University of Pavia

Department of Brain and Behavioral Sciences

Risk-taking behaviour

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Abstract

The environment we interact with constantly confronts us with challenges that may cause us potential harm or provide a reward depending on our choices. The ability to evaluate and weigh the trade-off between a potential win and a harmful loss is called risk-taking ability. This Thesis aims to better clarify some of the many unknown aspects regarding this function. As an index of real-life risk-taking tendencies, we chose to use the Balloon Analogue Risk Task (BART).

This Thesis is divided into two chapters. The first chapter describes the effects on risk-taking behaviour of 2 techniques of vestibular stimulation: Caloric Vestibular Stimulation (CVS) and Galvanic Vestibular Stimulation (GVS). More in detail, contrary to our predictions, results in *Study 1* show how the CVS can selectively increase risk tendencies only for bodily-related stimuli, implying that the CVS is not sufficient to modify risk-taking behaviour as a whole, but a biologically salient and bodily-related stimulus is necessary to allow the effects of the CVS on the representation of the body to interfere with the decision regarding dangerous situations. As a continuation, *Study 2* directly deals with the influence of the vestibular input on risk-taking. To assess that, the BART is administered to subjects undergoing GVS. A significant reduction of hazardous tendencies is reported during L-GVS when compared with the opposite polarity, highlighting the vestibular contribution to high cognitive functions, risk-taking in particular, with a polarity specific effect that mainly excites the activity of the right hemisphere.

In continuity with the previous, chapter 2 shows the effects on risk-taking of more ecological and natural tools. More precisely, *Study 3* reports our findings regarding short-term alterations of the gravitational signals to the brain and how they influenced the willingness to take risks. Our results demonstrated an effect of head orientation on risk propensity, where an upright head position showed behavioural patterns directed towards more conservative and less risky choices compared to a

downward head position (i.e. “bed rest”). A coherent and well-integrated vestibular input to the brain is needed to properly cope with different environmental situations.

Lastly, *Study 4* displays an attempt to detect possible changes in risk-taking after the prolonged time spent in isolation during the Covid-19 lockdown. No significant modification in risk tendencies was found as the time spent in isolation increased.

Together, these results highlight the importance of a preserved ability to judge risk situations and have the ability to cope with challenging environments. In particular, the understanding of the neurocognitive substrates underpinning this function is of primary importance in order to begin to sort out the many unknown sides of this topic.

General Introduction

Risk is always present in our everyday life. The environment we live in and interact with constantly puts us in such situations that require decision-making abilities balancing our previous experiences, internal states, expectations and understanding of the potential positive or negative consequences. Whenever this evaluation of the costs/benefits ratio involves a potential economical, physical or moral harm we talk about risk-taking behaviour (Leigh, 1999).

Withing the umbrella term of “decision-making”, a central component of these processes is risk-taking, which can be defined as the propensity to select actions with potentially greater advantageous and/or adverse consequences, compared to alternatives with relatively low favourable and/or unfavourable effects (Paulus et al., 2003). In real life, risk-taking manifests itself by taking part in numerous behaviours that involve a potential danger to oneself or others, often of uncertain magnitude, although this is counterbalanced by the opportunity to obtain some form of reward (Leigh, 1999). Therefore, an adaptive decision-making process requires the ability to weigh reward-seeking and harm-avoidance behaviours, which can be defined as the individual tendency to respond respectively to appetitive or aversive stimuli through approaches or distancing behaviours (Ernst & Paulus, 2005). It would be more appropriate not to refer to risk-taking as a one-dimensional construct, but rather to adopt a multidimensional perspective in which the levels of risk-taking vary according to the nature of the activities undertaken and the situational context, e.g. monetary, social, physical and ethical risks (Leigh, 1999). Furthermore, risk-taking behaviours can be differentiated based on the temporal dimension of the adverse consequences, in the short or long term, as well as concerning the nature of the consequent damages, in varying degrees of psychological, physical, legal and interpersonal types (Hunt et al., 2005).

To study and measure the concept of risk-taking, various types of tasks have been formulated and used in a wide range of research. For example, one of the most famous and used paradigms is the Iowa Gambling Task (IGT) (Bechara et al., 1994), where a set of 4 decks of cards is presented and each deck has an associated probability to give a monetary reward or loss. Two decks are advantageous with smaller gains but overall net win, while the others are disadvantageous with larger gains but lead to an overall net loss. The subject is asked to extract one card at a time choosing from these decks and therefore needs to understand which deck is more convenient to gain as much money as possible. As mentioned, this task has been used on a series of studies as a measure of decision-making and risk-taking and how they change with age (Cauffman et al., 2010), or between sexes (for a review: van den Bos et al., 2013) and as the testosterone level varies (Stanton et al., 2011), on patients with lesions to the prefrontal cortex (Bechara et al., 1994), Parkinson's disease (Kobayakawa et al., 2008), anxiety (Miu et al., 2008), depression (Must et al., 2013), schizophrenia (Shurman et al., 2005), borderline disorder (Haaland & Landrø, 2007), anorexia (Tchanturia et al., 2007), bulimia and obesity (Brogan et al., 2010), on alcohol abusers (for a review: Kovács et al., 2017), and even a version for rodents has been created (van den Bos et al., 2006). Given its ease of administration and its frequent usage in research, the IGT has arguably become one of the most famous decision-making paradigms in the cognitive and neuroscientific landscape for research purposes. Not only that, but the IGT also became a clinical instrument to evaluate executive functions. However, some authors raised concerns regarding the IGT's validity and reliability (Buelow & Barnhart, 2018; Buelow & Blaine, 2015; Buelow & Suhr, 2009; Lin et al., 2013; Xu et al., 2013). In particular, it appears that the IGT has scarce test-retest reliability, especially influenced by state mood, making its application (especially in clinical assessments) debatable (Buelow & Barnhart, 2018). Again, in Xu et al (2013) the IGT showed lower reliability when compared to other risk-taking paradigms: the Balloon Analogue Risk Task (BART) (Lejuez et al., 2002a, 2003) and the delay discounting task (DDT) (Johnson et al., 2010). The authors argued that the scarce correlation between the performances at these tasks can be explained considering risk-taking as a multi-layered construct, and each one of the tasks measures a different dimension of it. Nevertheless, the BART has been proved to have moderate to high reliability for the assessment of risk-taking and impulsive behaviour when compared to the IGT (Xu et al., 2013) and these two paradigms are sensitive to different aspects of decision-making and risk propensity (Buelow & Blaine, 2015). The original version of the BART was created by Lejuez and colleagues (2002, 2013) and was designed as a measure of real-life risk propensity. The task is usually performed on a computer and it shows a small simulated balloon and a pump. Moreover, a reset button labelled "Collect $$$" is shown on the screen, as well as a permanent money-earned display ("Total Earned"), and a second display listing the money earned on the last balloon ("Last Balloon"). Clicking on the pump inflates the balloon, giving the participant a small amount of money (5 cents in the original version), accumulated in a temporary bank. When a balloon is pumped past its breaking point, it explodes and a popping sound effect is generated, all money accumulated in the temporary bank is lost, and the next uninflated balloon appears on the screen. At any moment during each trial, the participant could stop pumping the balloon and click the "Collect $$$" button, transferring all the accumulated money from the temporary bank to the permanent bank while a slot machine payoff sound effect is played. A total of 90 balloons are presented during the task. In the original version of the BART, the 90 trials are divided into 3 different balloon types: blue, yellow, and orange balloons. Each balloon colour has a different probability of exploding, but participants are not instructed regarding this difference, neither any detailed information about the probability of an explosion is given. They were simply told that at some point each balloon would explode, starting from the first pump to the point the balloon is expanded to fill the entire screen. The range of pumps a balloon can reach varies between 1 to 128, and according to the explosions algorithm the average break point across all balloons is 64 pumps. As it is conceptualised, during the BART the subject should try to gain as much money as possible balancing small but safer wins (i.e. clicking fewer times on a single balloon) and bigger but less safe gains (i.e. pumping a balloon more risking to make it explode). Since this very first construction, the BART has been modified in different versions and applied on a wide range of settings due to its versatility (for a meta-analysis: Lauriola et al., 2014). In fact, this task has been used to assess risky tendencies, for example, in adolescents (Lejuez et al., 2003), drug abusers (Campbell et al., 2013; Canavan et al., 2014), brain-injured patients (Balagueró et al., 2016), and psychopathic inmates (Swogger et al., 2010). Moreover, the BART has been administered various times during neuroimaging exams, providing an anatomical account underlying the performance. These studies described a widespread pattern of activations in the brain, including the Anterior Cingulate Cortex (ACC), medial-frontal cortex and dorsolateral-frontal cortex and insula (Li et al., 2020; Schonberg et al., 2012).

To sum up, the BART enjoys a very wide range of applications, high reliability and validity, as well as being proven to measure real-life risk tendencies and a well known functional activity pattern. Due to these reasons, we chose to use this paradigm in different forms and experimental settings to explore how risk-taking behaviour can be modulated in healthy subjects to deepen our knowledge regarding this specific domain of decision-making.

In **Chapter 1**, we discuss how and why two of the most famous vestibular stimulation techniques (the Caloric Vestibular Stimulation – CVS; and the Galvanic Vestibular Stimulation – GVS) can be used to manipulate risk-taking behaviour during the performance of the BART. As matter of fact, this chapter focuses mainly on artificial vestibular stimulations as a tool to manipulate decision-making to answer specific theoretical questions that will be displayed in detail later in the Thesis. In particular, in *Study 1* we used the CVS on 21 healthy subjects during the performance of an alternative version of the BART created by this research group (Salvato et al., 2019). As matter of fact, in Salvato et al. (2019) we demonstrated that people with higher interoceptive abilities are more prone towards conservative choices when the shape of the balloon is substituted with the shape of a body. Since CVS is known to be able to modify a series of bodily-related abilities both in brain-injured patients and healthy subjects (for example: Bottini et al., 2005, 2013; Lopez et al., 2012; Sturt & Punt, 2013), we hypothesized that this kind of stimulation might be able to enhance participants' ability to better perceive their bodily states during this version of the BART, reducing their risky behaviour. To preview our results, contrary to our predictions, we found a significant increase towards risky choices after CVS only for body-shaped balloons. These results imply that the CVS is not sufficient to modify risk-taking behaviour per se, rather a biologically salient and bodily-related stimulus is necessary to allow the effects of the CVS on the representation of the body to interfere with the decision regarding dangerous situations. On the other hand, in *Study 2* we present the results we obtained in a recent publication (De Maio et al., 2021) specifically aimed at providing novel findings regarding the influence of the vestibular input on risk-taking. In fact, numerous neuroimaging studies have identified several cortical areas involved in vestibular processing in a widespread network primarily located in the right hemisphere of the brain that suggests a vestibular contribution to cognition that goes far beyond the traditional conceptualization of the vestibular function. Hence, artificial vestibular stimulation has been shown to modulate an impressive range of cognitive functions, including decision-making and body representation (Ferrè, Arthur, et al., 2013; Ferrè, Longo, et al., 2013; Ferrè, Vagnoni, et al., 2013b; Ferrè et al., 2015). The arising questions regard the possibility that this pattern of vestibular activations may interest risk propensity as well, proving once again the influence of the vestibular input on high-level cognitive functions. To do that, we applied left-anodal and right-cathodal GVS, the opposite polarity (i.e. right-anodal and left-cathodal GVS) and sham stimulation on 20 healthy subjects while performing the BART. What we found was a significant reduction of hazardous tendencies during left-anodal/right-cathodal GVS when compared with the opposite polarity. These result highlights the vestibular contribution to high cognitive functions, risk-taking in particular, with a polarity specific effect, meaning that a general vestibular stimulation is not sufficient to manipulate these tendencies, rather a specific stimulation that mainly excites the activity of the right hemisphere is necessary to observe such a modification.

As an extension of our findings presented in Chapter 1 regarding the manipulation of risk-taking, **Chapter 2** focuses on less artificial, therefore towards more ecological and natural ways to modulate hazardous tendencies. More precisely, in *Study 3* our goal was to test the short-term alterations of the gravitational signals to the brain could influence the willingness to take risks. In fact, alterations in decision-making have been described in altered gravitational conditions that simulate the typical conditions experienced during spaceflights (Lipnicki et al., 2009; Steinberg et al., 2015; Strangman et al., 2014), in particular their effects on behavioural control strategies (Gallagher et al., 2019). To test the effect of these gravitational alterations on cognition, we manipulated how the vestibular organs sense gravity by changing the body's orientation with respect to the direction of the gravitational acceleration on 20 healthy subjects. Thus, participants completed the BART while being either standing upright or lying supine, the so-called "bed rest posture". Our results demonstrated an effect of head orientation on risk propensity, where an upright head position shows behavioural patterns directed towards more conservative and less risky choices compared to a downward head position. We argue that these results are consistent with other findings in literature pointing out the importance of a coherent and well integrated vestibular input to the brain to properly cope with different environmental situations, providing new data about this topic in the frame of risk-taking.

Finally, *Study 4* has been conducted during the first months of the Covid-19 global pandemic, in the middle of the massive lockdown most of the people around the world had to face. With differences in terms of the extension of time spent in lockdown and the number of people being closed in lockdown with, almost everyone experienced a period of relative isolation, not being able to go to work, meet with friends and relatives and loved ones. Isolation is known to be extremely detrimental for almost all social animals, humans included, undermining physical and psychological health (for a review: Cacioppo & Hawkley, 2009). The most evident impairment caused by isolation within the cognitive functions is the decline of the executive functions. This causes a reduction in the capacity to control attention, cognition, emotion, regulation of social behaviour, the capacity to pursue personal goals and self-regulation (Cacioppo & Hawkley, 2009). Especially during a global pandemic that is still causing thousands of deaths every day, the impairment of such capacities may affect one's ability to properly judge and adequately respond to a risky situation. Of course, the very tangible risk to be infected by a potentially lethal virus constitutes a plastic example of the fundamental role of preserved decision-making strategies in a challenging environment that can put you in life or death situations. Therefore, our aim was to measure if the prolonged isolation caused by the lockdown may affect the ability to regulate hazardous tendencies. We administered the BART to 179 subjects using an online platform, also collecting data regarding the time spent in lockdown and the number of people the lockdown was spent with. To preview our results, we found that as the time spent in isolation increased, the risk tendencies increased. Unfortunately, this result was imputable to a methodological flaw: the statistical result was mainly driven by few people who participated at the experiment who did not spent time in lockdown due to their work commitments. In fact, their performances were remarkably less hazardous on average than the performances obtained by those who experienced around 2 months of isolation. Even if this is not a methodologically appropriate result, we believe that the huge difference in risk tendences performed by the two groups is worth being mentioned at least to reason about possible future directions that this branch of research regarding risk-taking may take under consideration.

To summarize, this Thesis aimed at contributing to a better understanding of that particular aspect of decision-making that is risk-taking. In particular, we used a gold-standard task to assess hazardous tendencies, the BART. Firstly, we investigated the interplay between interoception and an alternative version of the task after CVS, proving a specific effect of this type of vestibular stimulation on bodily-related stimuli. We then used another type of vestibular stimulation, the GVS, to test the vestibular contribution to those high cognitive functions involved during the BART, bringing novel data regarding the hemispheric-specific effects of this technique on risk-taking. Further, we naturally manipulated the vestibular input to the brain using the bed rest technique, showing an alteration in the behavioural pattern regarding risky choices when the head is in a tilted position. Finally, we tried to measure how the isolation caused by the Covid-19 pandemic may have affected our capacity to properly deal with dangerous situations. Together, our results provide new information regarding risk-taking, highlighting the relevance of this ability to safely interact with the environment surrounding us.

Chapter 1: Artificial vestibular manipulations affect risk-taking tendencies

Study 1: Caloric Vestibular Stimulation (CVS) increases risky choices towards body-related stimuli

Introduction

As anticipated in the introduction, this study aimed to investigate the relationship between body awareness capacity (i.e. interception) and risk propensity. In its narrowest meaning, the term "interception" has traditionally been associated with the sensations that originate from the internal organs of the body, in a privileged way from the viscera, in theoretical opposition to the term "exteroception", referring to the perception of exogenous stimuli on the surface external body (Ceunen et al., 2016). However, starting from the neuroanatomical observations made by Craig (Craig, 2003), interception has been redefined as the perception of the physiological condition of the body as a whole, thanks to the ability to identify and interpret the signals coming from the organism (Khalsa et al., 2018). Interoception would represent a moderating variable between the physiological modifications of the organism and the affective-cognitive processes, to the point that individuals endowed with high interoceptive accuracy would be able to perceive more intensely the link between bodily signals, emotional experience and/or cognitive processing (Dunn et al., 2010). One of the most relevant cognitive domains affected by interoceptive capabilities is decision-making, especially in complex and uncertain contexts, where potential gains or losses are expected. An adaptive decision-making process, therefore, requires the ability to weigh reward-seeking and harm avoidance behaviours, which can be defined as the individual tendency to respond respectively to appetitive or aversive stimuli through approaches or distancing behaviours.

As already mentioned, in a recent study conducted by this group (Salvato et al., 2019) the interoceptive abilities of 50 participants were measured using a paper-and-pencil questionnaire, the Body Perception Questionnaire (BPQ) (Porges, 1993). The experimental design also contemplated the measurement of participants' tendency to risk by means of the BART as well as using an alternative version of it. In this alternative version, images of balloons were replaced with a silhouette of bodies. The individual interoceptive sensitivity score on BPQ negatively predicted the risk index only in the experimental paradigm with stimuli in the shape of a human silhouette, while the level of interoceptive sensitivity was not able to predict the result with the classic BART.

In recent decades, vestibular caloric stimulation (CVS) has been used to study aspects of body representation, mainly in relation to awareness and social cognition disorders, in the distinction between one's own body and that of others. In light of our group's results (Salvato et al., 2019), the present research aimed to investigate whether CVS, which is supposed to modify aspects of interoceptive and bodily awareness, modulates risk-taking behaviour as the type of stimuli (object or body) is manipulated. Vestibular caloric stimulation (CVS) is a non-invasive stimulation technique, put into practice by irrigating the external auditory canal with hot or cold water (Bottini & Gandola, 2015). By inducing a temperature variation in the endolymph of the semicircular canals, the vestibular portion of the eighth cranial nerve is stimulated, directed to the vestibular nuclei and cortico-subcortical structures and then to the cortical areas implicated in the integration of the vestibular input (Ferrè, Bottini, et al., 2013; Lopez, Blanke, et al., 2012). In patients, cold water CVS on the left ear is effective in bilaterally remedying several neurological deficits and body awareness disorders (Bottini & Gandola, 2015). As stated in a review by Bottini (Bottini et al., 2018), CVS can induce a selective and transient remission of numerous awareness disorders, e.g. neglect, anosognosia and somatoparaphrenia. Furthermore, as mentioned in the general introduction, CVS would increase various perceptual abilities relating to the body (Ferrè et al., 2011; Lopez et al., 2010a; Sedda et al., 2016). Given these notions, we hypothesise that CVS contributes to the modulation of some interoceptive dimensions and, consequently, facilitates the processing of bodily-related stimuli during risk decision-making processes. Therefore, the first hypothesis is that vestibular stimulation induces a variation in the tendency of risk assumption in the presence of stimuli related to the human body, causing a reduction of risk tendencies. Furthermore, it is hypothesized that some aspects of interoceptive awareness may act as moderators of risk-taking behaviour, especially in the presence of bodily related stimuli.

Method

Participants

Twenty-one participants (8 males, 13 females; age range = 20-30 years; M=22.10; SD=2.3), were recruited from the students of the University of Pavia. All were native Italian speakers with no history of neurological or mental disorders. The exclusion criteria included the presence of disorders of the vestibular system and/or of pathologies affecting the ear. The experimental procedures were approved by the Ethics Commission of the Department of Sciences of the Nervous System and Behavior of the University of Pavia. Each participant provided their informed consent.

Task and Procedure

CVS

The experimental design included two distinct sessions, separated by an interval of at least 24 hours between them. During these sessions, CVS (with cold water) or the sham condition (with water at room temperature) were administered in randomized order among the participants. In both conditions, the water was applied to the left ear. In the first session, the participants filled out the questionnaires on interoceptive awareness and trait anxiety (both described below), in randomized order. Then, before continuing with the administration of CVS or sham, the frequency of the heartbeat was recorded by means of a pulse oximeter on the right middle finger; the heart rate measurement was repeated one minute after the administration procedure. This measurement was aimed at checking for any physiological activations caused by CVS that could represent a confounding factor. In both sessions, participants performed the modified version of the BART implemented with balloon-shaped stimuli and a human silhouette. After completing the computerized task, they were asked to complete the state anxiety questionnaire. In line with other studies (Been et al., 2007; Ferrè, Bottini, et al., 2013; Salvato et al., 2016), CVS was performed by irrigating with 30 ml of cold water (temperature ~2°C) the left external auditory canal, using a syringe equipped with a soft plastic cannula. The participants' head was tilted 30 ° backwards from the horizontal plane and tilted to the right to facilitate the irrigation. Some participants reported transient feelings of dizziness and nausea, which decreased over a few minutes; none withdrew from the study due to these sensations. The experimental paradigm was structured to be terminated within 15 minutes, in line with the indicated temporal efficacy of CVS (Bottini et al., 1995). The sham procedure was performed in a similar way, with the difference that the water was at room temperature.

The BART

In order to assess the risk-taking trend, the participants carried out the BART and a modified version of the original BART. In line with the study by Salvato (Salvato et al., 2019), the experimental paradigm included stimuli depicting a balloon or a human silhouette. However, some changes were made: firstly, the stimuli were not divided into two separate tasks (Balloon and Body task), but 30 balloons and 30 virtual bodies were presented in random order in each session of the experimental task, for a total of 60 stimuli. Secondly, the stimuli were not differentiated by colour categories, as each stimulus had a different probability of pseudo-randomized explosion within an interval between 1 and 128 insufflations, in line with the original BART. The explosion probability was balanced between balloon and body stimuli.

Interoceptive and mood measurement

As a measure of interoceptive awareness, the participants completed the Italian version of the Multidimensional Assessment of Interoceptive Awareness (MAIA) (Mehling et al., 2012). The questionnaire consists of 32 items on a six-point Likert scale, from "never" to "always", and returns distinct scores for each of 8 subscales, regarding different ways of paying attention to one's physiological signals: Noticing, Not-Distracting, Not-Worrying, Attention Regulation, Emotional Awareness, Self-Regulation, Body Listening, and Trust. Furthermore, to collect data about trait anxiety, the participants were subjected to the Italian version of the Trait Anxiety Scale (STAI X-2), and the State Anxiety Scale (STAI X-1) was chosen as a measure of state anxiety (Spielberger et al., 1970). We chose to measure these components of the emotional state to check for any confounding factors, given that, as mentioned, mood can significantly affect performance in risk paradigms.

Analysis

Following the indications in the literature, as a risk index, we used the average adjusted number of insufflations for the unexploded balloons on each subject. Therefore, in the analysis, we excluded the number of pumps for the exploded balloon and averaged the number of pumps for the unexploded ones (Lejuez et al., 2002; White et al., 2008). The indices for balloons and human silhouettes were calculated separately. To compare the obtained performance, an ANOVA 2 (Condition: CVS and sham) x 2 (Stimulus: balloons and bodies) was conducted. Since the BART shows a slight variation in the performance as the paradigm progresses over time (MacLean et al., 2018a), we decided to put the administration order as a covariate. Pre and post-CVS heart rates were also compared by means of a t-test to check that there were no significant changes in physiological activation.

To verify if the results of this study were in line with what we found in Salvato (2019), we performed Correlations between the scores obtained in the MAIA subscales and the differences between the scores obtained in CVS and sham in the Body BART.

The analyses were conducted using Jamovi (Version 1.6.13.0) (www.jamovi.org).

Results

The results showed a main effect for Stimulus, as participants showed a greater tendency to take risks in the presence of biological stimuli in the shape of a virtual body than in balloon-shaped object stimuli (F(1,19)=4.54, MS=130.36, p=.046). On the contrary, the main effect of the Condition (CVS/sham) on the risk indices was not significant (F(1.19)=0.34, MS=4.47, p=.567). The Condition x Stimulus interaction, on the other hand, was instead significant, as CVS selectively caused an increase in the average number of insufflations only in the presence of virtual bodies (F(1,19)=6.269, MS=18.95, p=.022) (See "Table 1"). This interaction was significantly influenced by the administration order between sham and CVS, whereas performing the BART for the first time during CVS led to a smaller decrease in risky behaviour in the second administration during sham compared to a much bigger increase in the number of pumps when the subject performs the BART for the first time during the sham and is subsequently administered with the BART after CVS. This issue is further discussed later on. "Figure 2" graphically represents the distribution, means and standard deviations relating to the number of insufflations in the Body and Balloon task. "Table 1" shows the results obtained in the ANOVA.

On the other hand, no significant correlations were found between the 8 subscales of the MAIA and the average number of insufflations in the Body task, in either of the two conditions. There was also no significant correlation between the risk indices in the Body or Balloon task and the status and trait anxiety scores. Performing a t-test for related samples, it was found that state anxiety levels (STAI X-1) following sham or CVS were comparable (t(20)=.81, p=.43). To exclude effects related to a general increase in physiological activation, two t-tests were conducted for dependent samples regarding the heartbeat rate before and after administration. No significant difference in heart rate was found either between pre- and post-CVS (t(19)=1.504, p=.15) or between pre- and post-sham (t(19)=.778, p=.45), proving that our main results were not imputable to the possible physiological activation caused by the CVS.

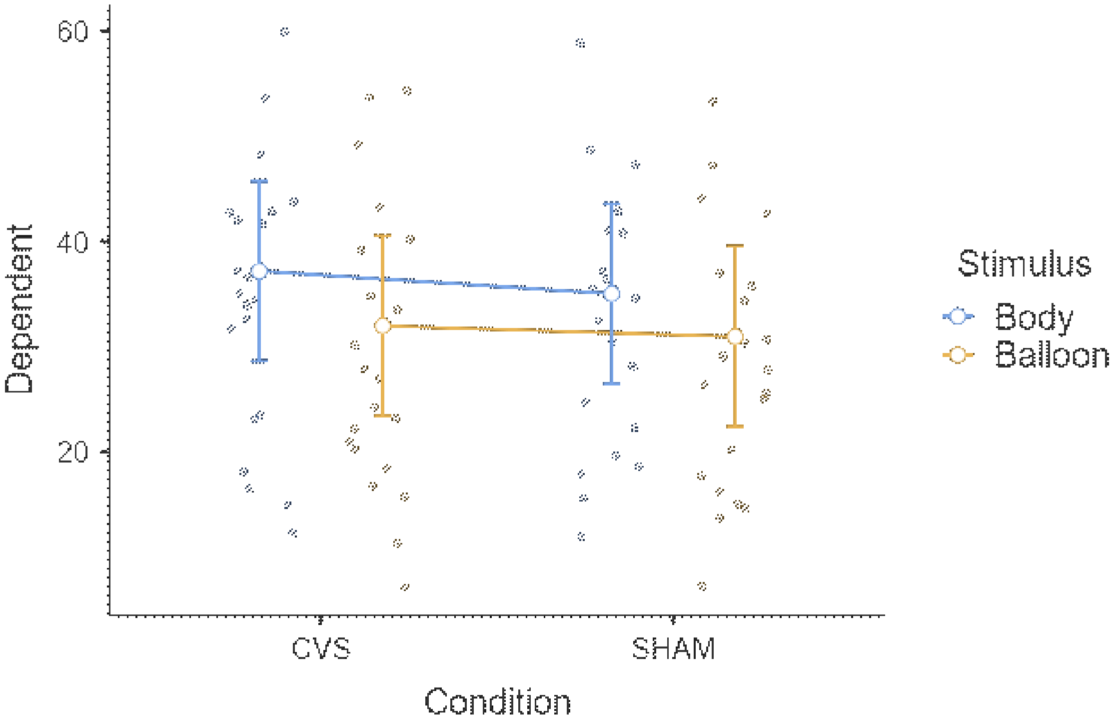

Figure 1 - This graph reports the performances obtained by each subject in the BART. The results are divided for each condition (CVS and sham) and by type of stimulus (Body in blue and Balloon in orange).

Within Subjects Effects

	Sum of Squares	**df**	**Mean Square**	**F**	**p**	**η^2_G**
Condition	9.47	1	9.47	0.340	0.567	0.001
Condition ✻ Order	31.56	1	31.56	1.134	0.300	0.002
Residual	528.75	19	27.83			
Stimulus	130.36	1	130.36	4.540	0.046	0.010

Within Subjects Effects

	Sum of Squares	**df**	**Mean Square**	**F**	**p**	**η^2_G**
Stimulus ✻ Order	22.81	1	22.81	0.794	0.384	0.002
Residual	545.62	19	28.72			
Condition ✻ Stimulus	18.95	1	18.95	6.269	0.022	0.001
Condition ✻ Stimulus ✻ Order	13.33	1	13.33	4.410	0.049	0.001
Residual	57.44	19	3.02			

Table 1 *- Results obtained in the 2 (Condition) x 2 (Stimulus) ANOVA, with administration order as a covariate.*

Interim discussion

The interaction between interoceptive abilities and risk-taking tendencies is a complex conundrum, especially when bodily-related stimuli are used to influence hazardous behaviour. Starting from our previously published findings on the different ways of processing object and bodily stimuli (Salvato et al., 2019b), we expected that a high level of interoceptive sensitivity would allow the participants to make primarily reliance on one's internal bodily signals during the BART, leading towards less risky choices. However, the results only partially confirmed this hypothesis. Contrary to our expectations, no correlation was found between the interception dimensions, measured by the 8 subscales of the MAIA and the risk indices, not even following CVS. In particular, is peculiar the lack of correlation with the *Attention Regulation* and *Body Listening* subscales, respectively the ability to pay attention to body sensations and to actively listen to the body during cognitive and emotional processes. In fact, it was supposed that thanks to a multidimensional tool such as the MAIA (Mehling et al., 2012), it was possible to differentiate the specific dimensions of interoceptive awareness that intervene in modulating risk-taking behaviour, especially in the presence of salient stimuli such as bodies. However, it's important to notice that interoception is not a unique construct, rather a multidimensional function. In general, the ability of an individual to accurately monitor the physiological changes within the organism is called interoceptive accuracy, as opposed to the concept of interoceptive awareness, which would refer to the metacognitive ability to correctly evaluate body signals; nonetheless, as found by Ceunen (Ceunen et al., 2013), numerous researches erroneously use these two terms interchangeably. To overcome this terminological ambiguity present in the literature, it is more appropriate to refer to interoception as a multidimensional construct, as proposed in the model by Garfinkel and colleagues (Garfinkel et al., 2015). According to these authors, the concept of interception can be divided into three dissociable dimensions:

- *Interoceptive Accuracy* (IAc): that is the ability to perceive and monitor one's body states (i.e. objective performance in behavioural tasks);
- *Interoceptive Sensibility* (IS): the tendency to pay attention to one's internal body states, investigated through questionnaires or other self-assessment scales, such as the MAIA and the BPQ;
- *Interoceptive Awareness* (IAw): metacognitive awareness of one's ability to pay attention to internal body states.

In this multi-layered structure, it is not trivial to understand how CVS would impact these dimensions and in what way. It is therefore possible that using the MAIA (i.e. interoceptive sensibility) as a measure of interoception might not be sufficient to prove the effects of this vestibular stimulation on interoception as a whole.

However, it is fundamental to notice that the main finding of this study is the selective modulation of risk propensity in the presence of biological stimuli after CVS, while this stimulation did not make significant differences in the risk indices referred to object stimuli. Assuming that CVS is associated with a variation in the subjectively perceived intensity of body states, the participants tended to risk more in the presence of the human silhouette stimuli. It was expected that CVS, thanks to the contribution of vestibular afferents in the body representation, would be able to facilitate the detention of internal physiological modifications and thus support a better interoceptive awareness, therefore it was hypothesized that this improvement in interoceptive awareness would selectively provide support for decision-making processes regarding body-related stimuli. A possible solution to this counterintuitive result comes from recent findings regarding the relationship between the lowering of body temperature and the sense of ownership (Crivelli et al., 2021). In this paper, the authors argue that body temperature constitutes a fundamental dimension in order to maintain a coherent sense of body ownership. As matter of fact, it is known that CVS also causes a significant body temperature drop (Sedda et al., 2016). It might be possible that this lowering in temperature caused by the CVS may have compromised the normal process of information integration coming from the body, disrupting the coherent sense of the embodied self, harming the modulating effect of interoception abilities on risk-taking towards bodily stimuli. Further studies are necessary to better clarify this hypothesis.

In conclusion, I would like to briefly address the issue regarding the significant effect of the administration order between sham and CVS on the interaction between stimuli and condition. As already mentioned, the difference between the performances at the BART during the two conditions varied if the CVS was executed before the sham (i.e. smaller difference) or vice versa (i.e. bigger difference). One may speculate that since CVS was the main tool to modulate risk-taking, while the sham should not create any cognitive or behavioural modification, performing the sham first would simply lead to a great enhancement in risky behaviour during the subsequent session under CVS. On the other hand, performing the CVS while performing the BART for the very first time may have created a sort of “anchoring effect” for the second session under sham, whereas participants more or less explicitly used their performances during the previous session as a target for that second assessment, trying to replicate the previous accomplishment that was, after all, boosted by CVS. Future studies may better address this issue as well.

In the light of the al above-mentioned considerations, in future studies it might be interesting to a) explore the neural correlates selectively involved in risk-taking behaviour depending on the nature of the stimuli; b) investigate all of the 3 interoceptive dimensions to better frame the effect of the CVS on the Body BART; and c) include temperature measurement during the session, to better understand if temperature variation may be correlated with the increase of risky choices for bodily stimuli. In particular, in order to properly comprehend the interaction between CVS effects on interoception and temperature variations, a novel experimental design should be structured to explore this fundamental matter.

Study 2: Galvanic Vestibular Stimulation (GVS) influences risk-taking behaviour[1]

Introduction

To further understand the mechanisms underlying the influence of vestibular stimulation and risk-taking, we decided to use another type of artificial vestibular stimulation, the Galvanic Vestibular Stimulation (GVS). For this study, we decided to formulate our hypotheses based on anatomical and physiological accounts.

It is fundamental to know that the vestibular information has been classically considered a specific sensory input for basic orienting behaviours, such as oculomotor adjustments, postural control, balance and gaze stabilisation (Angelaki & Cullen, 2008). The vestibular system in the inner ear is composed of three orthogonal semicircular canals that mainly sense rotational acceleration of the head in space, and two otolith organs that sense translational acceleration, including the orientation of the head relative to gravity. Some studies have identified several cortical areas involved in vestibular processing in the brain, including the Temporo-Parietal Junction (TPJ), posterior insula, superior temporal gyrus, Inferior Parietal Lobule (IPL), Anterior Cingulate Cortex (ACC), fronto-parietal operculum, both primary and secondary somatosensory cortices and the prefrontal cortex (Lopez et al., 2012; Eulenburg et al., 2012), primarily located in the non-dominant right hemisphere in right-handed subjects (Dieterich et al., 2003; Duque-Parra, 2004). Notably, this widespread vestibular cortical network suggests a vestibular contribution to cognition that goes far beyond the traditional role, which was limited to automatic, low-level reflex motor circuits for balance, gaze stabilisation and orientation (Ferrè & Haggard, 2020). In fact, recent findings regarding artificial vestibular stimulation have been shown to modulate a consistent range of cognitive functions, including but not limited to spatial attention, decision-making, body representation, memory, motor and spatial imagery and emotion perception (Ferrè et al., 2013a; 2013b; Ferrè & Haggard, 2020;

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[1] – This part (*Study 2*) has been largerly extracted and adapted from De Maio, Bottini and Ferrè (2021), Neuropsychologia.

Hilliard et al., 2019; Lenggenhager et al., 2008; Lopez et al., 2012; Miller, 2016; Pasquier et al., 2019; Preuss et al., 2017; Schmidt et al., 2013a; 2013b; Wilkinson et al., 2008).

Even more relevant to the present dissertation, recent studies have demonstrated that vestibular signals play an important role in behavioural control strategy, influencing the balance between novel and routine responses in implicit decision-making tasks (Ferrè et al., 2013a, 2013b). Bipolar GVS has been widely used to non-invasively stimulate the vestibular organs (Fitzpatrick and Day, 2004). An anode and cathode were placed on the left and right mastoid, and vice versa. Perilymphatic cathodal currents are known to depolarize the trigger site and lead to excitation, whereas anodal currents hyperpolarize it resulting in inhibition (Gensberger et al., 2016; Goldberg et al., 1984; Minor & Goldberg, 1991). Galvanic currents equally affect the afferents innervating all vestibular end organs resulting in a change in the vestibular nerve afferent discharge. Hence, GVS results in a diffuse activation of the cortical and subcortical vestibular projections in the already mentioned areas (Fitzpatrick & Day, 2004). Interestingly, neuroimaging evidence has shown that left-anodal and right-cathodal GVS (L-GVS) caused a unilateral activation of the right hemisphere vestibular projections, while the inverse polarity (R-GVS) activated both left and right hemispheres (Fink et al., 2003). Previous findings have demonstrated polarity-specific effects in decision-making tasks. For example, L-GVS, which primarily activates the right hemisphere vestibular projections, increased novel responses compared to right-anodal and left-cathodal GVS (Ferrè et al., 2013a, 2013b). These results raise questions regarding the potential effects of the different GVS polarities on risk-taking. To answer these questions, in this Study we combined bipolar GVS with the BART, which is also been demonstrated in neuroimaging studies to activate ACC, medial-frontal cortex and dorsolateral-frontal cortex (Li et al., 2020; Schonberg et al., 2012). Given this anatomical overlap between vestibular areas and cortical regions involved in risk during the BART, we hypothesized that GVS might induce a polarity-specific modulation of risk-taking behaviour during this paradigm enhancing cortical excitability of these areas, therefore reducing the tendency to take risks.

Method

Participants

Twenty healthy right-handed participants volunteered in the study (19 women; age range 18-22 years; M=19 years; SD=1.28 years). Participants with a history of neurological, psychiatric, vestibular or auditory disorders were excluded. Informed consent was obtained prior to participation in the experiment. The experimental protocol was approved by Royal Holloway University of London research ethics committee, where the data collection took place. The study was designed according to the ethical standards of the Declaration of Helsinki.

GVS

Bipolar GVS was delivered using a 1mA squared waveform via a commercial stimulator (Good Vibrations Engineering Ltd., Nobleton, Ontario, Canada). Carbon rubber electrodes (area ~10cm2) were then fixed binaurally with adhesive tape. Electrode gel was applied to reduce skin impedance. As in previous studies, an anode and cathode were placed on the left and right mastoid, or vice versa (Figure 2). GVS polarity-dependent differences in postural, sensorimotor and cognitive functions have been demonstrated both in healthy volunteers and in brain-damaged patients (Ferrè et al., 2013a, 2013b; Fitzpatrick et al., 1994, 1999; Fitzpatrick & Day, 2004; Lenggenhager et al., 2008; Lopez, 2016; Lopez et al., 2010; Oppenländer et al., 2015; Smith et al., 2010; Utz et al., 2011; Wilkinson et al., 2008, 2014). These behavioural effects can be explained by the specific hemispheric cortical projections activated by GVS, as demonstrated by neuroimaging studies (Bense et al., 2001; Lobel et al., 1998). For example, Fink et al. (2003) found that left-anodal and right-cathodal GVS caused unilateral activation of the right hemisphere vestibular projections, while the reverse polarity activated both left and right hemispheres (Fink et al., 2003). A sham stimulation, based on that used by Lopez et al. (2010), was applied with a left-anodal and right-cathodal electrodes configuration to the neck, 5 cm below the mastoids. This causes a similar tingling skin sensation, and it functions as a control for non-specific alerting effects but does not activate the vestibular system and its inputs. Electrodes for L-GVS, R-GVS and sham were placed at the beginning of the experimental session and remained in place for the entire duration of the experiment. The electrodes and the polarity of stimulation were selected under randomized computer control.

Figure 2 *– The subjects performed the BART during L-GVS and R-GVS applied on the mastoids and during a sham condition, applied on the neck.*

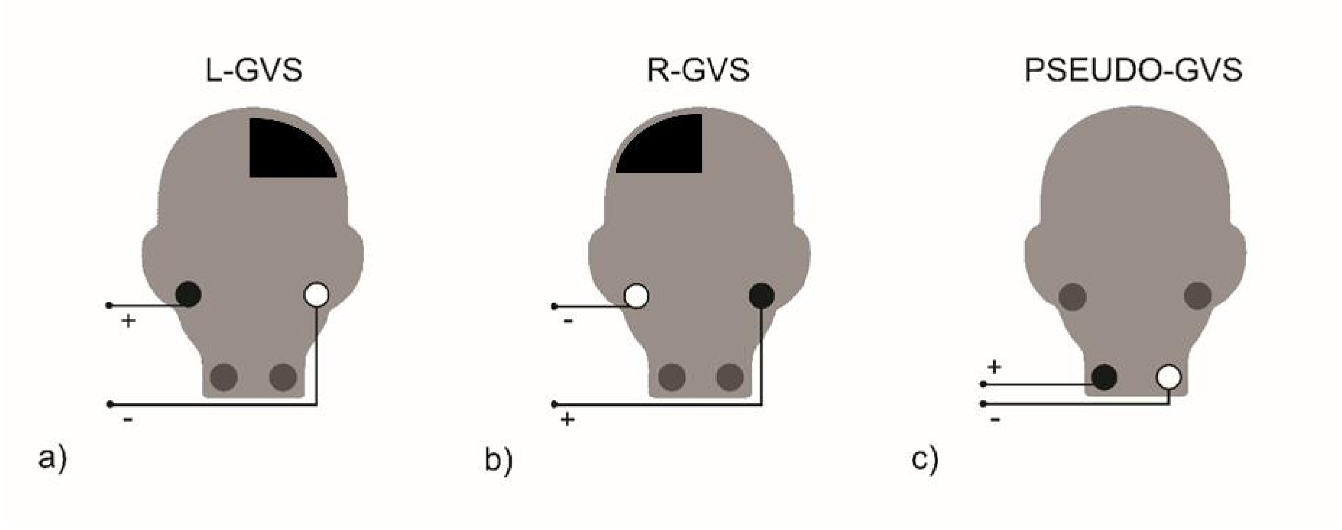

Figure 3 *– a) Left-anodal and right-cathodal GVS is applied to mainly stimulate the right hemisphere, while b) right-anodal and right-cathodal GVS activates the left hemisphere; c) left-anodal and right-cathodal configuration is applied to the neck, causing a similar tingling sensation to control for non-specific effects without any activation of the vestibular system.*

<ins>Task and Procedure</ins>

Data from each participant was gathered in a single experimental session; verbal and written instructions about the task were given to participants at the beginning of the session. The experiment was conducted in a sitting position and with the participant's head kept straight and steady on a chinrest to decrease the postural consequences of vestibular stimulation. This allowed avoiding any potential GVS-induced postural adjustments (Day et al., 1997).

Participants performed a shortened version of the BART during L-GVS, R-GVS, and sham. These three stimulation conditions were randomised between participants to control for potential order effects and the tendency to increase risky behaviour as the BART progresses over time (MacLean et al., 2018). In this version, a total of 30 balloons were presented during the task. To get familiar with the paradigm, participants performed a brief practice block of 5 trials. The BART was designed to last less than five minutes to prevent any potential sensory habituations during GVS.

Between each GVS/sham condition participants took a break of at least 5 minutes to avoid potential stimulation after-effects.

Analysis

The adjusted average pumps, namely the average number of pumps for the unexploded balloons (Lejuez et al., 2002; White et al., 2008), was estimated for each vestibular stimulation condition (L-GVS, R-GVS and sham) for each participant. For this study, we tried to avoid anticipation responses, therefore participants were not allowed to start pumping or collecting the money for the subsequent balloon before the “losing” or “winning” phrase disappeared from the screen and the balloon was visually presented. Hence, we decided to exclude responses given within this period of time (i.e. 1.5s), that were generally 0 (meaning the participant clicked to collect money without having given a single pump) or 1 (only one pump given) (excluded responses=0.67%).

We a priori hypothesized that vestibular stimulation might influence risk-taking behaviour in two distinct ways, and we consequently tested these hypotheses as planned contrasts. First, any activation of the vestibular system might influence risk-taking behaviour independent of GVS polarity and hemispheric effects. For instance, a pure arousal account would predict changes in behavioural tasks independently from the GVS polarity. To test this *generic vestibular effect* hypothesis, we compared the adjusted average pumps for the L-GVS and R-GVS conditions to the sham condition. Second, we hypothesised that the effects of vestibular stimulation might be specific and related to the hemisphere mainly activated by GVS. In fact, several studies reported different effects induced by L-GVS and R-GVS in both neurological patients and healthy volunteers (see for a review Utz et al., 2010). To test the *specific vestibular effect* hypothesis we directly compared L-GVS and R-GVS conditions. Paired t-tests were conducted using both frequentist and Bayesian approaches using JASP (JASP Team, 2019). Bayes factors were calculated using the default Cauchy prior distribution with a scale factor of 0.707.

Results

The proportion of exploded balloons in each GVS condition was numerically similar (L-GVS=.24, SD=.12; R-GVS=.28, SD=.15; sham=0.29, SD=.16) ruling out a potential impact of the exploded balloons on subsequent choices made by participants.

First, we investigated whether any activation of the vestibular system might influence risk-taking behaviour independently of GVS polarity and hemispheric effects, perhaps because of non-vestibular effects such as changes in general arousal. Thus, the *generic vestibular effect*, defined as (L-GVS + R-GVS)/2 (mean number of pumps =23.25; SD=9.723), was compared to the sham condition (mean number of pumps =26.03; SD=12.103). This analysis revealed no significant differences (t(19)=-1.715; p=.103; Cohen's d=.384). In addition, a low Bayes factor was estimated (BF10=.83; Posterior Median=.334; 95% CI: [-.084, .787]), indicating no evidence in favour of either H1 or H0. Taken together these results suggest no support for a generic vestibular effect on risk-taking behaviour.

We next compared L-GVS (mean number of pumps =21.23; SD=10.37) and R-GVS (mean number of pumps =25.27; SD=10.42) conditions to investigate the effects of vestibular stimulation specific to the hemisphere activated (specific vestibular effect). This analysis revealed a significant difference (t(19)=-2.451; p=.024; Cohen's d=-.548). "Figure 4" reports violin plots representing these results. To better understand if this difference in the number of pumps during the BART was actually caused by L-GVS, we performed another comparison that was not initially planned in our first conceptualization: we directly compared L-GVS and the SHAM, proving a difference between the two kinds of stimulation in modulating risk-taking was mainly L-GVS causing a significant reduction in the number of pumps (t(19)=2.354; p=.094; Cohen's d=.526).

Bayes factor showed a moderate index (BF10=4.893; Posterior Median=-.484; 95% CI: [-.947, -.090]) in favour of H1 over H0. These results suggest a polarity-specific effect: compared to right-anodal and left-cathodal GVS, left-anodal and right-cathodal GVS caused a reduction in the number of pumps in the BART. In other words, L-GVS triggered a change in decision-making strategies towards less risky choices.

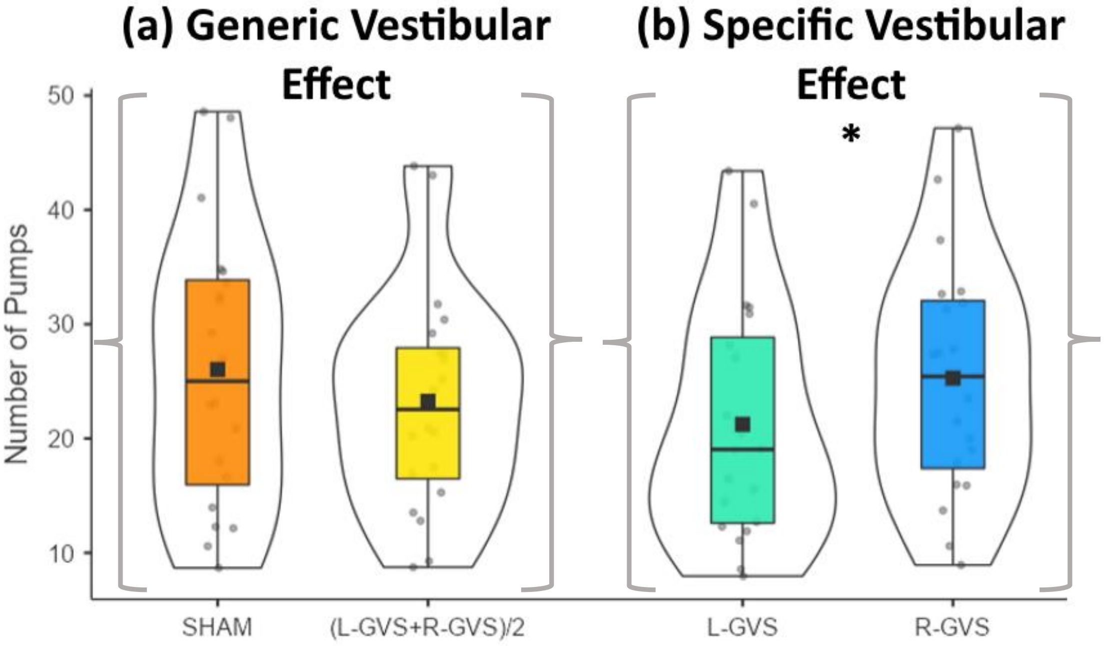

Figure 4 – *a) the difference for the scores in the BART between the sham condition and the average between L-GVS and R-GVS was not significant, not providing support for the existence of a generic vestibular effect on risk-taking; while b) the comparison between L-GVS and R-GVS proved a significantly lower risk tendency for L-GVS, therefore after stimulation of the right hemisphere of the brain.*

Interim discussion

In this Study, we show that vestibular input, in general, did not modulate the cognitive processes involved in risk-taking propensity. However, specific polarities of vestibular input, associated with activation of vestibular projections in each hemisphere separately, had differential effects on risk-taking behaviour as predicted. In particular, L-GVS induced a significant reduction in risk tendencies compared to R-GVS. That is, during left anodal and right cathodal GVS, which primarily activates the vestibular areas in the right hemisphere, participants adopted more conservative strategies in evaluating the probability to gain or lose a virtual monetary reward.

Our results confirmed the already mentioned recent findings of a vestibular contribution to decision-making and strategy control behaviour. Other studies focused their attention on the relationship between the vestibular system and decision-making. For example, Preuss and colleagues (Preuss et al., 2014) have described a vestibular influence on one's desirability to buy a product in economic decision-making tasks. Further, left-anodal and right-cathodal GVS has also been shown to influence heuristics involving emotional context and framing susceptibility in risky choice games (Preuss et al., 2014, 2017). In particular, left-anodal and right-cathodal GVS increased the willingness to take risks when the focus of the framing was given to potential losses while it decreased risk-taking behaviour when the focus was on potential gain (Preuss et al., 2017). In our study, participants were asked to decide whether to keep pumping the balloon to gain a monetary reward while increasing the risk of making the balloon explode and therefore losing their potential reward, or refrain from risk for a larger reward. According to Preuss and colleagues (2017), the observed decrease in risk-taking behaviour induced by left-anodal and right-cathodal GVS could be potentially related to the conceptual framing of the BART which focuses on the reward rather than loss (i.e., participants are explicitly instructed to try to make as much money as possible). Left-anodal and right-cathodal GVS might have therefore modulated the perceived desirability of the reward. Interestingly, in decision-making tasks in which neither reward nor risk is involved, left-anodal and right-cathodal GVS increased the proportion of novel responses, and right-anodal and left-cathodal GVS promoted routine stereotyped ones (Ferrè et al., 2013a, 2013b). Importantly, taken together these results support a functional interaction between vestibular signals and high level cognitive processes involved in behavioural control.

Moreover, polarity-dependent GVS effects have been observed both in brain-damaged patients and in healthy participants (Utz et al., 2010). Here we report a polarity spec*ific vestibular effect* in risk-taking behaviour. Neuroimaging studies have identified an asymmetry in the cortical vestibular network, suggesting a right hemisphere dominance in right-handed participants (Bense et al., 2001; Dieterich et al., 2003; Janzen et al., 2008; Suzuki et al., 2001). Thus, the observed hemispheric-specific effects in risk-taking propensity might arise because of this cortical asymmetry, or because one polarity of GVS has stronger effects in the brain. We suggest that the difference between L-GVS and R-GVS in hazardous decisions may be caused by changes in cortical excitability in widespread hemispheric networks for behavioural control. Brown and Braver (Brown & Braver, 2007) have shown a strong hemispheric specialization in behavioural control: the right hemisphere ACC, temporal gyrus, and middle/superior frontal gyrus are selectively involved in preventing errors, minimising losses, and predicting adverse outcomes. Similarly, activation of the right ACC and insula have been observed when people were taking risks during the BART (Li et al., 2020; Schonberg et al., 2012). Importantly, these regions are also core areas receiving vestibular projections and might be therefore good candidates for subserving the observed vestibular modulation of risk-taking behaviour. The sudden artificially-induced activation of these areas might have triggered changes in the overall cortical excitation, which might have been reflected in behavioural changes, such as an increase of risk-averse choices and therefore more conservative responses.

Our willingness to take risks is often influenced by the actual or even perceived value of the reward. For instance, Bornovalova and colleagues (Bornovalova et al., 2009) highlighted how hazardous tendencies were dramatically reduced as the reward/loss ratio (e.g., the pay-out) increased, suggesting that decision-making is intrinsically influenced by the awareness of potential losses. Accordingly, people with higher impulsivity have been shown to be much less susceptible to the reward/loss ratio. Importantly, several studies have highlighted differences in behavioural responses when participants were presented with a real vs. hypothetical reward during the BART. In particular, the real pay-out induced a reduction in risk-taking behaviour compared to a virtual scenario (Xu et al., 2016), similar to the one used in the present study. L-GVS might have altered the perceived trade-off between gains and losses towards less hazardous strategies. Changes in motivation might account for our findings and potentially provide an explanation that does not directly involve decision-making. However, we argue that these two accounts might not necessarily be mutually exclusive and since no real-life monetary reward was given here, it is unlikely that the changes induced by L-GVS are merely driven by motivation.

We also considered other potential alternative explanations that may explicate our results. It has been largely reported that artificial vestibular stimulation influences spatial attention (Utz et al., 2011). Attentional shifts of attention towards one side of the personal and/or extra-personal space have been observed in neurological patients and healthy participants (Dilda et al., 2012; Kerkhoff, 2001; Rorsman et al, 1999; Utz et al., 2011). For example, left anodal and right cathodal GVS induced a leftward attentional bias, while R-GVS reversed this bias, in a bisection task (Ferrè et al., 2013). Thus one might argue that the hemispheric effect in risk-taking behaviour might be driven by attention mediated mechanisms, for instance, a preference for pressing the left or right button. However, our data do not fully support this account. An attentional driven effect would have caused a L-GVS preference towards the leftmost button, which in our task corresponded to the ‘inflate the balloon’ key. Thus, a completely opposite pattern of results should have been observed. Further, recent studies excluded a direct influence of GVS on motor effectors (Abekawa et al., 2018; Ferrè, Arthur, et al., 2013).

Artificial vestibular stimulation may also influence emotional responses and anxiety levels (Pasquier et al., 2019; Sailesh et al., 2016). Critically, anxiety levels may influence risk-seeking behaviour during the BART (Lighthall et al., 2009). Therefore, one might speculate that the observed changes in risk-taking measures are indirect anxiety-driven, rather than directly vestibular modulations. However, an account based on indirect anxiety-driven changes cannot fully explain our results. First, previous studies have shown changes in anxiety levels only after prolonged GVS exposure (for example 38 or 78 minutes GVS for 3 sessions in Pasquier et al. 2019; 146 ± 5.6 days GVS in Sailesh et al. 2016). In our study, GVS lasted less than a few minutes in each block (max. 4.86 minutes). Second, an account based on indirect vestibular effects based on changes in anxiety would have predicted differences in risk index between sham and vestibular conditions (i.e. generic vestibular effect), which we did not observe. Finally, in our knowledge, no evidence has so far supported GVS polarity-specific changes in anxiety.

In conclusion, the results of this experiment showed polarity-dependent effects of GVS on risk-taking behaviour, providing novel data regrading the involvement of vestibular input to high cognitive functions. Our suggestion is a vestibular-mediated balancing of risk-seeking behaviour as an important element of the brain’s capacity to adapt to the environment.

On a side note, it is interesting to observe that these results somehow contradicts our findings in *Study 1*. As matter of fact, left-cold CVS and L-GVS are considered to cause very similar effects in terms of stimulated areas in the right side of the brain (Lopez, 2016; Preuss et al., 2017), still, we didn’t find any modulation of risk tendencies for the classic BART after CVS, while we found a reduction in the number of pumps after L-GVS. Of course, some differences distinguish the two types of stimulation, for example, L-GVS is known to modulate the activity of the entire vestibular nerve, including afferents from both the semicircular canals and the otoliths, while CVS predominantly affects the endolymphatic fluid in the horizontal semicircular canals only (Gensberger et al., 2016; Preuss et al., 2017). Yet, the stimulation of the vestibular nerve leads to comparable stimulations of the vestibular areas, providing equivalent effects (Lopez, 2016). Therefore, it is not trivial to understand why this difference emerged in our two studies. As already stated, a first explanation can be found in the body temperature drop caused by CVS (Sedda et al., 2016), which is itself known to modulate the sense of body ownership (Crivelli et al., 2021). As far as I know, no effects on body temperature have been reported in literature after GVS. Therefore, it is possible that this diverse effect on body temperature between CVS and L-GVS might have differently influenced the performance during the BART. Moreover, it is significant to remember that in *Study 1* the body-shaped balloons and the classic balloons have been both presented during the same task in randomised order. It might be possible that the influence of CVS might have caused a major drift of the attention towards the body-shaped balloons because of their specific biological saliency, compared to the normal balloons, leading to a reduced effect of CVS on the classic type of stimuli. Future studies can better address these speculative hypotheses.

Chapter 2: Natural vestibular manipulations and their impact on risk tendencies

Study 3: Altered gravitational input modulates hazardous choices

Introduction

This study was conceived as an extension of *Study 2*. As already highlighted, we chose to manipulate the vestibular input using a more natural and ecological system. We already saw that the basic functions of the vestibular system are mainly activated by the force of gravity. As matter of fact, since the beginning of time, all living organisms have evolved under a terrestrial gravitational acceleration of 9.81 m/s^2, known as 1g. It's hard to imagine a more fundamental and ubiquitous aspect of life on Earth than gravity. On Earth, when the head moves with respect to gravity, the vestibular otoliths in the inner ear shift with the direction of gravitational acceleration, moving the hair cells receptors and signalling to the brain the magnitude and direction of gravity (Green et al. 2005; Merfeld et al. 1999). These vestibular-gravitational signals are integrated with sensory signals from vision, proprioception, and viscera to form an internal model of gravity (Lacquaniti et al., 2014). Critically, the internal model of gravity is optimal in the terrestrial environment and permits the regulation of multiple aspects of behaviour. However, in non-terrestrial gravities – as during spaceflights, for example – sensory conflicts arise between the altered gravitational afferent information sensed by the vestibular otoliths and the internalised model of gravity, leaving astronauts disoriented and cognitively debilitated (Strangman et al. 2014). Making the *right* decision is vital in these high-pressure environments. Alterations in decision-making have been described in gravity conditions typical of spaceflight (Lipnicki and Gunga 2009; Steinberg et al. 2015; Strangman et al. 2014; Gallagher, Arshad, & Ferrè, 2019). As we already saw, some authors have recently demonstrated sub-optimal decision-making and biases towards routined and stereotyped responses while participants were exposed to altered gravity signals, suggesting an important contribution of gravity in behavioural control strategies (Gallagher, Arshad, & Ferrè, 2019). Similarly, Lipnicki et al. (Lipnicki et al., 2009)found that participants exposed to altered gravity conditions were more prone to fail to adapt their decisional strategies during the Iowa Gambling Task, compared to controls.

In this Study, we investigated whether lab-controlled short-term alterations in gravitational signals could influence the willingness to take risks. We manipulated how the vestibular organs sense gravity by changing the body's orientation to the direction of the gravitational acceleration. Thus, participants completed the BART while either being upright or lying supine, the so-called *bed rest posture*. Bed rest posture has been used for at least 50 years in space research as a ground-based analogue for weightlessness, which allows to reliably mimic the effects of vestibular-gravitational alterations on human physiology (for a review: Pavy-Le Traon et al., 2007). Based on previous literature on the effect of altered gravity exposure on both perception and cognition (Lipnicki et al. 2009), we hypothesised that short-term bed rest posture may increase risk propensity.

Methods

Participants

Twenty healthy right-handed participants volunteered in the study (8 women; age range 20-69; M=32.5; SD=13.01). The sample size was estimated a priori based on similar experimental procedures (Ferrè, Vagnoni, & Haggard, 2013; Ferrè, Arthur, & Haggard, 2013) as well as based on our findings on *Study 2*. Once again, participants with a history of neurological, psychiatric, vestibular or auditory disorders were excluded. Informed consent was obtained prior to participation in the experiment. The experimental protocol was approved by Royal Holloway University of London research ethics committee. The study was designed according to the ethical standards of the Declaration of Helsinki.

Task and Procedure

Since data collection started during the Covid-19 pandemic, according to UK Government Covid restrictions, the experiment was done in social distancing, therefore participants taking part in the study performed the BART online, using the Gorilla Experiment Builder platform (https://gorilla.sc/). Data from each participant was gathered in a single session using their smartphone. Verbal and written instructions about the task were given to participants at the beginning of the experimental session via video call. Participants performed the 20 balloons version of the BART, administered in upright and bed rest posture. In upright condition, participants were asked to stand against a wall keeping their head and back as straight as possible and to keep their phones right in front of them to prevent head movements towards the floor. During the tilted condition, they were asked to lay on the floor with their legs straight, their head placed right on the floor facing the ceiling and their phone right above it. To ensure that somatosensory and proprioceptive information was similar across body postures, participants were instructed to keep the back, head, and heels in contact with the supporting surface. The experimenter visually monitored their body posture throughout the task. Again, upright and bed rest experimental conditions were administered in counterbalanced order between participants to control for order effects and the reported tendency to increase risky behaviour as the BART progresses (MacLean et al., 2018b).

Analysis

Once again, we calculated the adjusted number of pumps, which is the average number of pumps for the unexploded balloons (Lejuez et al., 2002b; White et al., 2008b) for both upright and bed rest conditions and for each participant. To investigate whether altered gravity signals influence risk-taking behaviour, we directly compared the mean adjusted pumps between upright and bed rest conditions with t-tests using both frequentist and Bayesian approaches using Jamovi (version 1.6.13.0 (www.jamovi.org). Bayes factors were calculated using the default Cauchy prior distribution with a scale factor of 0.707. The difference between the two conditions is represented in "Figure 5".

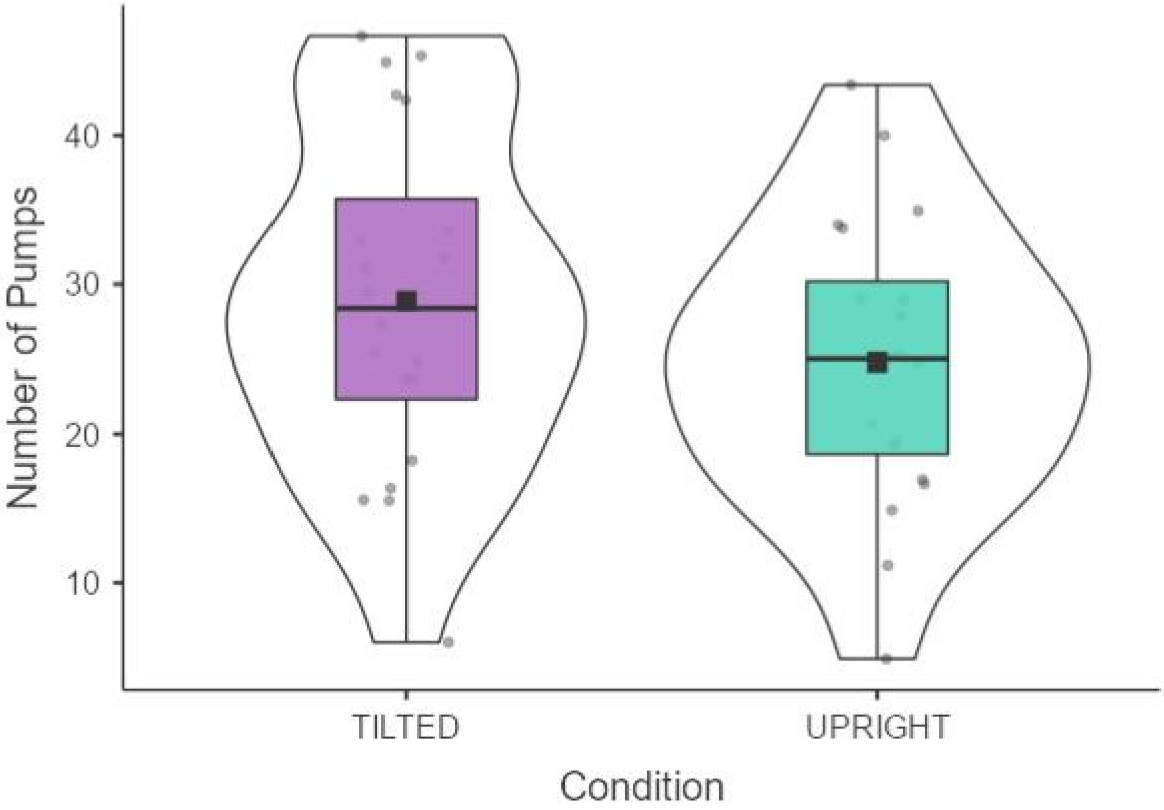

Figure 5 *– The performances at the BART significantly turned towards more risky choices when the subjects were lying down in the tilted condition (i.e. with an incongruent vestibular signal) compared to the upright body posture (i.e. congruent vestibular signal).*

Results

To investigate whether altered gravity might influence risk-taking behaviour we compared the average adjusted number of pumps performed in the BART in the upright position (M=24.780; SD=9.662) with the same index obtained by participants in the bed rest position (M=28.868; SD=11.486). This analysis revealed a significant difference between the two conditions (t=-2.219; p=.039; Cohen's d=-.496). Further, Bayes factor was estimated (BF10=3.307; 95% CI: [-.893, -.438]), indicating moderate evidence in favour of H1 over H0. Overall, these results suggest an effect of head orientation on risk propensity, where an upright head position shows behavioural patterns directed towards more conservative and less risky choices compared to a downward head position.

Interim discussion

By 2030, humans will once again walk on the surface of the Moon, travel to Mars and potentially enjoy 10 minutes sub-orbital vacations. However, space is an extremely hostile environment. Space missions have shown that exposure to non-terrestrial gravities leads to dramatic structural and functional changes in human physiology, including alterations in the cardiovascular, musculoskeletal and neural systems. Spatial disorientation, perceptual illusions, balance disorders, motion sickness and altered sensorimotor control have been reported by astronauts during spaceflight (Reschke et al., 1998). With an eye towards deep-space human missions and space tourism, it is a pressing goal to get a better insight into how non-terrestrial gravities influence human behaviour. Humans have always aspired to explore new frontiers. Recent advancements and investment in technology are ushering in a new age of space exploration and possibility which will lead to sustainable lunar habitats, orbiting space hotels and the first humans on Mars. However, the upcoming exploration missions will present much greater challenges to health and performance than the challenges currently faced. Unprecedented distance, duration, isolation and increasingly autonomous operations will be combined with prolonged exposure to non-terrestrial gravities. It is therefore a pressing goal to get a better insight into how terrestrial and non-terrestrial gravities impact human behaviour.

On Earth, gravity is stable, permanent and unchanging. The physical constraints of Earth's gravity must be internalized in the human brain. That is, we are exceptionally adapted to terrestrial gravity. Several studies have described the effects of non-terrestrial gravities on sensorimotor coordination, spatial perception, motor control and decision-making (Gallagher et al., 2019, 2020; Steinberg et al., 2015). In this study, we demonstrated that altered gravitational input through the vestibular system influences risk-taking behaviour. That is, participants were more prone to take risks while in bed rest posture relative to upright posture. Thus, online gravitational signals may shape hazardous tendencies.

Bed rest is commonly used by international space agencies as a ground-based analogue to investigate the effects of spaceflight stressors on human physiology and performance. However, findings investigating the effects of bed rest on cognitive performance have been inconclusive so far (Lipnicki 2009; Koppelmans 2015; Liu 2012; Liu 2015, Liu 2015, Yuan 2017; Dolenc 2013). As far as we know, only two studies have investigated whether prolonged exposures (>45 days) to bed rest might modulate risk-taking behaviour (Basner et al., 2021; Rao et al., 2014). Both studies did not find any significant changes in performance. However, neuroimaging investigations highlighted a significant deactivation of the Ventro-Medial Prefrontal Cortex (VMPFC) when performing the BART after prolonged bed rest. The VMPFC is considered a primary cortical region of decision-making circuits, especially for risky decisions and value estimates (Bechara et al., 1999; Kable and Glimcher, 2009; Xue et al., 2009; Rushworth et al., 2011). The observed decrease in VMPFC deactivation may be indicated changes in value calculation that were not directly captured by the BART.

Conversely, our results indicate an increased propensity for hazardous choices after short bed rest exposure. It is likely that prolonged bed rest exposure may have caused physiological habituation to the altered vestibular inputs and compensation in cognitive performance. In other words, the subject acclimatizes to the altered gravity condition and compensates - at a behavioural level - for the cognitive alterations that the tilted position caused. In our experiment subjects did not have to spend too much time lying on the floor before they were asked to perform the BART, therefore they may not have been got used to the vestibular input alteration. Of course, deep space exploration is clearly something that entails a large amount of time spent in a zero-gravity environment, so prolonged bed rest studies are fundamental to understand the long-term effects of the absence of gravity on cognition. However, astronauts may not always have the time to adapt to the completely new gravitational ambient before they are asked to undergo potentially risky actions and make dangerous decisions. Hence, short-term gravitational manipulation also appears to have to be taken into consideration when discussing the effects of the gravitational pull on cognition. As matter of fact, gravity is something that can deeply alter our cognition due to its effects on the vestibular system both in a short period of time and for prolonged time spans. Nonetheless, until now this topic has been almost completely neglected in neuroscientific and cognitive research. Still, the rapid evolution of space tourism in recent years should push us to dedicate more attention to this issue. Not only that, but even for those patients who suffer from diseases affecting the vestibular system and its connectivity pathway to the brain, it is important to understand if and in what ways these kinds of problems may affect their ability to properly face those situations involving risk. An adequate grasp of this issue is fundamental to conceptualize and enforce behavioural strategies aimed at compensating for these possible shortcomings which, for some, may occur on a daily basis.

Study 4: Can isolation modify risk tendencies?

Introduction

This last study was conceived in the middle of the very first year of the global Covid-19 pandemic. All around the world billions of people were experiencing a period of distress, tension and uncertainty. To make things worse, that difficult moment was exacerbated by a prolonged and intense period of lockdown in most countries, preventing people from moving, working, and meeting with friends, relatives and loved ones. This extended period of isolation deeply impacted the general population also from a psychological point of view, causing a detrimental effect on mental health including stress, anxiety, depression, and frustration (Serafini et al., 2020). As we have already pointed out during this thesis, isolation also causes various effects on cognition, including heightened sensitivity to social threats, a confirmatory bias in social cognition (Cacioppo & Hawkley, 2009).

As far as we know, risk-taking tendencies are sensitive to social interaction. For example, in a series of seminal studies, Wallack and colleagues showed that people tend to perform riskier decisions when group interaction occurs, compared to individually-made decisions (Wallach et al., 1962, 1964, 1965). These conducts can be explained in two ways: a) shared/spreading of responsibility in the group in such a way that risky decisions are perceived as more affordable in terms of consequences, ii) persuasion exercised by the most influential individuals in the group (usually high-risk takers) and perceived as holders of greater forcefulness by the group. These interesting results proved a prominent influence of the group on risky attitudes towards even riskier choices. On the other hand, very recent findings proved that prolonged isolation may cause a reduction in risk tendencies as the isolation time increases (Wang et al., 2020). In fact, Wang and colleagues (2020) measured risk propensity with the BART on a group of 12 subjects during a prolonged "voyage" in a self-developed maritime chamber simulator. What they found was a constant decline in the number of pumps during the BART, providing interesting information regarding the effects of reduced social interaction on risk-taking. Still, the very limited number of participants, the massive sleep deprivation caused by working shifts made by the experimental subjects, and the lack of demographical diversity in this study could make the results non-generalizable for isolation in the broad sense. Moreover, the peculiarly stressful situation we all experienced during the pandemic might have influenced risk-taking in many different ways, since stress, depressive mood and anxiety can significantly impact risk-taking paradigms (Buelow & Blaine, 2015; Lighthall et al., 2009).

With the purpose of understanding how risk-taking propensity in the general population might have been affected during the prolonged period of isolation caused by the Covid-19 pandemic, we assessed an online version of the BART.

Methods

Participants

One-hundred seventy-nine healthy subjects (114 females) volunteered for the study (age range 20-85; M=34.8; SD=14.4). Informed consent was obtained prior to participation in the experiment. The experimental protocol was approved by Royal Holloway University of London research ethics committee, where the data collection took place. The study was designed according to the ethical standards of the Declaration of Helsinki.

Task and Procedure

Participants were administered with the 20 balloons version of the BART. According to UK Government Covid restrictions, the experiment was done in social distancing, therefore participants taking part in the study performed the BART online, using the Gorilla Experiment Builder platform (https://gorilla.sc/). Data from each participant was gathered in a single session using their smartphone. Verbal and written instructions about the task were given to participants at the beginning of the experimental session via video call.

They were also asked to fill out a brief survey to collect data regarding:

1) how many days of lockdown they have been into;

2) how many people there were in their houses;

3) how many times per week they were able to go out;

4) how many hours they spent communicating with others using smartphones and/or laptops.

Also, 3 questions regarding the sense of loneliness were asked to assess the perceived feeling of isolation. Moreover, they were asked to compile the Depression Anxiety Stress Scale (DASS) (Parkitny & McAuley, 2010) as a measure of their mood during the test.

Analysis

Again, the adjusted number of pumps for the unexploded balloons was taken into consideration as a risk index. Since our intention was mainly to measure how this index changed depending on the time spent in isolation, a Linear Regression was conducted using the adjusted number of pumps as the dependent variable and the time spent in lockdown as the main factor. Since preliminary analyses did not show non-normal distributions in the variables explored in the initial survey, they were not included in the analysis as covariates.

Results

The final model was significant (R2=.026, t(177)=2.181, p=.0305), see “Table 2” for detailed results. We found that the adjusted number of pumps in the BART increased as the time spent in isolation during the lockdown increased.

Yet, looking at the plots representing the data distribution (Figure 6), we can clearly see a relatively small group of subjects "dragging down" the number of pumps on the left side of the graph. Interestingly, this small group of people did not spend any time in isolation due to job responsibilities that allowed them to keep working and, therefore, not spent time in isolation. For this reason, we decided to exclude those participants (n=33) and ran the Logistic Regression a second time (see "Figure 7" for the plot). The final model was not significant (R2=.006, t(144)=.992, p=.322), proving no effect of time on risk tendencies (see "Table 3" for detailed results).

Model Fit Measures

			Overall Model Test			
Model	**R**	**R^2**	**F**	**df1**	**df2**	**p**
1	0.16178	0.026172	4.7569	1	177	0.03050

Omnibus ANOVA Test

	Sum of Squares	**Df**	**Mean Square**	**F**	**p**
Isolation_Duration	665.71	1	665.71	4.7569	0.03050
Residuals	24770.70	177	139.95		

Model Coefficients – PUMPS

			95% Confidence Interval			
Predictor	**Estimate**	**SE**	**Lower**	**Upper**	**t**	**p**
Intercept	20.652454	1.972768	16.7592815	24.54563	10.4688	< .00001
Isolation_Duration	0.082621	0.037882	0.0078632	0.15738	2.1810	0.03050

***Table 2** – Detailed results obtained in the Linear Regression with the adjusted numbers of pumps at the BART and the number of days spent in isolation during the lockdown.*

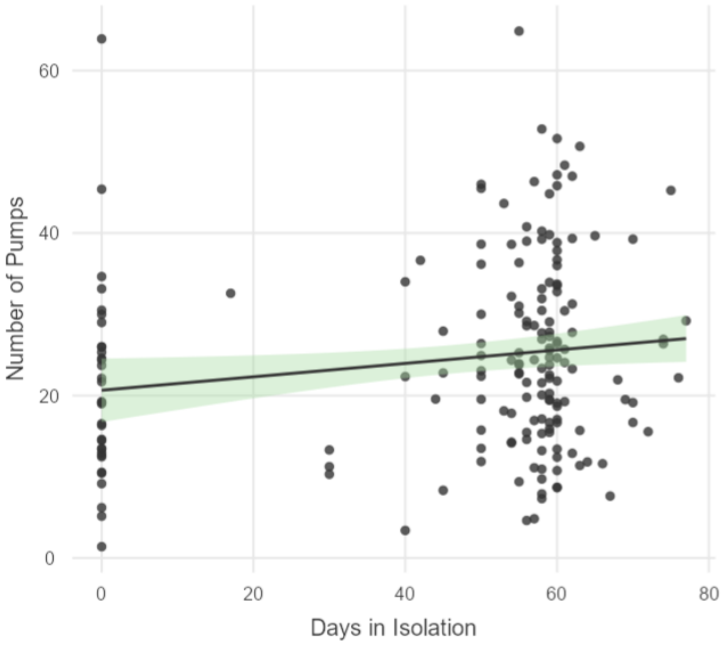

Figure 6 *– The scatterplot clearly shows that the effect is "dragged" by a few subjects that did not spend any time in lockdown. This flaw makes it difficult to properly interpret the results.*

Model Fit Measures

			Overall Model Test			
Model	**R**	**R²**	**F**	**df1**	**df2**	**p**
1	0.082397	0.0067893	0.98434	1	144	0.32279

Omnibus ANOVA Test

	Sum of Squares	df	Mean Square	F	p
Isolation_Duration	136.58	1	136.58	0.98434	0.32279
Residuals	19979.80	144	138.75		

Model Coefficients – PUMPS

			95% Confidence Interval			
Predictor	**Estimate**	**SE**	**Lower**	**Upper**	**t**	**p**
Intercept	18.60244	6.84713	5.06858	32.13630	2.71682	0.00740
Isolation_Duration	0.11781	0.11874	-0.11690	0.35252	0.99214	0.32279

Table 3 *– Excluding those who did not spend time in isolation from the regression, the final model was not significant.*

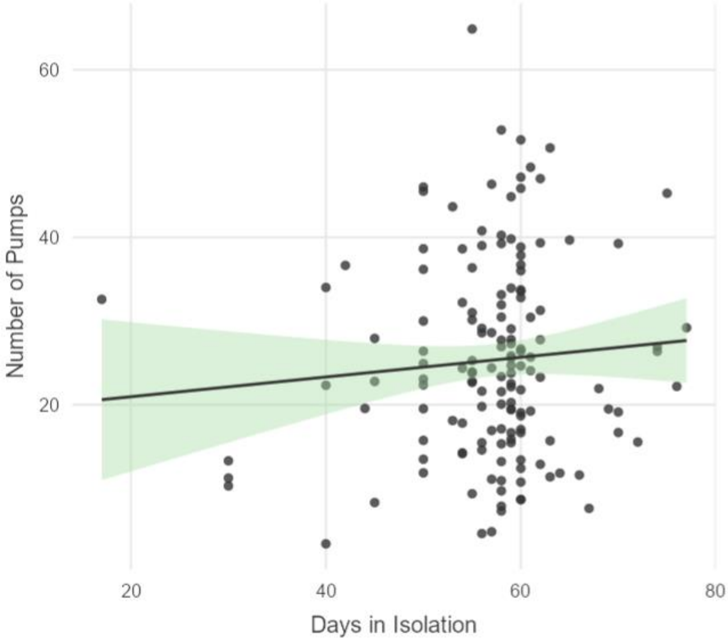

Figure *7 – The plot represents the data distribution after the exclusion of the 33 subjects who did not spend time in isolation during the quarantine.*

Interim discussion

Unfortunately, our results were affected by a methodological flaw that made their interpretation extremely hard. One may say that even if the Logistic Regression is not the proper way to explore the data, a difference in risky choices can be detected between those who experienced a prolonged period of isolation and those who did not. Yet, we believe that a more cautious approach should be adopted, excluding those how did not spend time in isolation. As matter of fact, since our main interest was to measure how forced isolation could affect risk tendencies over a period of time, having a sub-group of people who were not isolated would have been a counter sense, based on our initial hypothesis. After their exclusion, we could say that the analysis did not reveal any variation of the risk index over time during the lockdown in our sample.

Another important aspect regarding our data that might explain this non-significant result, is the massive concentration of our distribution along with the “time” dimension around the 60 days of isolation. This might be caused by the fact that each of us who experienced the lockdown was forced into isolation in the same period of time. Since the data collection did not cover a significant period of time, the majority of the subjects participating in the experiment had spent approximately 2 months in lockdown at the moment of the data collection, significantly reducing the variability along this dimension. Perhaps, a better distribution of the subjects along the "isolation duration" variable could have made the results clearer and more easily interpretable. Moreover, a second testing session at 1 or 2 months from the first collection would have been ideal to properly assess the possible influence of isolation on risk-taking. Unfortunately, even if a softer version of the lockdown remained, the extreme form of isolation we underwent at the very beginning of the pandemic ended a few days after the data collection was finalized, making a second data collection impossible since the isolation conditions radically changed.

Even if this study resulted inconclusively, we believe that a brief reflection should be done in any case. Even if this study did not obtain any results, it is vital to further explore if and how social distancing can influence risk. After all, even if social interactions have significantly increased since the very first lockdown, we are still living in a period of social distancing, where human interactions have not yet fully returned to their previous form of social connections. As we have seen, a reduced social interaction leads to severe cognitive impairment and also has effects on risk parameters. It is therefore essential to further investigate the relationship between isolation and risk craving. In fact, Covid-19 is still widespread in the world and still kills thousands of victims a day. In an extremely dangerous situation like this, a deficit in risk aversive attitudes is definitely not desirable. A better understanding of this eventuality would also help us to create effective tools to counter it.

General discussions and conclusions

Risk-taking tendencies are very complex to be conceptualized despite being something we interact with all the time. Whenever we decide to cross the street with the red light is on, when we drive (even for a little bit) without our seatbelt on, or even when we decide to stop to have a coffee in the morning knowing that our boss is going to lecture us, we are always making decisions that involve risk at some level. Given the pervasiveness of risk in our lives, it is fundamental to deepen our knowledge regarding this topic from a cognitive and neuroscientific point of view.

As a measure of risk-taking tendencies, we chose to use the BART, a gold-standard task to assess risk propensity also in real life. In fact, this task has been used to assess risky tendencies, for example, in adolescents (Lejuez et al., 2003), drug abusers (Campbell et al., 2013; Canavan et al., 2014), brain-injured patients (Balagueró et al., 2016), psychopathic inmates (Swogger et al., 2010). Plus, the BART has been administered various times during neuroimaging exams, providing an anatomical account underlying the performance, including the Anterior Cingulate Cortex (ACC), medial-frontal cortex and dorsolateral-frontal cortex and insula (Li et al., 2020; Schonberg et al., 2012).

In Chapter 1, we discussed the interplay between vestibular signals and risk-taking behaviour. In particular, in *Study 1* we showed how the CVS was able to selectively increase risk tendencies only for bodily-related stimuli. We hypothesized that this kind of stimulation might be able to enhance participants' ability to better perceive their bodily states during this version of the BART, reducing their risky behaviour. Yet, we found a significant increase towards risky choices after CVS only for body-shaped balloons. These results imply that the CVS is not sufficient to modify risk-taking behaviour per se, rather a biologically salient and bodily-related stimulus is necessary to allow the effects of the CVS on the representation of the body to interfere with the decision regarding dangerous situations. Plus, in *Study 2* we aimed at providing novel findings regarding the influence of the vestibular input on risk-taking. To do that, we applied left-anodal and right-cathodal GVS, the opposite polarity and sham stimulation subjects performing the BART. What we found was a significant reduction of hazardous tendencies during L-GVS when compared with the opposite polarity. These result highlights the vestibular contribution to high cognitive functions, risk-taking in particular, with a polarity specific effect, meaning that a general vestibular stimulation is not sufficient to manipulate these tendencies, rather a specific stimulation that mainly excites the activity of the right hemisphere is necessary to observe such a modification.

As an extension of these findings, Chapter 2 focuses on more ecological and natural ways to modulate hazardous tendencies. More precisely, in *Study 3* we tested short-term alterations of the gravitational signals to the brain and how they influenced the willingness to take risks via the so-called "bed rest posture". Our results demonstrated an effect of head orientation on risk propensity, where an upright head position showed behavioural patterns directed towards more conservative and less risky choices compared to a downward head position. We argued that these results highlight the importance of a coherent and well-integrated vestibular input to the brain to properly cope with different environmental situations and properly cope with them, providing new data about this topic in the frame of risk-taking.

Finally, in *Study 4* we showed an attempt to detect possible changes in risk-taking after the prolonged time spent in isolation during the Covid-19 lockdown. We administered the BART to 179 subjects using an online platform, but we did not find any significant modification in risk tendencies.

As a whole, the major findings of this Thesis identify the influence of the vestibular system a fundamental component to comprehend and make decisions regarding situations involving risk. From a naïve point of view, the relationship between the vestibular signals and one's propensity to take risks could appear meaningless and nonsensical. Yet, the explanation of such influence has to be found in the anatomo-functional organization of the vestibular projections to the brain: as already mentioned, the vestibular system directly interacts with a widespread network of cortical and subcortical areas, including the TPJ, posterior insula, superior temporal gyrus, IPL, ACC, fronto-parietal operculum, both primary and secondary somatosensory cortices and the prefrontal cortex (Lopez et al., 2012; Eulenburg et al., 2012) which are, interestingly, mostly located in the non-dominant right hemisphere in right-handed subjects (Dieterich et al., 2003; Duque-Parra, 2004). These complex and widely distributed connections suggest a pervasive implication of vestibular inputs to several other cognitive functions due to the clear structural overlap in these areas (Lopez, 2016; Preuss et al., 2014b). As matter of fact, recent findings regarding vestibular stimulation have been shown to modulate a very consistent range of cognitive functions, including spatial attention, decision-making, body representation, memory, motor and spatial imagery, emotion perception, and most importantly behavioural control strategy, influencing the balance between novel and routine responses in implicit decision-making tasks (Ferrè et al., 2013a; 2013b; Ferrè & Haggard, 2020; Hilliard et al., 2019; Lenggenhager et al., 2008; Lopez et al., 2012; Miller, 2016; Pasquier et al., 2019; Preuss et al., 2017; Schmidt et al., 2013a; 2013b; Wilkinson et al., 2008). Therefore, our anatomo-functionally based model identifies in the structural overlap between areas involved in the already mentioned cognitive functions and the vestibular projections the source of the interplay between the vestibular system and risk-taking behaviour.

From a more speculative and philosophical standpoint, my personal opinion is that the roots of the implication of the vestibular input in higher cognitive functions, decision-making in particular, can be found in the most essential purposes of the vestibular system: orienting action. Indeed, as we already widely told, the vestibular system is prominently structured to sustain motor reflexes for balance, gaze stabilisation and spatial orientation. It is not that much of a surprise if more evolutionarily recent cognitive functions that assume a coherent perception of the surrounding environment and a correct understating of the contingent situation involving risk are deeply supported by information coming from the very system that is responsible for processing information about space and one's position in relation to it. This should motivate us to reflect on the embodied nature of our mind and cognition, which are intrinsically and inextricably linked to the nature of our body and the characteristics of the environment with which we evolved and constantly interact.

In conclusion, this Thesis demonstrated that risk-taking is not only pervasive in our life, but it could also be influenced and modulated in various ways, such as through vestibular artificial stimulation and natural manipulation. Better understanding this relationship is an exciting scientific challenge that may uncover many of the still unknown aspects of our cognition, providing novel insights regarding the nature of our brain and mind. Moreover, a deep knowledge of the relationship between the vestibular system and hazardous tendencies can be extremely helpful to understand the potential effects of vestibular damage on cognition in patients with traumatic injuries. In fact, lesions that may directly affect the vestibular system or a brain injury affecting the vestibular brain network might undermine one’s ability to properly perceive and cope with situations that involve some degree of danger. Moreover, the fact that an abnormal vestibular input to the brain might increase risk-taking tendencies leads us to ask ourselves what negative effects this phenomenon can have on pilots of aeroplanes or helicopters who, in situations of perceived altered gravity, have to make decisions on which their lives and those of many other people depend. Also, since risk is so pervasive in our existences, it is not obvious how hazardous tendencies may influence other cognitive domains pervasively impacting the everyday life of each individual.

We deeply hope that our attempt to better clarify some of the unknown aspects surrounding this fascinating conundrum can inspire other fellow researchers to further explore and clarify this fundamental yet undervalued topic.

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