influence of perceived pathogen threat on cognitions, emotions, and behavior. These studies have recently been extended to explore the effects of such perceptions on the immune system and the potential role of endocrine system. For example, it seems that pathogenic pictures have the capacity to induce not only disgust, but also elevate body temperature, and rise in salivary concentrations of TNF-alpha and albumin *(51)* and production of IL-6 *(52)*. These findings, if they replicate, would provide the evidence that behavioral immune system might proactively induce immunological responses when the threat of infection is perceived.

Even more complex than that, there is some evidence suggesting that these responses are calibrated, i.e., that organism's physiological needs impact behavioral immune activity. Recently and frequently ill people show greater activation of behavioral immune system than healthier peers *(53)*. Pregnancy is yet another example of immunosuppression, and a study has shown that pregnant women expressed more ethnocentrism in the first trimester, when their immune systems are weakest *(54)*.

Ideally, to conceptually complete the notion of behavioral immune system, we would have to know the underlying neural mechanisms. The emotion of disgust has been investigated on both central (anterior insula being the most often implicated) and peripheral (the blood pressure, pulse and skin conductance decrease and there is a change in respiratory rate; 9) level. We *(55)* have recently shown that exposing participants to pathogen-salient pictures (as compared to neutral stimuli) resulted in shorter latency periods of skin conductance responses and that magnitude of these responses correlated positively with the scores on pathogen disgust scale *(33)*, providing some tentative autonomic nervous system correlates of behavioral immune system activation. Here, we opted to explore how its central nervous system correlates. More precisely, the aim of this study was to determine whether frontal alpha asymmetries (previously used as a neural marker of avoidant motivations) can function as neural indicators of behavioral immune system activation. Furthermore, we wanted to explore the possible interplay between a stable trait-like dimension of behavioral inhibition and behavioral immune system reactivity. More precisely, we hypothesized that individuals high on behavioral inhibition dimension shall pay more attention to the pathogen-threat and that this tendency shall be reflected in greater frontal alpha asymmetries while exposed to the disgust-inducing stimuli as compared to the low behavioral inhibition individuals.

METHOD

Participants and procedure

The participants were enrolled from a pool of students at the Department of Psychology, and most of them received course points in compensation for participation in the study. There were no specific exclusion criteria, but the participants were informed that some of them shall receive an invitation for a follow-up EEG study and were asked to check the opt-out option if they did not wish to participate in the EEG part of the study. Initially, 62 participants (M_age= 19.86) completed the Behavioral inhibition/ activation scales *(41)*. Cronbach alpha for the BIS scale on this sample was α =.74. Their scores on the behavioral inhibition scale were then z-transformed, and two extreme groups were formed: high behavioral inhibition group (z>1; n=9; 6 female) and low behavioral inhibition group (z<-1; n=9; 5 female). The rationale for the formation of extreme groups was that large main effects were not expected, and we opted to maximize the chance that underlying differences in neural responsivity, if they were any, were not obscured by the errors in psychometrical assessment of the BIS as a trait (with the extreme groups, there is less chance that random effects influenced the score). Future studies, conducted on larger samples, would benefit from inclusion of the whole range of BIS scores as a covariate.

These 18 participants underwent continuous EEG recording which consisted of two baseline situations (eyes closed and eyes opened, no stimuli) followed by two blocks of stimuli: a set of neutral photographs and a set of pathogen related disgust inducing photographs (infected wounds, soiled public toilets, helminths etc.). The order of these two sets was counterbalanced across participants. During the presentation, all lights remained turned off to minimize visual stimuli interferences, besides the PC screen monitor. Individuals sat comfortably in order to minimize muscle artifacts in a sound-attenuated room. All the procedures were in accordance with the ethical standards defined in the Ethical Code of Conduct of Croatian Psychological Association and in compliance with the Declaration of Helsinki guidelines.

The EEG was recorded using a Nihon Kohden electroencephalograph with electrodes placed according to the international 10-20 system, using the Cz and linked earlobes as reference electrodes. Impedances were kept below 5 kΩ. Since central and linked earlobe referencing has been criticized (56) and is not recommended when indices of asymmetry are calculated, all recordings were re-referenced offline using the grand average reference algorithm. The EEG data were filtered using a 0.3–30 Hz band-pass filter. Noisy trials and epochs containing eye movements and/or muscle contractions were excluded by visual inspection to remove artifacts from the neural data. Clear EEG epochs were then extracted using a time window of min 3s (512 data points) during the stimuli presentation. These epochs were then fast Fourier transformed in order to extract spectral power bands.

All further analyses were carried out using SPSS v25. The frontal asymmetry indexes lnR – lnL were calculated within both the low (8-10 Hz) and high (11-13 Hz) alpha frequency bands on all analogue pairs of frontal electrodes (fp1/fp2, f3/f4, f7/f8). Only these three anterior pairs of electrodes were of interest, as frontal alpha symmetry indices have been previously shown to correspond with affective states.

RESULTS

After calculating the FAAs for each condition and within each spectral power band, a series of mixed model ANOVAs was performed, with condition (baseline, neutral stimuli, pathogen disgust inducing stimuli) as a source of variance within participants, and behavioral inhibition score (high vs. low) as a source of variance between groups. FAAs on each pair of electrodes were dependent variables.

Main effects: behavioral inhibition (low vs high)

There were no overall FAA differences between low and high behavioral inhibition groups (lower alpha band: $F_{fp1\text{-}fp2}$=0.84, p=.77; $F_{f3\text{-}f4}$=0.25, p=0.62; $F_{f7\text{-}f8}$=1.57, p=.23;

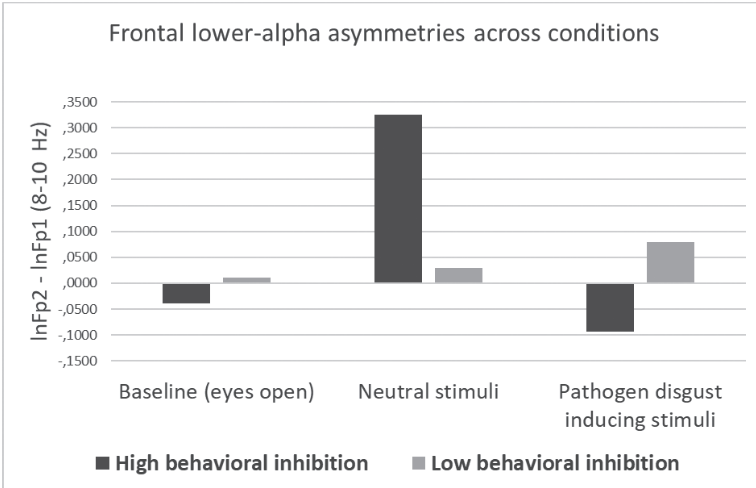

Figure 1. *Shifts in lower (8-10 Hz) frontal alpha asymmetries as a function of experimental condition and behavioral inhibition.*

higher alpha band: $F_{fp1\text{-}fp2}$=4.12, p=.06; $F_{f3\text{-}f4}$=1.97, p=.12; $F_{f7\text{-}f8}$=1.58, p=.23).

The overall differences here (between high and low behavioral inhibition groups) were not expected, as it has previously been shown that individual differences in affective tendencies as measured by FAAs will emerge as a function of the interaction between the innate capabilities of the individual and the situational context (i.e., emotion-eliciting stimuli).

Main effects: experimental condition (behavioral immune system activation)

There were no main effects of the experimental condition either (lower alpha band: $F_{fp1\text{-}fp2}$=2.70, p=.08; $F_{f3\text{-}f4}$=2.57, p=.09; $F_{f7\text{-}f8}$=0.93, p=.42; higher alpha band: $F_{fp1\text{-}fp2}$=0.11, p=.90; $F_{f3\text{-}f4}$=1.97, p=.10; $F_{f7\text{-}f8}$=0.09, p=.91). In order to claim that shifts in FAAs are a useful neural indicator of behavioral immune system activation, we would have to see significant main effects here. The possible reasons for lack of these effects are discussed in the discussion section.

Interaction: behavioral inhibition x experimental condition

There was a significant behavioral inhibition x condition interaction on the frontopolar pair of electrodes, among both lower ($F_{fp1\text{-}fp2}$=4.03, p=.028) and higher ($F_{fp1\text{-}fp2}$=3.81, p=.037) alpha power band FAAs. As can be seen

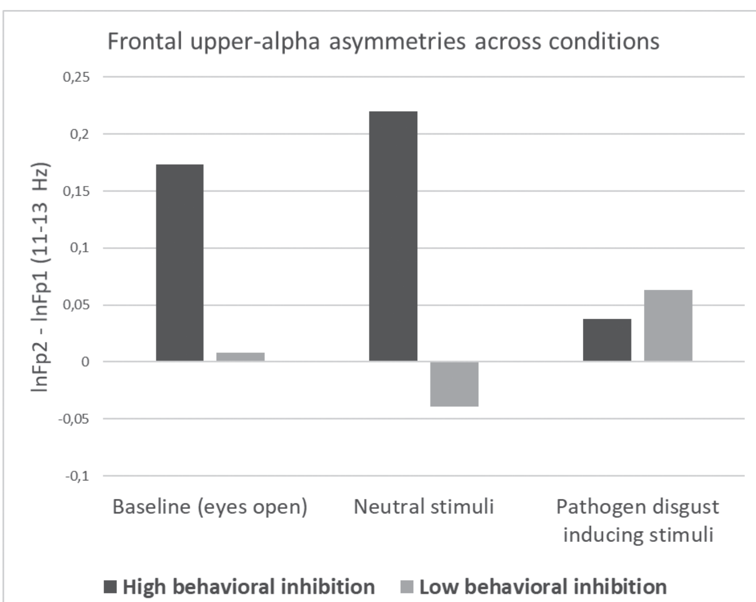

Figure 2. *Shifts in upper (11-13 Hz) frontal alpha asymmetries as a function of experimental condition and behavioral inhibition.*

from Figures 1 and 2, this interaction stemmed from the fact that individuals from high behavioral inhibition group showed a significantly larger shift in FAAs while watching the disgust-inducing photographs, as compared to neutral photographs, than did the low behavioral inhibition group, suggesting they attend to pathogen threat cues more readily.

DISCUSSION

This study had two aims: 1) to compare the frontal EEG activity (baseline and during the presumed activation of the behavioral immune system) between participants with high vs. low scores on the Behavioral Inhibition Scale and 2) to explore the usefulness of FAAs as neural indicators of behavioral immune system activation.

Regarding our first research problem, i.e., exploring the role of behavioral inhibition system in pathogen induced feeling of disgust, our results suggest that highly behaviorally inhibited individuals probably attend to pathogen related threats more readily. Shifts in their FAA indices across conditions (baseline / neutral / disgust-inducing stimuli) were larger in both alpha power bands. Since various bands of alpha frequency spectra have been shown to reflect different aspects of information processing (with changes in the lower alpha band being associated with attention and working memory and the ones in the higher alpha band reflecting specific components of the stimuli processing; *56–58*), the robustness of this interaction across the bands is relevant. However, this effect was found on frontopolar locations only. Based on previous reports, we expected the same pattern of results on all frontal locations. Our small sample size probably resulted in lack of statistical power, which is why these results should be considered as preliminary only. However, it is also possible that the effect was seen on these locations only because EEG asymmetries on frontopolar locations are particularly affected by state factors and emotional states *(59)*.

Furthermore, in line with theoretical expectations, and the fact that pathogen threat related cues have the potential to draw attention easily *(22, 23)*, it is not unconceivable that individuals who usually attend to cues of potential danger and negative consequences more readily (the high behavioral inhibition group) also show greater frontal alpha power shifts while exposed to pathogen disgust inducing stimuli. On one hand, this might be a reflection of their generally heightened avoidance tendencies. But from an evolutionary medicine perspective, it would be interesting to explore the possibility that this is an adaptively calibrated response, an interplay between their immune status and perceptual/behavioral domain. The rationale for this interpretation lies in the fact that there seems to be a link between dominant activity of the left vs. right hemisphere and increased immunocompetence vs. immunosuppression *(60–63)*. The exact mechanism underlying this link is not yet completely understood, but several hypotheses have been proposed, including the role of the right prefrontal cortex in the modulation of the stress response, the role of sympathetic nervous system, and the possible hemispheric specialization in autonomic control of the heart *(61)*.

This, along with findings that the mere visual perception of diseased-looking people has the potential to stimulate the white blood cells to respond more aggressively to infection *(52)* leaves some space for speculation about a complex adaptive psychoneuroimmunological response, fine-tuned by one's immune status and immediate pathogen threat cues from environment. It has already been suggested that the behavioral immune system might promote both short-term and long-term pathogen management *(49)* and that personal control over pathogen exposure might be a key factor predicting investment in behavioral (e.g., avoidance) versus physiological (e.g., tolerance) immunity. Furthermore, there are studies suggesting that individual differences in the genetic bases of immunocompetence correlate with individual differences in behavioral tendencies associated with the behavioral immune system. For example, the individuals who possess gene variants associated with greater susceptibility to certain infectious diseases and poorer immunological function reported lower levels of extraversion and openness to experience and higher levels of harm avoidance *(64, 65)*.

Regarding the second research problem we opted to answer, the frontal alpha asymmetries did show variations as a function of interaction between experimental condition and group. Moreover, a certain trend was seen toward marginally significant shifts in lower alpha power band as a function of experimental condition, and we believe our small sample size and the lack of statistical power caused this lack of statistical significance in FAA shifts. A larger study should be conducted in order to determine whether with more statistical power FAAs would show predictable shifts as a function of experimental condition (i.e., presumed behavioral immune system activation) only. Based on numerous earlier studies *(30–34)* showing that state-dependent frontal alpha asymmetries do indeed correlate with motivational drives, we believe this index has the potential to be used in future studies as an additional biological marker of behavior immune system (re)activity. As we have previously argued, the behavioral immune system research program could benefit greatly from implementation of neural indices underlying the relation between perceived pathogen threat and resulting behaviors.

Limitations of the present study and recommendations for future studies

Even though it is not unusual to see small sample sizes in EEG studies, especially with a dependent design like in our case, a larger sample would be required before reaching any definite conclusions. We have observed trends toward statistical significance in some of our main effects; however, given the sample size the statistical power is limited. Furthermore, in order to test a possible role of behavioral inhibition, we used extreme groups of high vs. low behavioral inhibition individuals, and so any information regarding potential non-linear relation between behavioral inhibiting and behavioral immune system reactivity would be lost. The rationale for this procedure was the fact that earlier literature reports of non-consistent correlations between behavioral inhibition scores and resting frontal alpha asymmetries, and we wanted to minimize the within-group variance in the behavioral measure in an attempt to minimize the noise in the data. However, this finding should be replicated using continuous behavioral inhibition variable. Finally, the low spatial resolution of the EEG makes it impossible to elucidate possible BIS-related changes in neural activity of more specific brain regions. As it is, due to the combination of limitations related to both the small sample size and the lack of spatial resolution, the question whether different pattern of activity on frontopoloar vs. F3/4 and F7 /F8 locations was incidental or stemming from the affective nature of our stimuli, remains unanswered.

Since behavioral immune system is conceptualized as a behavioral extension of the physiological immune system (i.e., a crude first line of defense against disease-causing pathogens), we plan to broaden this preliminary study and investigate the potential relationship among one's overall health status, perceived vulnerability to disease and both baseline asymmetries and pathogen-disgust induced shifts in FAAs. More precisely, we plan to explore whether people who perceive themselves as more vulnerable show greater FAA shifts in response to pathogen cues, and whether behavioral inhibition system plays a role as a potential mediator in their responsiveness.

In conclusion, even though this study is preliminary in its nature, our results suggest that there is an interplay between one's behavioral inhibition system activity and their behavioral immune system reactivity, as measured by shifts in frontal alpha asymmetries. Building upon previous body of research about the relation between neural asymmetries and immunocompetence, we hypothesize that these variations in readiness to attend to pathogen related cues reflect a specific feature of disease avoidance motivational system, i.e., a sort of calibrated adaptive response promoting long-term health management.

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