Body Posture Alters Brain Imaging Data

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Table of Contents

Abstract

In this thesis, I propose that body posture is an important, underappreciated, variable to consider in neuroimaging research. Thousands of brain imaging experiments are published each year, but few consider how the postures that participants assume may influence the data collected. Whereas participants in most behavioural, cognitive, and psychology experiments sit upright, one of the most prominent functional neuroimaging techniques, functional magnetic resonance imaging (fMRI), requires participants to lie supine. Many cognitive processes in our everyday life, moreover, are executed while neither sitting nor lying, but rather when standing, moving, or interacting with other people and the surrounding environment. A growing literature suggests that posture weighs heavily on both cognitive functions and physiological processes that are relevant to brain imaging. This thesis aims to elucidate how body posture shapes neuroimaging data.

We directly investigated the effect of posture on spontaneous brain dynamics by recording electrical activity (EEG) in four orthostatic conditions (lying supine, inclined at 45°, sitting upright, and standing erect) and magnetic activity (MEG) in three postures (lying supine, sitting reclined, sitting upright). We found that posture altered electromagnetic brain imaging data. Upright postures (sitting and standing), compared to reclined and supine postures, were associated with widespread increases in high-frequency oscillatory activity regardless of whether participants were involved in a mental task or had their eyes open or closed. Using MEG recordings alongside associated structural MRI scans, we were able to more precisely localize posture-driven changes in brain activity. Sitting upright versus lying supine was associated with greater high-frequency (i.e., beta and gamma) activity in widespread parieto-occipital cortex. Moreover, upright and reclined postures correlated with dampened activity in prefrontal regions, especially across lower frequency bandwidths. Our findings highlight the importance of posture as a determinant in neuroimaging. Generalizing results—from supine neuroimaging measurements to erect positions typical of ecological human behavior—would call for considering the influence that posture wields on brain dynamics.

Résumé

Dans cette thèse, je propose la posture corporelle comme une variable importante à prendre en compte dans la recherche en neuroimagerie. Des milliers d'expériences d'imagerie cérébrale sont publiées chaque année, mais peu d'entre elles considèrent comment les postures que les participants adoptent peuvent influencer les données collectées. Alors que les participants à la plupart des expériences comportementales, cognitives, et psychologiques se tiennent debout, l'une des techniques de neuroimagerie fonctionnelle les plus utilisées, l'imagerie par résonance magnétique fonctionnelle (IRMf), exige que les participants soient allongés. De plus, de nombreux processus cognitifs sont exécutés sans n'être ni assis, ni couché, mais plutôt en étant debout, en mouvement ou en interaction avec d'autres personnes et l'environnement immédiat. Une littérature croissante suggère que la posture pèse lourdement sur les fonctions cognitives et les processus physiologiques pertinents pour l'imagerie cérébrale. Cette thèse vise à élucider comment la posture du corps façonne les données de neuroimagerie.

Nous avons directement investigué l'effet de la posture sur la dynamique spontanée du cerveau en enregistrant l'activité électrique (EEG) dans quatre conditions orthostatiques (couché sur le dos, incliné à 45°, en position assise, ainsi que debout) et l'activité magnétique (MEG) dans trois postures (couché sur le dos, assis-incliné, assis droit). Nous avons constaté que la posture altérait les données d'imagerie électromagnétique du cerveau. Les postures droites (assis et debout) par rapport aux postures inclinées et en position couchée étaient associées à une augmentation généralisée de l'activité oscillatoire à haute fréquence, peu importe si les participants étaient impliqués dans une tâche mentale ou non et si leurs yeux étaient ouverts ou fermés. En utilisant les enregistrements MEG parallèlement aux examens IRM structurels associés, nous avons trouvé des modifications plus détaillées de l'activité cérébrale liées à la posture. Les postures assises en position verticale ou couchée étaient associées à une plus grande activité à haute fréquence (c.-à-d., bêta et gamma) généralisée dans le cortex pariéto-occipital. De plus, les postures droites et inclinées corrélaient avec une activité atténuée dans les régions préfrontales sur toute pour l'activité à basse fréquence. Nos résultats soulignent l'importance de la posture en tant que déterminant de la neuroimagerie. Ainsi, généraliser ces résultats—des mesures de neuroimagerie en position couchée à des positions droites typiques du comportement humain écologique—nécessiterait de prendre en compte l'influence de la posture sur la dynamique du cerveau.

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I am very grateful to have had Amir Raz as my Supervisor. He has provided me with invaluable guidance over the years and helped me develop into the researcher I am today. I would further like to thank my academic advisors: Stevan Harnad for helping me think critically and showing the importance of working on research that I am passionate about; and Ian Gold for providing guidance and motivating me to progress. I am also grateful to many other scholars I have met throughout my PhD who have helped me carve my path. It has been a pleasure to be surrounded by an inspiring team of graduate students along the way: Michael Lifshitz, Jay Olson, Mathieu Landry, Rémi Thériault, and others.

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Structure of the thesis

I have prepared this thesis in accordance with the article-based thesis guidelines of McGill University. The goal of this package of scientific contributions is to highlight posture as an important variable to consider in neuroimaging and psychology research. This thesis includes a general introduction, followed by five published articles and a general discussion. The introduction discusses four topics: embodied cognition, imaging methods and imaging posture, how postures influences cognition, and how posture alters physiology. My supervisor Amir Raz and I consolidated many of the subjects we discuss in the introduction, plus additional material, into an edited volume on crucial, but often overlooked, considerations in neuroimaging. The introduction makes reference to a number of these book chapters. The first article of this manuscript-based thesis is taken from a chapter I prepared for our edited volume. This chapter serves as an extension to the thesis introduction and discusses important factors to consider when conducting and interpreting (f)MRI research.

The main body of this thesis proposes posture as an additional factor to consider in (f)MRI research and beyond. It consists of Articles 2-4, which are original empirical research I conducted during my degree and published in the scientific journals *Cortex*, *Brain Imaging and Behavior*, and *Journal of Cognitive Neuroscience*. In Article 2 we used EEG to record brain activity from participants in four postures (standing, sitting, reclined, lying down) with both eyes closed and open, as well as with and without a task. We found widespread changes in high-frequency electrical activity in more upright postures regardless of eye closure and task conditions. Article 3 extends our original findings with a resting state multi-posture study that uses magnetoencephalography (MEG). MEG provides an advantage over EEG in that the signals it records (magnetic versus electrical) are less disturbed by cranial fluids and tissues. We attempt to replicate our sensor-level EEG findings with a sensor-level MEG analysis. Due to the limitations of current algorithms to standardize head placement in relation to the magnetic sensors across body postures, our results only partially replicated. In Article 4 we combine resting state multi-posture MEG recordings with structural MRIs from each participant. We conduct a source-level analysis and find that upright posture increase posterior high frequency activity, as observed in our initial

EEG study. We further find that upright postures are associated with lower levels of low-frequency oscillatory activity.

Article 5 discusses one of the key implications of our findings. To record brain activity in more ecological everyday environments, some researchers propose to use inexpensive EEG systems that are available to consumers and can connect to their smartphones. The text in Article 5 is an excerpt from a review I published in *Journal of Cognitive Enhancement* with a co-author. The complete review establishes that there is a dearth of the evidence to support the research use of consumer EEG devices (this is my work and is included in thesis) alongside a discussion of the regulatory implications of our findings (my co-author drafted this section; not included in thesis). We then proceed to the *General Discussion* section where I summarize our findings, relate this thesis to additional work I conducted as a doctoral student, discuss the potential mechanisms underlying our group's results, and suggest how scientists can move forward in light of our findings. The *Introduction* and *General Discussion* sections of this thesis quote text from a review I published in *Frontiers in Human Neuroscience* with Amir Raz (Thibault & Raz, 2016a). **All quoted text, unless otherwise marked, refers to my own work published in this review.**

Author Contributions

Article 1. I wrote the first draft of this book chapter. My co-author, Amir Raz was available for discussion and helped edit the final version.

Article 2. I developed the experimental design with input from Amir Raz and Jennifer Jones. I led data collection, with assistance from Jennifer Jones. I cleaned the data, performed the statistical analyses, produced the figures, and drafted the manuscript. All authors worked together to craft the final article.

Article 3 & 4. Michael Lifshitz and I designed the experimental protocol. We collected data together with additional assistance from members of the MEG lab at the Montreal Neurological Institute (Ishan Walpola, Sylvain Baillet, Elizabeth Bock). I cleaned the data, performed the statistical analysis, produced the figures, and drafted the manuscript for Article 3. All authors worked together to craft the final manuscript. For Article 4, I led data cleaning, statistical analysis, and figure development with assistance from an undergraduate student, Raquel Roth. Michael Lifshitz and I prepared the initial draft together and refined it with guidance from Amir Raz. Michael Lifshitz and I are co-first authors on Article 4. He has completed his Ph.D., did not use this article in his thesis, and has provided permission for me to include it in my thesis.

Article 5. My co-author, Anna Wexler, and I conceived the idea for this review together. The review is divided into two sections: scientific arguments and regulatory implications. I drafted the first section, Wexler the second section. We worked together on the final version. In this thesis I include only the paragraphs which I wrote.

Review (from which I quote text in the *Introduction* and *General Discussion*)**.** I conceived the idea for this review and wrote it. My co-author, Amir Raz, provided guidance and helped craft the final version.

Edited volume (from which I draw on in the *Introduction* and *General Discussion*). Amir Raz and I developed the idea for this book together. I invited the majority of the contributors and provided each author with detailed comments and edits.

All other text. I am the sole writer of all other text included in this thesis.

Introduction

“From psychiatry and cognitive science to education and marketing, many experts draw on discoveries from human brain imaging to inform their practice. However, few consumers of neuroimaging findings fully appreciate the methodological and environmental variables that these techniques often impose. For example, in a typical functional magnetic resonance imaging (fMRI) experiment, participants lie motionless in a body-sized bore while piercing screeches, thumps, and hums thunder around their head for up to an hour. In a customary electroencephalography (EEG) experiment, participants sit upright, alone, in a small, silent, and often dimly lit room, while staring at and responding to a computer screen for extended periods of time. Of the many glaring discrepancies between such imaging environments and everyday life, this [thesis] focuses on the role of body posture” (p. 1)[1]. This introduction surveys research on body posture and how it relates to neuroimaging through four lenses: (1) embodied cognition, (2) brain imaging methods, (3) body position and cognition, and (4) body position and physiology.

1. Embodied cognition

“Neuroimagers seldom draw on research suggesting that environmental variables impact human cognition. Meanwhile, an entire field of research, entitled *embodied cognition*, highlights the intricate relationship among our cognitive capacities, ongoing sensorimotor state, and surrounding environment (Di Paolo & Thompson, 2014; E. Thompson, 2005; E. Thompson & Varela, 2001; Wilson, 2002). Relevant postural findings highlight that slouching increases measures of helplessness and stress (Riskind & Gotay, 1982) and expansive postures increase testosterone, decrease cortisol, and amplify feelings of power and risk-tolerance (Carney, Cuddy, & Yap, 2010) [Note, these latter findings have been falsified since we originally published this review, discussed further on page 22 of this thesis]. Static imaging environments further diminish cognitive loads related to balance, moving visual fields, and social interaction (Hari & Kujala, 2009). Considering these factors, some scientists demand a new neuroscientific model—the

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[1] All quoted text in the introduction comes from a review I published (Thibault & Raz, 2016a). This practice follows the McGill thesis guidelines.

embodied brain—to better account for the ongoing interactions between brain, body, and environment (Kiverstein & Miller, 2015)" (p. 1-2).

The embodied brain approach is at odds with the proposal of Thomas Insel, ex-director of the United States National Institutes for Mental Health (NIMH), to conceptualize mental disorders as brain disorders. This proposal has gained traction and offers part of the framework for the NIMH's Research Domain Criteria Initiative (RDoC), which largely aims to understand mental disorders in the bottom-up terms of physiology. It may one day be used for a similar purpose as the Diagnostic and Statistical Manual of Mental Disorders (DSM). The concept of mental disorder as brain disorders is attractive because it attempts to reduce complex cultural and biopsychosocial phenomena to simple physiological units. However, this proposition has a conceptual shortcoming. We discuss this shortcoming in one of my major contributions as a doctoral student: an edited volume. In particular the invited chapters: *From Mind to Brain: The Challenge of Neuro-reductionism* by Ian Gold, and *Is Addiction a Brain Disease* by Scott Lilienfeld. Gold highlights that reductionism in science can be extremely fruitful and he provides the successful case of reducing genes to DNA, and DNA to molecules. At the same time, he argues that reducing the psychology and human behavior of mental disorders to neuroscientific theories misses the fact that mental disorders play out in a social and cultural landscape. Moreover, even if we could reduce mental disorders to brain processes, it may only prove more complicated to speak in the reduced terms.

Lilienfeld argues that mental disorders as brain disorders is partially unfalsifiable. He uses addiction as an example and notes that psychosocial variables including life stressors and neighborhood factors play key roles in addiction risk and in turn suggest that focusing primarily on a disordered brain as the culprit in addiction is misplaced (Hart, 2013). Opponents can argue that even these psychosocial factors are no more than products of the brain. However, with this reasoning, we could further argue that the brain is no more than the actions of atoms. Speaking of psychosocial phenomena in terms of atomic principles, however, does little to address the main issues scientists are interested in.

Various lenses and levels of analysis are available. Neuroimaging is a useful one, among many. A recent target article in *Behavioral and Brain Sciences* proposes a network model of mental disorders that integrates multiple levels of analysis (neurobiological, psychological, social) as well as the interplay between them (Borsboom, Cramer, & Kalis, 2018). Together, this article and the abovementioned chapters argue that scientists can benefit from espousing the view that the brain not only affects behavior and the environment, but that behavior and the environment also affect the brain. Body posture is but one example of a behavioural variable that influences the brain.

In line with the non-neuroreductionist approach Gold and Lilienfeld embrace, some researchers now discuss cognition in terms of the *4Es*—embodied, embedded, enacted, and extended. This framework implies that cognition take place in the body as well as the brain—*embodied*; always functions in relation to an environment—*embedded*; involves actions rather than neural computations alone—*enacted*; and includes more than just the individual (e.g., books, calculators, other people)—*extended*. Body posture becomes important when considering the 4Es. Certain postures offer the scaffolding for different activities. For example, when lying down, someone will not engage in the cognitive task of deciding where to step next; they need not worry about balancing or maintaining a posture. The 4Es hold an important place in current theories of *enactivism*, which proposes that cognition is geared towards action. The subset of cognitive tasks that people can perform in each posture is limited and can be more difficult to execute in certain postures compared to others.

The 4Es weigh heavily on cognition, and many neuroimaging experiments study cognitive processes; thus, brain imaging researchers stand to benefit from integrating this concept into their thinking. Two case examples that illustrate this point come from our edited volume. In *Beyond the brain: Toward an integrative cross-disciplinary understanding of human behaviour and experience*, Laurence Kirmayer highlights the interdependence regarding how culture shapes the brain and how the brain shapes culture. He explains how “cultural gadgets” provide new affordances for us to use our brain in different ways. Depending on one’s environment and posture, certain cultural gadgets will be more available than others. In *What’s wrong with the mindful brain? Moving past a neurocentric view of meditation*, Michael Lifshitz and Evan Thompson argue that meditation is not just about training brains, but rather a highly social, and necessarily embodied, collection of cultural practices. Many traditions of meditative practice propose the body as a mirror of the mind and highlight posture as an important element of meditation (W. Johnson, 1996).

Knowledge from embodied cognition, the 4Es, enactivism, and neuroreductionism all suggest that evaluating neuroimaging data alongside non-brain factors can only help gain a more complete understanding of brain processes and human behavior.

2. Imaging methods and imaging postures

"Popular functional neuroimaging modalities collect electromagnetic or hemodynamic brain data (Table 1). Electroencephalography (EEG) and magnetoencephalography (MEG) record electric and magnetic signals from pyramidal neurons; fMRI [generally] measures deoxygenated blood concentrations that correlate with neural activity; and functional near infrared spectroscopy (fNIRS) measures oxygenated and deoxygenated blood flow. EEG and MEG come with spatial precision of about one centimeter, yet millisecond temporal resolution; fMRI provides millimetric spatial resolution but temporal precision of approximately one second; fNIRS excels in neither temporal nor spatial resolution (Cui, Bray, Bryant, Glover, & Reiss, 2011) [see Table 2]. Each imaging modality, moreover, permits a subset of body positions. Participants can wear EEG and fNIRS caps throughout a wide range of postures (see Table 1) and, with proper equipment, can move and interact with their environment; MEG restricts participants to an adjustable seat that can adopt any position between an upright chair and a horizontal bench; and most fMRI options constrain participants to horizontal positions. Compared to portable technologies (i.e., EEG and fNIRS), the large and static imaging devices (i.e., fMRI and MEG) permit fewer posture, yet provide higher-quality data. These intrinsic differences lend certain imaging modalities more advantageous for specific applications and research questions but less so for others (e.g., the postural constraints of most MRI scanners would make fMRI a good way to explore the [resting] brain, but less ideal to study the driving brain)."

"Two canonical imaging postures dominate brain research even though more ecological alternatives exist (see Table 1). These established positions include sitting upright—common in EEG, MEG, fNIRS, [transcranial magnetic stimulation (TMS), transcranial electrical stimulation (tES),] and most of cognitive and psychological research; and lying supine—the standard for fMRI [and positron emission tomography (PET)]. Whereas a limited number of imaging experiments stray from these standardized postures, humans perform many cognitive tasks while standing and moving, yet few while lying down. Experiments leveraging non-standard body positions often ask particular questions which demand these postures. For example, researchers have participants stand or walk to better understand balance, gait, and motor disorders such as Parkinson's disease (Bakker, Verstappen, Bloem, & Toni, 2007; Koenraadt, Roelofsen, Duysens, & Keijsers, 2014; Mahoney et al., 2016), lie supine titled 6-12° head-down past horizontal to simulate a microgravity environment (e.g., Spironelli and Angrilli, 2011), or lie prone to investigate gravitational forces on cranial fluids (Rice, Rorden, Little, & Parra, 2013). Whereas the execution of these experiments fully depends on the use of non-standard imaging postures, the supine and sitting positions hardly impede researchers from conducting most neuroimaging experiments. This situation may encourage neuroimagers to continue employing standardized imaging postures even when ecological comportments could better unveil the neural mechanisms of everyday cognition."

2.1 fMRI

Posture becomes an important factor when considering the source of neuroimaging signals. Rather than measure neural activity directly, fMRI records hemodynamic processes. The Blood Oxygen Level Dependent (BOLD) signal is the most common measure taken; Cerebral Blood Volume (CBV) and Cerebral Blood Flow (CBF) are two other options. Following neural activity, blood flow increases to replenish the oxygen and glucose that the neurons consumed. The relative increase in blood flow is greater than the oxygen consumed and this process generates a change in the BOLD signal. Because the BOLD signal measures blood oxygenation, holding the breath can drastically affect this signal (3-6%; Abbott, Opdam, Briellmann, & Jackson, 2005; Kastrup, Krüger, Glover, & Moseley, 1999; Thomason, Burrows, Gabrieli, & Glover, 2005). Subtle variations in breathing rate and depth, which occur naturally between postures, can also substantially sway the BOLD signal (Birn, Diamond, Smith, & Bandettini, 2006; Birn, Smith, Jones, & Bandettini, 2008). Changes in the way gravity acts on the upright and supine human body, (e.g., changes in the pressure and dynamics of cranial fluids) can further alter fMRI signals without necessarily altering neural activity itself. Under certain conditions fMRI signals can dissociate from neural activity (Maier et al., 2008) and they can also fail to detect sparse neural activity (Logothetis, Pauls, Augath, Trinath, & Oeltermann, 2001). Signals from fNIRS suffer from the same shortcomings (plus additional issues associated with decreased spatial resolution and imaging depth). Posture, thus, acts on fMRI signals through two processes: neural activity and hemodynamic physiology. This dual action makes it difficult to disentangle whether postural changes to the BOLD signal would come from neural activity itself, or from other hemodynamic factors.

Using the BOLD signal, scientists have discovered resting state networks (RSNs) in the brain. RSNs consist of multiple cortical regions that activate in a temporally and spatial consistent pattern and in the absence of goal-directed behavior (Damoiseaux et al., 2006). Multiple RSNs exist. They span functionally relevant regions involved in visual processing, auditory processing, motor function, executive function, memory, and attention. The default mode network (DMN) is a highly researched RSN that is particularly active in the absence of a task. Researchers have noted disturbances in these networks related to many clinical conditions (Fox & Raichle, 2007; Greicius, 2008). Notably, RSNs were established with recordings taken from participants in the supine posture. As I document in the later parts of this introduction, and as many people can intuitively feel, our cognitive and physiological resting state differs when lying down compared to when sitting upright. Few reports acknowledge this insight. Article 4 of this thesis looks at key nodes of the DMN in relation to posture.

Spatial precision is an additional issue at the intersection of (f)MRI and posture. Standard MRI scanners now have a field strength of 3.0 Tesla and allow researchers to analyze the structure and function of the brain down to about 1 mm^3. High field MRI, with a field strength of 7 Tesla or more, is becoming more commonplace and can provide sub-millimetric precision (De Martino et al., 2011; Ugurbil, 2016). The higher the spatial precision, the more head movement becomes an issue. Compensatory algorithms can partially correct for head motion, but they remain far from perfect. For example, even after applying these algorithms, head motion can still produce spurious functional connectivity patterns (Ciric et al., 2018; Power, Barnes, Snyder, Schlaggar, & Petersen, 2012). Thus, even if engineers were to develop upright MRI scanners with sufficient strength for useful functional sequences, for most applications, the loss of precision may outweigh the improvement in ecological positioning. Article 1 extends this conversation by discussing additional artifacts to consider in (f)MRI research.

2.2 MEG and EEG (M/EEG)

As with fMRI signals, posture may affect M/EEG data via both neural mechanisms and ulterior pathways. EEG records electrical activity from the synchronized activity of tens of thousands of pyramidal cells that sit perpendicular to the surface of the scalp. Eye movements and muscle activity, however, also produce electrical activity that reaches EEG sensors. These artifacts can be orders of magnitude greater than the recorded neural activity. Researchers can easily remove large artifacts by simply discarding portions of the recording—the smaller artifacts tend to be more pernicious. Even after standard cleaning procedures, M/EEG recordings often contain lingering artifacts, especially in higher frequency ranges that overlap with muscle activity (Muthukumaraswamy, 2013). MEG may outperform EEG when considering multi-posture research. Magnetic signals are much less perturbed when passing through the highly conductive cerebrospinal fluid (CSF) that surrounds the brain. Gravity affects the distribution of CSF differently depending on body posture, and thus could alter EEG signals substantially without necessarily impacting neural activity. Whereas EEG records neural activity mainly from gyri (the ridges of the cerebral cortex), MEG is capable of recording from both gyri and sulci (the furrows of the cerebral cortex), based on the physical properties of electric signals versus magnetic fields. Both EEG and MEG are recordable in a variety of postures, unlike fMRI. Researchers who draw on both M/EEG and fMRI in relation to a single experimental question, can benefit from considering the influence posture exerts on neural activity, artifacts, and signal quality.

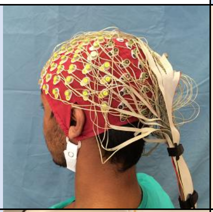
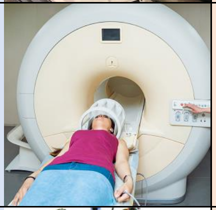
		Canonical imaging postures		Other everyday postures	
		Lying supine	**Sitting upright**	**Standing erect**	**Sitting reclined**
					
EEG		✓	✓	✓	✓
MEG		✓	✓	✗	✓
fMRI		✓	✗	✗	✗
fNIRS		✓	✓	✓	✓
Vigilance		low	medium	high	medium/low
Assumed in waking life		rare	common	common	occasional
Associated cognitive tasks		few	many	many	few
Actions possible		few	many	most	few

Table 1. *Each body posture raises particular considerations in terms of brain imaging modalities and cognitive experiments. To conduct fMRI beyond a horizontal body posture requires specialized scanners, which are extremely uncommon. Researchers can conduct EEG and fNIRS in any posture, but must care for occipital electrodes in the supine position. Humans execute most physical and cognitive actions when sitting or standing. To better depict the posture assumed in*

fMRI, this photo shows a participant before entering the bore. During scanning, the head and upper body remain inside the bore, which measures about 60 cm in diameter for standard scanners. This table and caption are taken from Thibault & Raz (2016a).

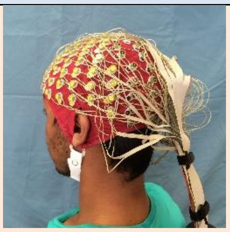
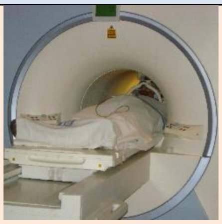
	EEG	**MEG**	**fMRI**	**fNIRS**
				
Underlying Signal	Electrical activity from pyramidal cells perpendicular to the scalp (mainly gyri)	Magnetic fields produced by pyramidal cells perpendicular and tangential to the cortical surface	Blood oxygenation level dependent contrast (which indirectly relates with neuronal activity)	Volume of oxygenated and/or deoxygenated blood (which indirectly relates with neuronal activity)
Resolution temporal spatial depth	Milliseconds Centimeters Superficial	Milliseconds ~10mm Depth constrains interpolation accuracy	Seconds Millimeters Deep (any region)	Seconds Centimeters Superficial (<4 cm)
Portable	Yes	No	No	Yes

Table 2. *Common functional brain imaging methods and their specifications. This table only discusses the BOLD signal from fMRI (as opposed to other, less common functional measures). Table and caption adapted from Thibault, Lifshitz, & Raz (2016).*

3. Posture influences cognition

“Posture alters sensory perception and behavior (Figure 1). For example, when upright compared to supine: olfactory thresholds increase for select odorants (e.g., Lundström et al., 2008), pain ratings amplify (e.g., Fardo et al., 2013; Spironelli and Angrilli, 2011), visual awareness improves (e.g., Goodenough et al., 1981; Marendaz et al., 1993), anticipatory anxiety heightens (e.g., Lipnicki and Byrne, 2008), approach motivation increases (Price, Dieckman, & Harmon-Jones, 2012), and conflicting thoughts decrease (e.g., Harmon-Jones et al., 2015). Posture further influences cognitive performance. Compared to lying supine, sitting upright improves non-verbal intelligence (e.g., Raven’s Progressive Matrices; Lundström et al., 2008) and aids in composing mental images, but impairs the ability to inspect them (Mast, Ganis, Christie, & Kosslyn, 2003). Standing compromises performance on problems requiring a burst of insight (e.g., anagrams: Lipnicki and Byrne, 2005) and improves psychomotor performance (Caldwell, Prazinko, & Caldwell, 2003; Caldwell, Prazinko, & Hall, 2000)” (p. 2).

3.1 Olfaction

“The fMRI environment may alter the very phenomena researchers aim to study. This concern has motivated diverse research groups to test how posture and cognition interact” (p. 2). For example, researchers who use fMRI to study functional brain responses to scents, tested whether standard experiments on olfaction—which are generally performed with participants sitting upright—would replicate in the supine posture used in fMRI research (Lundström et al., 2008). They found comparable sniffing behavior between sitting and supine postures, yet participants were less able to detect some, but not all, perithreshold odors. They found no effect on participant’s ability to detect suprathreshold odors, or rate them for pleasantness, familiarity, or intensity. A related pilot study reported that participants had no difference in taste perception between supine and sitting positions (Hort et al., 2008).

3.2 Emotion

Emotion researchers found a divergence between EEG and fMRI findings and proposed posture as the mediator (Harmon-Jones & Peterson, 2009). Their article highlights that over 15 EEG and TMS studies identify greater activity in the left, compared to right, prefrontal cortex during the experience of anger. Yet, fMRI studies found no such lateralization. To test the theory that posture accounts for the divergence in findings of lateralization, these researchers evoked anger in participants and recorded EEG when participants were either sitting up or lying down. Participants who were sitting up expressed greater EEG lateralization than those who were supine. The researchers theorized this difference stems from greater approach motivation when upright (as the principle of *enactivism* would suggest). They extended their initial experiment and discovered reduced motivation on a Stroop task and a lesser desire for dissonance reduction when supine (Harmon-Jones et al., 2015). Another set of participants expressed a smaller startle eye-blink response and a greater late positive potential (a type of event related potential (ERP)) when presented with appetitive photos, but not neutral photos, when sitting leaning forward compared to when sitting reclined (Price et al., 2012). A related study found that posture had no effect on risk taking in an experimental betting market (O’Brien & Ahmed, 2014). These findings, in general, suggest that certain body postures afford the scaffolding to act in different ways.

3.3 Pain and arousal

Body posture also influences how individuals experience pain. One experiment had participants either sit or lie down for 90 minutes and then electrically stimulation their arm at either 40% below or 40% above individually established pain thresholds (Fardo et al., 2013). Supine participants experienced less pain sensitivity to the sub-threshold stimulus, but there were no differences for the supra-threshold stimulus. In a comparable study researchers had participants sit or lie on a bed at a 6° head-down angle from horizontal (often used to mimic a microgravity environment). They applied a 30% sub- and 30% supra-threshold painful stimulus to the arm and found that lying down inhibited pain for both stimulation intensities (Spironelli & Angrilli, 2011). The changes in pain perception may be related to levels of arousal, which also differ between postures. For example, before taking a difficult mental test, anxiety is greater if standing compared to sitting (Lipnicki & Byrne, 2008). Although, in this experiment, differences were absent between postures during the test and at a 10-minute follow-up. Another experiment suggests that mild to moderately depressed patients speak more positively after holding an upright, as opposed to slouched posture (Wilkes, Kydd, Sagar, & Broadbent, 2017).

3.4 Vision

Body posture alters visual perception. When sitting, compared to lying supine, participants could better align a rod with the horizontal in spite of illusory background visual information (Goodenough et al., 1981). A similar experiment demonstrated that participants could more quickly identify a target item—a line at a given angle, among a visual display with many lines—when upright compared to when supine. These effects could be due to body posture, or simply the direction of gaze. Another study altered body posture and visual field separately and suggested that the direction of gaze with respect to gravity determines visual accuracy (Di Cesare, Sarlegna, Bourdin, Mestre, & Bringoux, 2014). Composing mental images also seems to be more difficult, but inspecting them easier, when supine. (Mast et al., 2003). Other experiments surrounded individuals with monitors and found that participants reacted more quickly to a moving visual field (Kano, 1991) and felt a visual illusion more strongly when upright compared to supine (Guterman, Allison, Palmisano, & Zacher, 2012). All these results suggest that vision relies on proprioceptive and vestibular information which are posture-dependent.

3.5 Performance

Humans perform most cognitive tasks better when upright, although few fMRI experiments raise this point. Participants make more mistakes and take longer to complete Raven’s Matrices, which are often used to index IQ, when supine compared to upright (Lundström et al., 2008). Many days of bed rest decreases performance on measures of executive function (Iowa Gambling task), yet results were inconclusive for a Flanker task and working memory task (Lipnicki, Gunga, Belavỳ, & Felsenberg, 2009). Performance on tasks of divergent thinking—in terms of completion, fluency, flexibility, and novelty—decreased stepwise from when participants were walking freely, to walking in a predetermined pattern, to standing still, to sitting, to lying (Zhou, Zhang, Hommel, & Zhang, 2017). In sleep deprived subjects, the effects of posture seem to amplify. After 20 hours without sleep, reaction time and lapses on a psycho-vigilance motor task increase when sitting, but not when standing (Caldwell et al., 2003). In fact, many participants fall asleep during resting-state MRI scans (Laufs & Tagliazucchi, 2014). The only task performance documented in the literature that seems to improve when supine is solving anagrams (Lipnicki & Byrne, 2005). Because many of the findings surrounding the effects of posture on cognition come from one-off studies with small sample sizes, we now proceed to a discussion on the reliability of these results.

3.6 Replication and reliability

Replication takes on particular importance when considering some of the most popularized findings that touch on embodied cognition. These include performing "power poses" to increase hormone levels and risk tolerance (Carney et al., 2010) and forcing a smile to feel happier (Strack, Martin, & Stepper, 1988). A presentation on power poses became the second most watched TED Talk with over 48 million viewers. A replication attempt with a much larger sample size and pre-specified analyses, however, showed that power poses affected neither hormones nor risk tolerance (Ranehill et al., 2015). The first author of the original power poses study issued a full retraction based on the flimsiness of the original experiment and analysis (Carney, 2016). Another popular, and now falsified, finding suggested that if you force yourself to smile, you will feel happier (Strack et al., 1988). Participants held a pencil in their mouth (to force a smile) and found that cartoons were 0.82 points more funny on a 10-point Likert scale. This paper has been cited almost 2000 times and has become part of popular knowledge. A systematic pre-registered replication attempt that included 17 independent studies, however, found a non-significant difference of 0.03 points on the Likert scale (Wagenmakers et al., 2016). These high-profile instances underscore the tentative nature of many scientific findings and the need for independent replication.

To improve the reliability and replicability of cognitive and brain science, researchers can employ larger sample sizes, aim to triangulate findings, and adopt more open science practices. In our edited volume, Marcus Munafò and colleagues highlight that average neuroscience experiments have somewhere between 8-31% power to detect a statistically significant result (Button et al., 2013). This statistic means that neuroscientists will label the vast majority of true findings as non-significant; in turn, obfuscating the conclusions drawn across the scientific literature. The authors further argue that *triangulating* findings from diverse experiments, that rely on different types of data and come with opposing biases, but aim to answer the same question, can help arrive at a solid conclusion (Munafò & Davey Smith, 2018). A classic example of triangulation is how many lines of evidence from genetics, paleontology, and animal biology all point to the same conclusion that natural selection drives evolution. Likewise, neuroimaging, cognitive science, psychology and other disciplines can merge to develop robust theories surrounding human cognition. Uploading scientific data, protocols, and analysis scripts to an open access repository, moreover, encourages replication and reproduction attempts and can bolster scientific conclusions. In our edited volume, the chapter *The Replication Challenge: Is Brain Imaging Next*, David Mehler highlights how open science remains widely under-practiced (e.g., Iqbal, Wallach, Khoury, Schully, & John, 2016).

Replication of the individual postural findings I discussed above remain sparse. Perhaps because posture receives more attention as a procedural caveat than a research field in its own right. However, findings from the various experiments (alongside the physiology studies I discuss next) *triangulate* to arrive at a general overarching consensus: that upright posture leads to a more alert state with additional affordances. In this sense, the foundation for my thesis rests on a broad and sturdy foundation developed from experiments conducted in different disciplines that rely on a variety of methodologies.

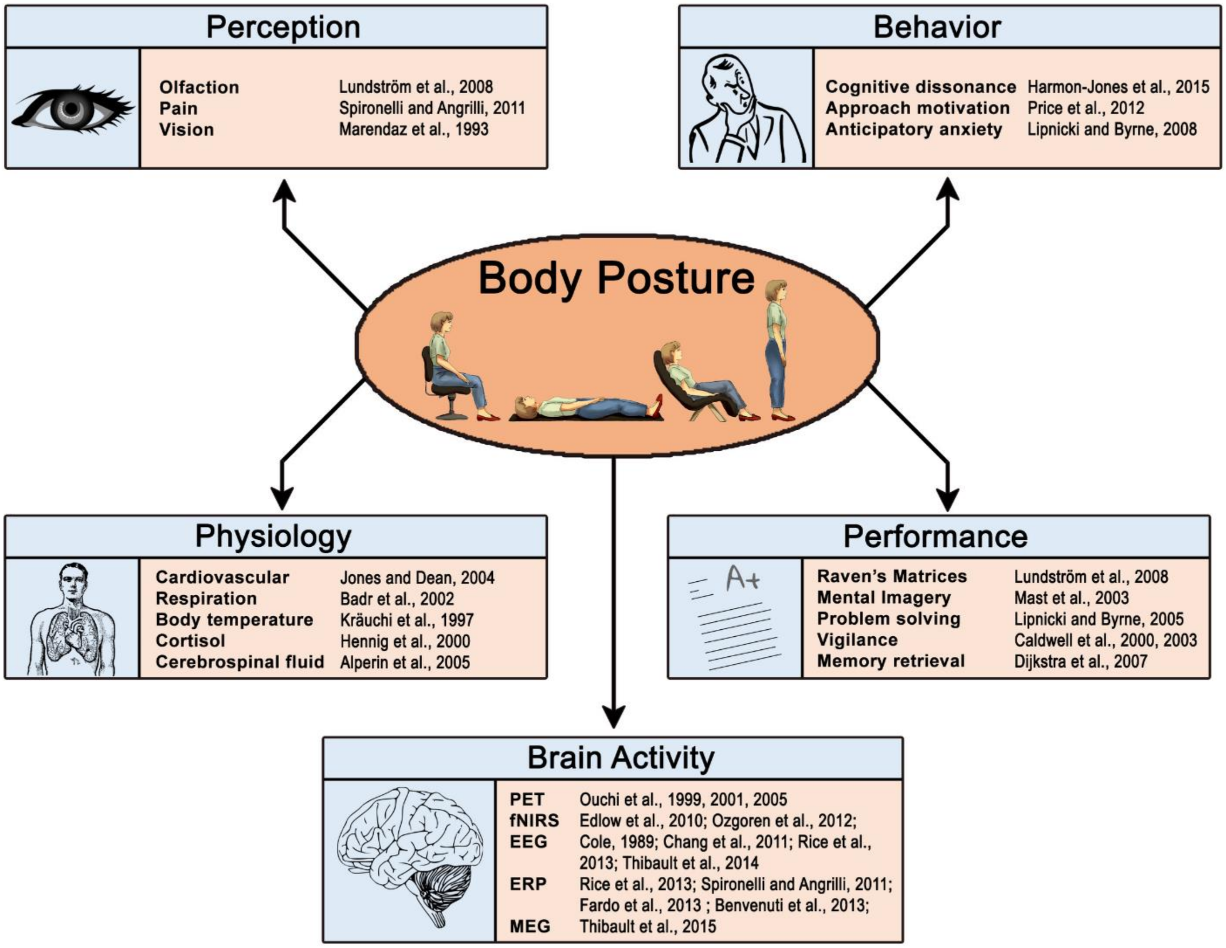


Figure 1. *Posture modulates physiology and cognition: select experimental findings. Figure taken from Thibault & Raz (2016a).*

4. Posture influences physiology

"Heart rate, respiratory volume, oxygen consumption, core body temperature, cortisol secretion, and other indicators of physiological arousal stabilize at higher levels when upright compared to supine (Figure 1; Cole, 1989; Badr et al., 2002; Jones and Dean, 2004; Kräuchi et al., 1997, Hennig et al., 2000). These physiological differences may influence the fMRI derived blood-oxygen-level dependent (BOLD) signal, regardless of whether or not brain processes actually change (Di, Kannurpatti, Rypma, & Biswal, 2013; Kastrup et al., 1999). fMRI measures neuronal activity indirectly (see Shmuel and Maier, 2015); the BOLD signal stems from the hemodynamic properties of neural populations and remains highly sensitive to cardiopulmonary variables (C. Chang, Cunningham, & Glover, 2009; C. Chang & Glover, 2009; Di et al., 2013; Weinberger & Radulescu, 2016). Thus, demonstrating that posture affects the BOLD signal falls short of confirming a change in neural activity; cardiopulmonary variables remain yoked to body position and also weigh heavily on BOLD activity.

Beyond BOLD, posture governs blood flow around the brain (Gisolf et al., 2004). A few experiments employ a stance-adjustable positron emission tomography (PET) gantry and report greater blood flow to both visual and cerebellar cortices when standing erect compared to lying supine (Ouchi et al., 2001; Ouchi et al., 1999). Using fNIRS, researchers document decreases in both oxygenated and deoxygenated cortical hemoglobin volume when participants move from lying supine to sitting upright (Edlow et al., 2010; Ozgoren, Tetik, Izzetoglu, Oniz, & Onaral, 2012). Due to a paucity of upright MRI scanners capable of functional sequences, researchers have yet to replicate postural fNIRS experiments with fMRI. Because fNIRS and fMRI measure similar signals (Cui et al., 2011), we can only presume that postural discrepancies would also influence fMRI data.

Beyond cardiovascular measures, posture exerts a quantifiable and direct impact on neural activity. A few EEG experiments demonstrate that, compared to lying horizontally, lying head-up on an incline [at 40° (Cole, 1989)] and sitting upright (L.-J. Chang et al., 2011) increase high-frequency neural activity, associated with alertness and sensory processing, and dampen down low-frequency oscillations associated with relaxed or drowsy states" (p. 2-4). In both these experiments researchers recorded from two central electrodes and instructed participants to keep their eyes closed. Cole (1989) analyzed only beta activity and found a greater amplitude when lying on an incline compared to lying flat. Chang et al. (2011) found lower amplitude low frequency activity and greater high frequency activity when sitting compared to supine. Another study recorded EEG and MRI from participants in supine and prone positions (Rice et al., 2013). They found an 80% decrease in occipital gamma amplitude which they explained with a head model that accounted for difference in CSF thickness observed between the postures with MRI. Whereas the majority of these studies employ healthy young adults, posture may exert a particularly strong influence on brain function in the elderly and specific patient groups (e.g., cardiovascular disease or tramautic brain injury: Ouchi et al., 2005; Thompson et al., 2005)" (p. 4).

One research group measured ERPs in response to a painful stimulus in both supine and seated postures. They found a flattened P1 response (Spironelli & Angrilli, 2011) and reduced slow cortical wave (300-600 ms) amplitude (Fardo et al., 2013) in supine versus seated participants. The P1 results, however, are not analyzed in this group's more recent paper and the slow wave results are not analyzed in the original paper. A visual inspection of the figures included in their articles suggests that neither of these results replicated. They performed a number of additional analyses with non-significant results and do not explain how they corrected for multiple comparisons. Thus, postural ERP results remain preliminary.

Taken together, "converging evidence from cognitive, medical, and neuroscientific research supports the *embodied brain* hypothesis and underscores the importance of postural variables in modern imaging experiments" (p. 4).

5. Contribution to original knowledge

The experiments composing the body of this thesis build on the literature I have discussed thus far. Article 2 is one of the first high-density multi-postural EEG studies. It is the first to measure EEG across more than two postures and across multiple conditions (eyes open vs. closed; task vs. no-task). This experimental design provides the data to obtain a more complete understanding of how posture alters brain activity, including where in the brain the effects occur and whether they follow a linear pattern in terms of body position relative to gravity. We are the first and only research group, to my knowledge, who compared MEG data taken from multiple postures. This seminal work contributed to original methodological considerations which we outline in Article 3. In Article 4 we performed the first multi-posture source analysis that draws on anatomical MRI scans. These published articles represent original empirical contributions to scientific knowledge.

Article One

Preface. The present article builds on section 2 of the introduction of this thesis, which discussed neuroimaging modalities. This article comes from a book chapter I wrote for the upcoming volume I co-edited with Amir Raz. The edited volume targets an academic audience, who are not brain imaging experts, with a light writing style. The book critically evaluates neuroimaging research and carves a path for how to conduct rigorous and reliable research with this set of tools. The chapter I include here overviews many caveats in (f)MRI research, a number of which relate to posture (e.g., respiration, resting state). I include this article because it provides overarching information that calls for increased nuance when conducting and interpreting neuroimaging experiments. Body posture is one of these nuances that many researchers and consumers of research findings overlook.

MRI Artifacts in Psychiatry:
Head Motion, Breathing, and other Systematic Confounds

Robert T. Thibault, Amir Raz

Book chapter in Thibault & Raz (eds.) Casting light on the dark side of brain imaging. Elsevier (2019).

To better understand psychiatric conditions, we rarely look at the brains of cadavers anymore; but that was common practice some hundred years ago. Today, magnetic resonance imaging (MRI) and functional MRI (fMRI), to give one example, permits structural/volumetric and functional investigation of the biology of psychiatric conditions in the living human brain. And yet, many subtle pitfalls linger when imaging the neural infrastructure, let alone neural activity, in search of higher brain functions.

Not only does the trade and popular science press burst at the seams with images of scanned brains and the results of studies, leading psychiatry journals now regularly include findings from brain imaging assays. A typical experiment may draw on about two dozen people from one group, often individuals diagnosed with a mental disorder, and compare these patients to a comparably-sized group of controls. Unfortunately, these findings tell us considerably less than most readers appreciate. Why? Mostly because of inadequate statistical power and systematic confounds. For example, patients and controls often differ with respect to traits that alter brain data (e.g., head motion in the scanner) without necessarily affecting the underlying neural activity. Such confounds pervade findings from both structural and functional brain imaging research.

With structural brain imaging, we often hear largely-accepted, but nonetheless questionable, statements such as: “anxiety alters amygdala volume”; “depression shrinks hippocampus and cingulate cortex”; and “schizophrenia eats away at cortical matter”. While debate wages on, many researchers acquiesce to the notion that structural brain changes are a primary characteristic of psychiatric disorders (Kahn & Sommer, 2015). Some researchers even claim that non-pathological behaviors, such as watching pornography (Kühn & Gallinat, 2014), alter the structure of our brain. Thus we apply diagnostic terms, such as “cortical thinning,” “atrophy,” “tissue loss,” and “abnormal connectivity,” and we assume that these are insights into the underlying nature of these conditions (Weinberger & Radulescu, 2016).

We’d like to make sure you fully understand our point: we don’t challenge the findings that these studies report; instead, we contest the jargon-filled, authoritative mode, which colors their seemingly conclusive claims. Such presentations conceal a largely-ignored, inconvenient truth: MRI scarcely allows us to make firm inferences about the neurobiology of mental disorders.

To begin to understand why, remind yourself what this imaging technique really measures. MRI does not directly assess brain structure. Rather, it measures the properties of hydrogen atoms and depends on the magnetic properties of the microenvironment surrounding the tissue. In other words, MR signals are susceptible to many physical-chemical phenomena possibly unrelated to the number (or structure) of cells in tissue.

When MRI scans emerge as evidence for a linkage between a given psychiatric condition and a certain pathology of brain structures, we must consider alternative, non-anatomical explanations. For example, some factors that influence MR signals include history of smoking, alcohol, cannabis/psychedelic drugs, exercise, body weight, lipid levels, ongoing stress, and medication.

Slight head motion during a scan can wield a substantial impact on MRI findings. So “professional” control participants—i.e., individuals who partake in multiple MRI experiments as paid volunteers—would likely have the advantage of keeping more still, compared to the uninitiated. Now imagine individuals diagnosed with a psychiatric disorder, their symptoms managed by medication, entering an MRI machine for the first time and asked to lie motionless for extended periods of time. Is it possible the image from the patient brain exhibits “cortical volume and thickness reduction,” or was the difference a function of how the patient subtly *moved* compared to a control participant?

To further illustrate this point, consider the “excessive tissue loss” in the hippocampus observed via MRI in schizophrenic patients. If this observation were a result of abnormalities in the neurobiology, then evidence of such tissue loss should be apparent upon a post-mortem examination. Alas, more than 100 years of post-mortem studies have scantily confirmed this MRI-based result (Weinberger & Radulescu, 2016).

In fMRI experiments we usually see “activation” studies, where participants perform a particular task, and “resting-state” studies where participants lie passively in the scanner without any specific cognitive goal. Over a thousand peer-review scientific reports on fMRI are published each year, and yet most of these articles neglect to mention common confounds—often the very same ones that plague structural MRI findings. While fMRI has improved dramatically since its inception in 1992, researchers still fall into the same traps of oversight and omission when comparing patients to healthy controls.

Within activation studies, rigorous experimental designs can offset many confounds. However, resting-state fMRI studies, where participants go through a scan without a specific task, pose a conundrum because they experience the scanning process very differently thereby exerting a dramatic impact on fMRI data. To demonstrate why many resting-state fMRI findings are likely spurious, one research group looked at a dataset of 500 brain scans, all taken from healthy controls, and tested every permutation of 20 brains compared to 20 other brains (Eklund, Nichols, & Knutsson, 2016). They found significant differences between the two groups of brains in up to 70% of cases. Moreover, they used the default setting in many statistical packages, which assumes that fMRI data follow a certain distribution, although that’s frequently untrue. In other words, some “standard methods” of analysis that rest on unreliable assumption can easily produce false positives. Thus, we must remain wary of the default statistical methods as we attempt to sort out results: from the robust to the flimsy.

Rather than direct neural activity, fMRI measures the content of oxygen in the blood circulating throughout the brain (the BOLD signal). If we hold our breath during a scan, we can drive a 3-6% change in the BOLD signal (Abbott et al., 2005; Kastrup et al., 1999; Thomason et al., 2005). Meanwhile, most fMRI studies find differences of less than 1% between experimental groups. Moreover, not just holding the breath, but subtle variations in respiratory rate and depth—patterns that occur naturally over time—can also markedly sway the BOLD signal (Birn et al., 2006, 2008). Can you imagine breathing differences when you cram anxious patients into an MRI scanner and compare them to healthy controls? It is likely that these two groups would breathe differently?

Two “hot” regions in brain imaging research—the anterior cingulate and the insula—are particularly susceptible to respiratory artifacts. Could their fame rely on such inhale-exhale confounds? Perhaps, but we would need further studies to confirm. With appropriate methodology, including a chest belt and some statistical modeling, we can control for and rule out a substantial portion of this potential artifact. And yet, not all neuroimagers pursue this direction.

Now consider imaging the brains of expert meditators, say Buddhist monks who have been practicing their contemplative tradition for decades. If we compared their resting-state to that of naïve controls, would you not expect the monks to be thinking about very different things? Would you not suppose that they breathe differently? Lining up a large sample of expert meditators would make for a tall order, so a small group would have to do and the possibility of a false positive would accordingly become more prominent, especially if we draw on default statistical tests. To properly evaluate fMRI resting-state findings, we would need to account, at the very least, for the sample size and what participants were pondering, whether the researchers had regressed out distortion from breathing, and whether they used appropriate stats.

The status of neuroimaging research in psychiatry seems tenuous. On the one hand, (f)MRI remains an important tool for understanding the psychopathology and pathobiology of mental disorders. On the other hand, to make further advances, researchers ought to keep in mind the caveats we have highlighted herein, and which remain heretofore largely unaddressed. Toward this end, clinicians and researchers stand to benefit from designing and interpreting experiments that account for such potential artifacts. We would do well to critically rethink the inferences we sometimes draw from (f)MRI studies of mental health.

Article Two

Preface. Now that we have established that easy-to-overlook variables, such as respiration, analytical choices, sample size, and posture, may drastically skew neuroimaging results, I now shift to the primary empirical research section of my thesis. This article was the first experiment our group conducted on body posture. We set out to test whether posture alters brain activity as a main effect or as an interaction with other variables (eyes open versus closed; mental task versus no task). Our main results were recently replicated by an independent group (Spironelli & Angrilli, 2017).

Posture alters human resting-state

Robert T. Thibault, Michael Lifshitz, Jennifer M. Jones, & Amir Raz

Cortex 58, 199-205, (2014).

Abstract

Neuroimaging is ubiquitous; however, neuroimagers seldom investigate the putative impact of posture on brain activity. Whereas participants in most psychological experiments sit upright, many prominent neuroimaging techniques (e.g., functional magnetic resonance imaging (fMRI)) require participants to lie supine. Such postural discrepancies may hold important implications for brain function in general and for fMRI in particular. We directly investigated the effect of posture on spontaneous brain dynamics by recording scalp electrical activity in four orthostatic conditions (lying supine, inclined at 45°, sitting upright, and standing erect). Here we show that upright versus supine posture increases widespread high-frequency oscillatory activity. Our electroencephalographic findings highlight the importance of posture as a determinant in neuroimaging. When generalizing supine imaging results to ecological human cognition, therefore, cognitive neuroscientists would benefit from considering the influence of posture on brain dynamics.

Introduction

Neuroimagers typically assume that body-position scantily affects neural activity (Raz et al., 2005). Here we challenge this tacit assumption by demonstrating that posture rapidly changes oscillatory dynamics of the resting brain as measured by electroencephalography (EEG). Sparse findings show that orthostatic variations (e.g., sitting upright, lying supine, standing erect) modulate specific cognitive processes and sensory thresholds; for example, body-position alters visual perception (Goodenough et al., 1981), problem solving (Lipnicki & Byrne, 2005), anticipatory anxiety (Lipnicki & Byrne, 2008), pain sensitivity (Spironelli & Angrilli, 2011), and odor discrimination (Lundström et al., 2008). Comparing postures using a stance-adjustable positron emission tomography (PET) gantry, moreover, studies reported signal differences across postures in a wide range of cortical and subcortical regions (Ouchi et al., 2001; Ouchi et al., 1999). These collective findings propose posture as a modulator of neural activity. Although a few studies have found changes in EEG as a function of posture (Chang et al., 2011; Cole, 1989; Rice et al., 2013), these efforts shied away from directly testing and addressing how posture may influence brain activity in canonical imaging contexts such as those common to fMRI and EEG. The present account addresses this lacuna.

Materials and methods

Participants

Nineteen participants provided written informed consent in accordance with the Research Ethics Board at McGill University and in compliance with the Code of Ethics of the World Medical Association—Declaration of Helsinki—before the experiment. We excluded data from seven participants because at least one of their recordings contained fewer than four two-second epochs without blinking artifacts. Although we excluded only 4% (13/304) of all 30-second trials, adhering to a fully factorial design required we exclude 37% (7/19) of participants. All twelve participants whose data we included (mean age = 20.5 ± 2.0 years; nine females) reported having consumed no nicotine and no more than one caffeinated beverage on the day of testing.

Experimental procedure

Participants randomly transitioned among four postures (supine, 45° incline, sitting, and standing; see Fig. 2.1). For each posture, participants underwent a 30-second adaptation followed by a 30-second EEG recording in four counterbalanced conditions: eyes closed with mental counting task, eyes closed with no task, eyes open with mental counting task, and eyes open with no task. To avoid electrode contact with the table and artifacts produced by neck muscles, participants used neck-support throughout the experiment.

Electroencephalography

We collected high-density EEG data from 128 pin-type active electrodes using an ActiveTwo system (BioSemi, Amsterdam, The Netherlands) acquiring data using ActiView

(BioSemi) at a sampling rate of 2048 Hz. We set filters to 0.5-70 Hz with a 60-Hz notch filter using 2-Hz width to eliminate electrical noise. Electrode impedances measured below 20 kOhms before each recording and neither drifted during the experiment nor changed as a function of specific postures. Throughout data acquisition and in line with the standard in the field, BioSemi equipment references electrodes to a signal formed by a Common Mode Sense active electrode and a Driven Right Leg passive electrode, located slightly occipitally from Cz (Metting van Rijn, Peper, & Grimbergen, 1990, 1991). Before analyzing the data, the Brain Electrical Source Analysis (BESA®) package re-referenced each electrode to the average of all EEG electrodes.

Setting

We partitioned an area of our laboratory measuring 3 x 2 x 2 m with grey-blue monochromatic sheets to control for visual stimuli across positions. We used squares of white tape measuring 3 x 3 cm as fixation points for conditions with open eyes. Depending on the specific posture, participants lay on a tilt table, sat upright in a chair, or stood flush with a wall in the middle of the testing area. The testing room was quiet throughout.

Data analysis

We manually scanned and labeled data with irregular high amplitude delta waveforms recorded by frontal electrodes as artifacts due to eye movement. We replaced electrode channels containing other ectopic waveforms with interpolated waveforms from surrounding electrodes using the BESA® package. We then fast-Fourier transformed all artifact-free 2-s epochs and calculated the average absolute power at each bandwidth using the *FFTaverage* function in BESA®. This function applies a cosine square window to the first and last 10% of each epoch to attenuate the amplitudes at the ends to zero. Using Statistical Analysis Software (SAS®), we performed a full-factorial three-way analysis of variance (ANOVA) (Posture x Task x Eye condition) on the logarithm of the absolute power (measured in μV^2) at each electrode for each bandwidth (delta (δ) 0.5-4 Hz; theta (θ) 4-8 Hz; alpha (α) 8-14 Hz; beta (β) 14-30 Hz; and gamma (γ) 30-50 Hz). To account for multiple comparisons, we calculated an adjusted p-value for each dimension of the ANOVA at each bandwidth using positive false discovery rate (Storey, 2002). We corrected all pairwise comparisons using Tukey's Honest Significant Difference Test. Using SAS® we confirmed normality and homogeneity of variance in each analysis. We generated color (heat) and electrode maps using MATLAB 7.11 (Mathworks, Natick, MA) and EEGLAB (Delorme and Makeig, 2004).

We performed a secondary analysis using a dipole source montage from BESA®. This montage employs spatial filtering to transform signals from recorded surface channels into fifteen virtual source channels inside the brain. These interpolated regions represent a single source with three single dipoles at the same location with orthogonal orientations. Finally, we corroborated our primary and secondary analysis on the main effect of posture using the power-spectrum density analysis function in *Brainstorm 3.1* (Tadel et al., 2011). This function applies Welch's method to obtain power spectra, and then performs Fourier transforms on the power spectra to obtain the average absolute power at each bandwidth.

Electromyography

To test whether muscle artifact contributed to our results we ran a control experiment on an additional six participants (mean age = 26 ± 10.7 years; three females) using flat-type active electrodes especially designed for recording electromyograms (EMGs). We placed six EMG electrodes at the following locations: the superior region of the left sternocleidomastoid; the superior region of the right trapezius; anterior to the earlobe on the left masseter; above the left eye; below it; and lateral to its temporal canthus (Fig. 3A). The EMG placed on the trapezius touched the neck support and received different amounts of pressure as a function of posture. To test whether postural effects on EEG signals are transient or long-lasting, we recorded two eight-minute runs with a one-minute break between runs. These participants either lay horizontally (supine) on a tilt table, lay at 45° (supine), or sat upright in a chair with eyes open and no task (Fig. 3C). Using BESA®, we removed vertical and horizontal electrooculogram (VEOG and HEOG) artifacts at a minimum of 250µV and 150µV, respectively, from the EEG electrodes only. We statistically analyzed both EMGs and EEGs using a two-way ANOVA (Posture x Run) using SAS®. All other aspects of the experiment (participants, experimental procedure, electroencephalogram, setting, data analysis) for these six participants matched the above-mentioned procedures (i.e., sections 2.1 through 2.5).

Results

Our primary analysis revealed a main effect of posture in the β and γ ranges (Fig. 2.1) and a main effect of eye condition across all waveforms except γ (Fig. 2.2). We found a main effect of posture on β-band activity over rostral frontal cortex as well as over medial and right occipital cortex (Fig. 2.1). Beta activity increased over frontal and occipital areas when inclined at 45° compared to supine (Fig. 2.1A), and increased over occipital regions when sitting upright compared to 45° incline (Fig. 2.1B). We also found a main effect of posture on γ-band activity distributed widely over the scalp. Gamma activity increased over lateral frontal regions when at 45° incline compared to supine (Fig. 2.1C), and increased over medial and right occipital regions when sitting compared to at 45° incline (Fig. 2.1D). Moreover, we observed widespread γ increases when sitting upright compared to lying supine (Fig. 2.1E). Both β and γ activity increased over frontal areas when at 45° incline compared to supine, and increased over occipital regions in sitting and standing erect positions compared to 45° incline. Across postures, eye closure instigated widespread increases in δ, θ, and α activity, as well as increases in β activity over dorsofrontal, parietal, and occipital regions (Fig. 2.2).

Our secondary analysis revealed a main effect of posture, eye condition, and task on the electrical activity of interpolated cortical areas (Fig. 2.3). Upright postures featured increased γ activity for all 15 brain regions and with increased β activity in all brain regions excluding central and left parietal areas (Fig. 2.3A). Eye closure featured increased δ, θ, and α activity in all cortical areas and with increased β activity in dorsofrontal, parietal, and occipital brain regions (Fig. 2.3B). When performing a task, δ, θ, and β activity decreased throughout the cortex, α activity decreased in frontal areas, and γ activity decreased in midline and right parietal regions (Fig. 2.3C).

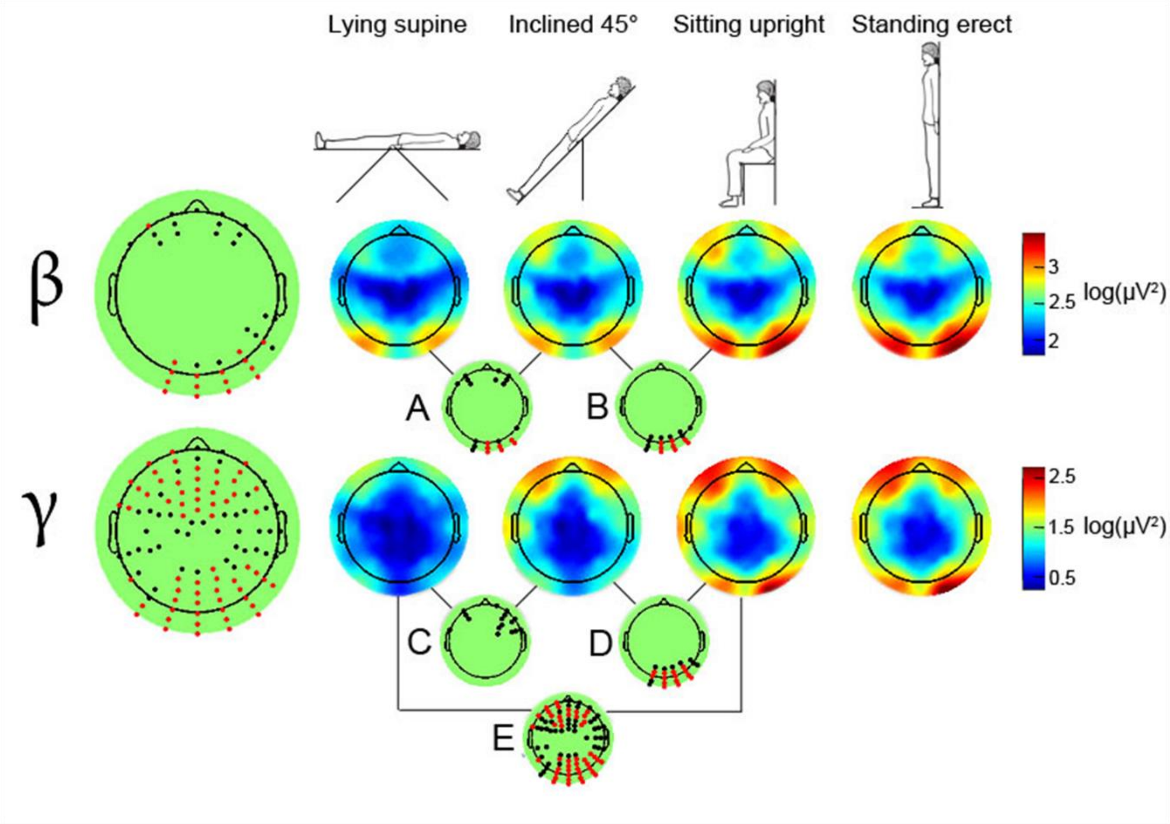


Figure 2.1 β and γ activity differences among postures.

Dots represent electrodes where three-way ANOVAs yielded a significant main effect for posture (black: p < .05; red: p < .005). Color maps represent the average power at each electrode for that particular posture and bandwidth. Small electrode maps show significant Tukey-corrected pairwise comparisons between select postures. Dots represent an increase in power when moving toward upright postures. ANOVAs for δ, Θ, and α bandwidths were not significant.

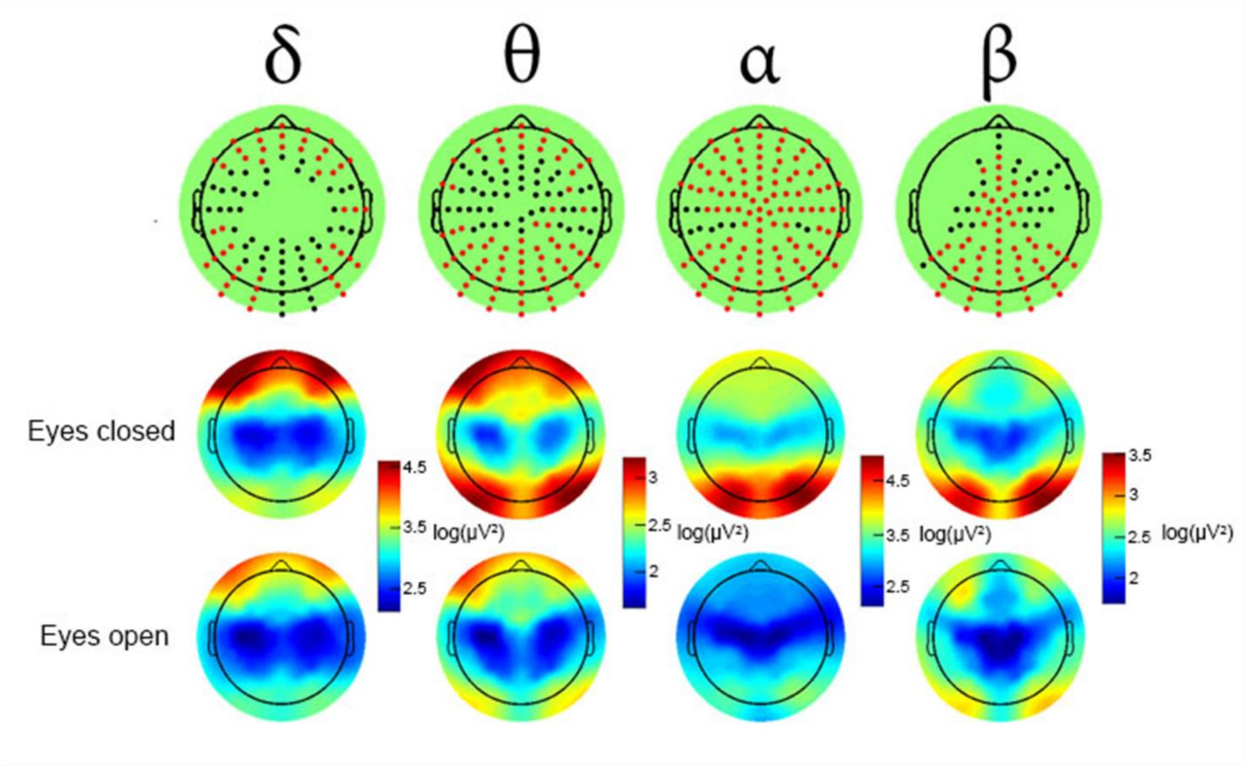


Figure 2.2 Resting-state changes associated with eye closure.

Color maps represent the average power across postures and tasks at each electrode with eyes closed and eyes open. Electrode map dots display sensors where three-way ANOVAs yielded a significant main effect of eye condition (black: $p < .05$; red: $p < .005$). Eye closure increased δ, Θ, α, and β power, but had no significant effect on gamma activity.

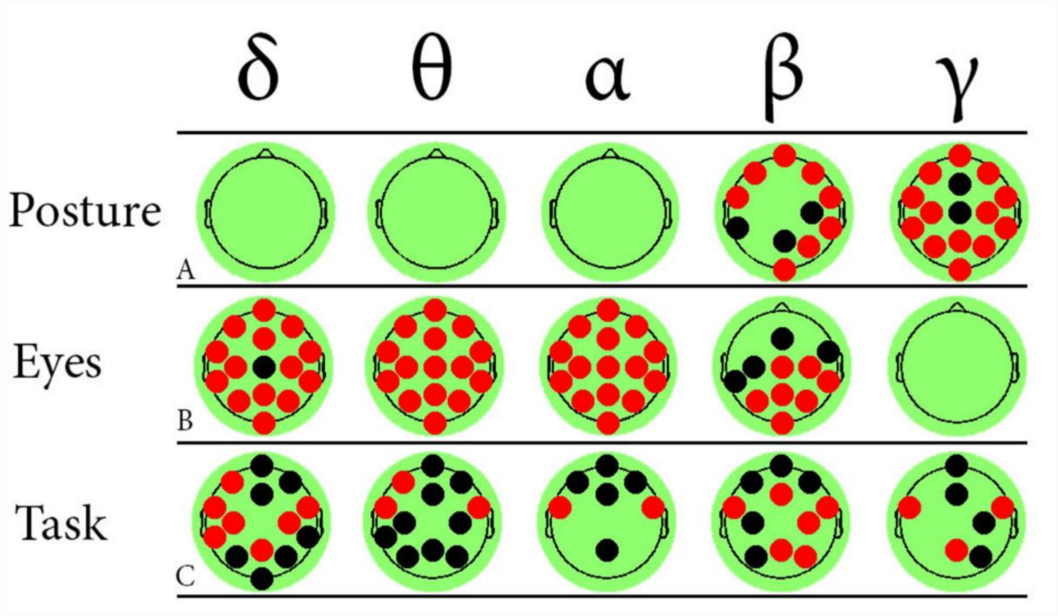


Figure 2.3 EEG changes in interpolated cortical regions.

Dots represent underlying cortical regions where activity differed between conditions of posture, eye closure, and task (black: p < .05; red: p < .005). Topographic maps display regional sources interpolated via a 3D dipole head model. The brain regions presented consist of ten lateral regions (i.e., temporal-anterior, temporal-posterior, frontal-lateral, central-lateral, and parietal-lateral) and five midline regions (i.e., pre-frontal, frontal, central, parietal, and occipital).

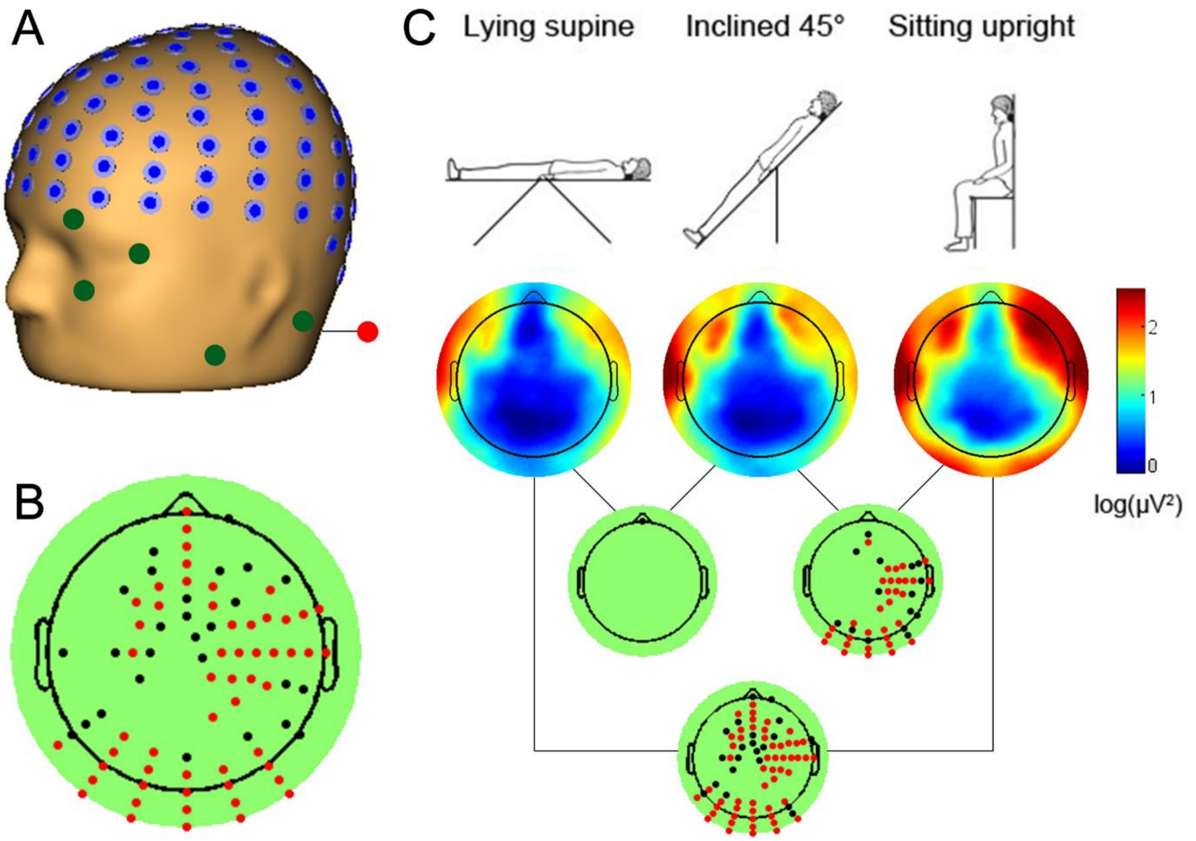


Figure 3. EMG and EEG related changes.

Dots represent sensors. Black and red dots show an increase in [gamma] power when moving toward upright postures. ***A.*** *Schematic depiction of the dense-array electrodes (light blue with a dark center) and six EMG electrodes where two-way ANOVAs yielded statistically significant (red: $p < .05$) and non-significant changes (green: $p > .1$) between postures in the gamma bandwidth.* ***B.*** *Same ANOVAs across EEG scalp electrodes (red: $p < .05$ and black: $p < .1$).* ***C.*** *Color maps represent the average power at each electrode for that particular posture. Small electrode maps show Tukey-corrected pairwise comparisons between select postures. ANOVAs for δ, Θ, α, and β bandwidths were not significant.*

Discussion

Our findings indicate that orthostatic condition rapidly influences high-frequency cortical activity. The most prominent alterations occurred over occipital and frontal brain regions. β and γ activity increased from laying supine to inclining at 45° and increased further when sitting upright. These changes manifested regardless of whether participants engaged in a cognitive task and irrespective of whether their eyes were open or closed. Changes appeared within 30 s and persisted for at least 16 minutes. Thus, our findings suggest a difference in baseline activity rather than transient event-related synchronizations or desynchronizations.

We obtained postural effects even for a small additional sample comprising the EEG data from six participants with EMGs. The EMG activity recorded from the trapezius changed across postures; both differential pressure on the electrode and increased neck tension across postures may account for this difference. However, muscle activity alone is unlikely to account for the present EEG findings: 1. While posture altered baseline gamma activity in the posterior of the neck (trapezius), all other measured muscles—lateral neck and superior jaw muscles (sternocleidomastoid and masseter) as well as muscles superior, lateral, and inferior to the eye (frontalis and orbicularis oculi)—remained unchanged; 2. We observed scalp-wide postural EEG effects; 3. Another muscle, the temporalis, located on the scalp superior to the ear, might also produce muscle artifact. While our EMGs did not measure temporalis activity, the EEG sensors did. However, many of the EEG electrodes located over the temporalis showed no differences across postures (Fig. 2.1 and Fig. 3B).

If the trapezius were responsible for the observed changes, we would have expected a gradient of postural EEG effects—greatest around occipital regions and diminishing further away, weakest towards frontal areas. However, our data are inconsistent with this pattern (Fig. 2.1). Moreover, moderate lateralization typifies our present findings of changes in gamma oscillations—a result difficult to attribute to neck tension because participants faced symmetrically forward in all postures. Thus, cortical activity appears primarily responsible for our results.

Two physiological mechanisms likely contribute to the influence of posture on electrical scalp activity: 1) alterations in cerebrospinal fluid (CSF) thickness and 2) changes in noradrenergic output. First, because CSF is highly conductive, minute shifts in CSF concentration can cause substantial alterations in EEG signals (Ramon et al., 2006; Ramon et al., 2004; Wendel et al., 2008). Using upright and recumbent MRI scanners, findings demonstrated that intracranial CSF concentration decreased when sitting up compared with lying down (Alperin et al., 2005). Thus, CSF scattering may influence the propagation and recording of high frequency cortical activity (Rice et al., 2013). Second, multiple reports suggest that altered noradrenergic output modulates EEG activity (Cole, 1989; Lipnicki, 2009; Schneider et al., 2008). When supine, gravity stimulates cardiopulmonary and arterial baroreceptors, reducing sympathetic system activation (Mohrman & Heller, 2003). This process decreases noradrenergic output from the locus coeruleus (Berridge & Waterhouse, 2003) and in turn dampens down cortical excitability (Rau & Elbert, 2001). Postural influences on EEG recordings, therefore, putatively involve alterations in both CSF thickness and noradrenergic output.

Head-direction neurons may also contribute to the observed changes between postures; however, this explanation is unlikely because head-direction cells are relatively insensitive to changes in the vertical planes (pitch and roll) and rely heavily on visual markers (Taube, 2007) which were absent in our visually uniform environment. Nonetheless, changes in vestibular inputs to head-direction cells (Yoder & Taube, 2014) may play some role in altering the recorded EEG signal. Future research relying on source localization would further elucidate the neural origin of posture-mediated EEG changes.

Triangulating data from converging methodologies would serve to illuminate the influence of posture on brain dynamics. Magnetoencephalography (MEG), for example, permits recording while sitting upright, reclining at a 0-90° angle, or laying supine—an advantageous feature for further characterizing neural patterns associated with body-position. MEG can complement other imaging modalities; for example, posture-induced changes in high-frequency cortical activity may confound fMRI data when investigating higher brain functions associated with β and γ oscillations (Siegel et al., 2012). Although upright MRI scanners for humans exist, they tend to employ low magnetic fields, which preclude fMRI sequences. Whereas posture may play an especially prominent role in regulating brain function in atypical populations such as the elderly (Edlow et al., 2010) and specific patient groups (Ouchi et al., 2005; Thompson et al., 2005), unraveling the effects of posture on the typical human brain has at least three broad implications: 1) Overcoming orthostatic caveats associated with distinct scanning environments; 2) Developing compensatory computational models to improve the specificity and generalizability of brain imaging; and 3) Providing insights into brain states that rarely lend themselves to imaging postures (e.g., in contemplative practices (Brewer et al., 2011; Tang et al., 2012)). Regardless of whether cortical sources, muscle artifacts, or other parameters influence changes in brain activity, our findings highlight the importance of considering posture when unraveling oscillatory dynamics in the human brain. Unlocking the influence of posture on neural processing would pave the road to a more scientific understanding of this pervasive, albeit little acknowledged, ecological nuance.

Article Three

Preface. Following our EEG results, we aimed to replicate and extend our findings with MEG. MEG has many benefits over EEG including a reference free recording, a higher density of sensors, improved superficial source analysis capacities, and less distorting of the signal due to cranial fluids and tissues. Because our original results found no interaction between posture, eye closure, and task engagement, our MEG experiment included only one condition—eyes open and no task—in three postures. To more closely reflect resting-state fMRI scans, we extended the recording time to 16 minutes in each posture. Our analyses aimed to replicate the sensor-level findings from our EEG study and examine a difference between the first and second 8-minute recording blocks. This publication is the first report, to our knowledge, that compares MEG data taken from different body postures. Thus, in addition to our primary goal of building on our EEG findings, we wrote a *caveats* section which highlights methodological consideration that future multi-posture MEG experimenters can benefit from considering. Due to the shortcomings of the algorithms designed to standardize head position relative to the sensors, the present sensor-level findings did not achieve the statistical significance apparent in our original EEG account.

Body position alters human resting-state:
Insights from multi-postural magnetoencephalography

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Abstract

Neuroimaging researchers tacitly assume that body-position scantily affects neural activity. However, whereas participants in most psychological experiments sit upright, many modern neuroimaging techniques (e.g., fMRI) require participants to lie supine. Sparse findings from electroencephalography and positron emission tomography suggest that body position influences cognitive processes and neural activity. Here we leverage multi-postural magnetoencephalography (MEG) to further unravel how physical stance alters baseline brain activity. We present resting-state MEG data from 12 healthy participants in three orthostatic conditions (i.e., lying supine, reclined at 45°, and sitting upright). Our findings demonstrate that upright, compared to reclined or supine, posture increases left-hemisphere high-frequency oscillatory activity over common speech areas. This proof-of-concept experiment establishes the feasibility of using MEG to examine the influence of posture on brain dynamics. We highlight the advantages and methodological challenges inherent to this approach and lay the foundation for future studies to further investigate this important, albeit little-acknowledged, procedural caveat.

Background

Cognitive neuroscientists rarely consider the influence body position wields on brain activity; and yet postural discrepancies hold important implications for the acquisition and interpretation of neuroimaging data (Raz et al., 2005). Moreover, converging evidence demonstrates that posture regulates physiological factors, including hemodynamics, and influences concomitant neurocognitive processing (Cole, 1989; Lipnicki & Byrne, 2005; Lundström et al., 2008; Ouchi et al., 2001; Spironelli & Angrilli, 2011). Such orthostatic variables take on particular significance as the field moves toward triangulating resting-state data from multiple imaging modalities involving different body stances (Agam et al., 2011). For example, whereas most functional magnetic resonance imaging (fMRI) scanners require participants to lie supine, occipital sensors impede pristine supine recordings with electroencephalography (EEG). Here we propose MEG as a promising imaging modality for elucidating how posture influences the temporal and spatial dynamics of the living human brain.

While a handful of fMRI studies report how environmental and contextual variables such as eye closure and gaze fixation alter the activity of resting state networks (RSNs) — i.e., networks of distributed brain regions demonstrating coherent activity at rest (Deco, Jirsa, & McIntosh, 2011; Yan et al., 2009) — these accounts shy away from addressing body-position as a potential caveat.

Posture likely influences the functional architecture of the resting brain (Lipnicki & Byrne, 2008; Lundström et al., 2008). Comparing postures using a stance-adjustable positron emission tomography (PET) gantry, studies have reported signal differences across a wide range of cortical and subcortical regions (Ouchi et al., 2005, 2001). In addition, a few studies have found changes in EEG as a function of posture (L.-J. Chang et al., 2011; Rice et al., 2013). Recent EEG findings, moreover, indicate that changes in orthostatic condition rapidly influence high-frequency electrical activity across the cortex (Thibault, Lifshitz, Jones, & Raz, 2014). In terms of physiology, gravity in the supine position stimulates baroreceptors that reduce sympathetic system activation (Mohrman & Heller, 2003), decreasing noradrenergic output from the locus coeruleus (Berridge & Waterhouse, 2003) and consequently dampening cortical excitability (Rau & Elbert, 2001). Furthermore, regardless of age, the supine posture associated with fMRI modulates respiration by altering diaphragm function (Rehder, 1998). This caveat holds special importance for confounds associated with independent component analysis (ICA)-based RSN measures (Birn et al., 2008). Such postural nuances come to the fore as researchers begin to compare supine fMRI findings with resting-state electrophysiological data from EEG and intracranial recordings typically acquired in the upright position (Agam et al., 2011; Lei et al., 2011; Lei, Hu, & Yao, 2012). Thus, understanding how posture alters resting-state brain activity permits a more judicious way to reconcile findings from disparate neuroimaging modalities and binds procedural nuances to the scientific investigation of neural processes.

MEG scanners permit recording while sitting upright, reclining at a 0-45° angle, or lying supine—an advantageous feature for characterizing neural patterns associated with body position. In contrast, although upright MRI scanners for humans exist, they tend to employ lower magnetic fields, which often preclude functional sequences. Furthermore, while previous posture studies employed either adjustable-gantry positron emission tomography (PET) or EEG, these methodologies lack integration of spatial and temporal signals. Whereas PET provides good (millimetric) spatial resolution but low temporal resolution, EEG offers millisecond temporal resolution but poor signal localization due to smearing of electrical signals when traveling through cephalic tissues to the scalp. In an EEG context, the highly conductive cerebral spinal fluid (CSF) causes a shunting effect that dampens the magnitude of electrical signals recorded at the scalp (Ramon et al., 2004; Rice et al., 2013; Wendel et al., 2008). In addition, this shunting effect propagates electrical currents through the CSF tangential to the scalp (Wolters et al., 2006). Because this tangential electrical current runs perpendicular to EEG electrodes, it exerts a negligible effect on the EEG signal. This electrical current, however, produces a circular magnetic fields that reaches MEG sensors. Thus, while magnetometers and gradiometers measure the intracellular currents from the dendrites of pyramidal cells both parallel and tangential to the scalp (Hillebrand & Barnes, 2002; Okada, Wu, & Kyuhou, 1997), they also record small additional magnetic fields originating from shunted currents in the CSF (Vorwerk et al., 2014). Otherwise, CSF and cephalic tissues leave magnetic signals emitted from the brain relatively undisturbed. Compared to EEG, therefore, in a MEG context CSF exerts an opposite effect on the magnitude of recorded brain signals (Vorwerk et al., 2014)—slightly increasing, rather than largely decreasing, the signal amplitude. Thus, MEG provides a useful complement to EEG studies of posture. In addition, advances in MEG source-localization and connectivity analysis permit fine-grained examination of temporospatial dynamics in the resting brain (de Pasquale et al., 2010). Such novel analytic approaches reveal MEG connectivity networks spatially congruent with classical fMRI RSNs. Furthermore, MEG may eventually permit researchers to examine temporal nuances otherwise difficult to probe with fMRI, including non-stationary dynamics among and within intrinsic connectivity networks — an emerging topic in resting-state research (de Pasquale et al., 2010; D. T. Jones et al., 2012). Comparing body positions with MEG, therefore, presents a powerful means of elucidating postural determinants of resting brain activity.

Here we present pilot findings from a MEG study comparing resting-state activity in three body postures — sitting upright, reclining at 45°, and lying supine. We hypothesized that our MEG findings would mirror previous multi-postural EEG results in which participants demonstrated widespread increases in beta and gamma activity in more upright postures (L.-J. Chang et al., 2011; Cole, 1989; Thibault et al., 2014). We highlight methodological issues inherent to this approach and explain how to control for such potential caveats. We submit our sensor-level analysis as proof-of-concept to encourage future analytic efforts to further unravel the influence body position imparts to resting-state network activity.

Materials and methods

Participants

Twelve participants (mean age = 26.4 ± 4.2 years; six females) provided written informed consent in accordance with the Research Ethics Board at the Montreal Neurological Institute and in compliance with the Code of Ethics of the World Medical Association—Declaration of Helsinki. Participants were right-handed, reported normal or corrected-to-normal vision, and received monetary compensation for their involvement.

Procedure

All sessions began with a 2-minute empty-room MEG recording. We then tested participants for magnetic artefacts in a brief preliminary MEG scan. Participants transitioned among three postures (sitting upright, sitting reclined at 45°, and lying supine; see Fig. 4) in a counterbalanced fashion. For each posture, participants underwent two eight-minute resting-state MEG scans separated by a brief (1-2 minute) verbal-response questionnaire concerning subjective experiences in the scanner (the present paper does not address the questionnaire data). Before each run we instructed participants to relax, stay still, and fixate on a point directly ahead while keeping their eyes open. We employed the eyes-open, rather than eyes-closed, condition to best match the present imaging context to everyday waking environments. Notably, recent findings from resting-state fMRI and EEG experiments demonstrate that the human brain assumes different default states when eyes are open rather than closed (Thibault et al., 2014; Xu et al., 2014). Accordingly, an eyes-closed paradigm may produce distinct results from the present eyes-open experiment. We standardized the visual environment by draping a white sheet around the immediate visual field.

Figure 4. *Posture and dewar positions*

Magnetoencephalography

We used the VSM/CTF system (MEG International Services Ltd.) at the Montreal Neurological Institute (McGill University, Quebec, Canada). The sensor array consisted of 275 axial gradiometers and an additional nine reference magnetometers and 17 reference gradiometers farther from the helmet to remove environmental noise. Recording used a sampling rate of 2400 Hz inside a magnetically shielded room (i.e., full 3-layer passive shielding). We used head-positioning coils and a 3-D digitizer system (Polhemus Isotrack) to register head position throughout. In line with standard guidelines, we recorded electrocardiograms (ECG) and electrooculograms (EOG) to capture heartbeat and eye-blink artifacts (Gross et al., 2013). Between postures participants left the scanning room while an experimenter adjusted the angle of the MEG dewar. We then waited 15 minutes to ensure that the liquid helium level outside the helmet had equalized and proceeded to conduct a two-minute empty-room recording to detect environmental noise. Based on tests conducted on the MEG system we used at the Montreal Neurological Institute, noise contamination from the sensors levels off within 15 minutes. While the helium boil-off rate increases when the dewar is horizontal, all sensors remain submerged in liquid helium and the temperature at each sensor is constant.

Data Processing

We processed and analyzed MEG data using *Brainstorm* (Tadel et al., 2011). Following the manufacturer's standard pre-processing (third-order gradient compensation), we applied a high-pass filter at 0.1 Hz and removed potential electrical contamination using a sinusoidal (notch) filter at 60, 120, 180, and 240 Hz. We then used the eye movement detection processes from *Brainstorm* to mark blink events based on EOG recordings from each participant. We designed a standard signal-space projector (SSP) in the 1.5-15 Hz frequency range and within ±200 ms of blink events to remove contamination from eye artifacts. Next, we discarded all data segments in which either of the two head localizer coils (left and right pre-auricular points) was farther than 5 mm from its position at the beginning of the recording. We set the threshold for excessive head motion at 5 mm. We chose this value in line with previous research (Brookes et al., 2011; B. W. Johnson, Crain, Thornton, Tesan, & Reid, 2010; Moradi et al., 2003; Poghosyan & Ioannides, 2007; Xiang et al., 2014) and the spatial precision of MEG, which lies around 5 mm (Moradi et al., 2003). We then detected heartbeats with an ECG recording and applied a standard SSP (13-40 Hz, ±40 ms) based on heartbeats events that occurred at least 250 ms from blink events to remove cardiac artifacts. Next, we visually inspected all data for muscle artifacts and discarded segments with transient high-amplitude and broadly distributed high-frequency activity. Lower-amplitude, sustained muscle activity persists in some recordings as is common in EEG and MEG data (Muthukumaraswamy, 2013). Lastly, we employed *Brainstorm* to calculate the average power-spectrum density (PSD) on each of the 275 MEG sensors, for delta (δ) 2-4 Hz, theta (θ) 4-8 Hz, alpha (α) 8-14 Hz, beta (β) 14-30 Hz, low-gamma (γ1) 30-58, and high-gamma (γ2) 62-90 Hz using 50% overlapping windows of two-seconds epochs. Here we conducted a sensor level analysis to extend our previous EEG effort (Thibault et al., 2014) and provide a direct comparison using MEG.

Statistical Analysis

Using Statistical Analysis Software 9.3 (SAS®), we performed two repeated measures full-factorial analyses of variance (ANOVA) on the logarithm of the absolute power (measured in fT^2) at each sensor for each bandwidth: (1) a two-way ANOVA (Posture x Run) on the data collected from participants, and (2) a one-way ANOVA (Posture) for the empty-room recordings. To account for multiple comparisons, we calculated an adjusted p-value (q-value) for each dimension of the ANOVA at each bandwidth using positive false discovery rate (Storey, 2002). We corrected all pairwise comparisons using Tukey’s Honest Significant Difference Test (Westfall & Tobias, 1999). Using SAS® we confirmed normality and homogeneity of variance in each analysis.

Results

We found a main effect of posture on high-gamma activity over left frontal and left temporal cortex (Fig. 5). High-gamma power increased in these regions when sitting compared to when reclined or supine (Fig. 5 C-D), but did not differ between reclined and supine postures (Fig. 5 E). Differences in delta, theta, alpha, beta, and low-gamma activity between postures lacked significance. We found no difference between the two runs in each posture for any bandwidth.

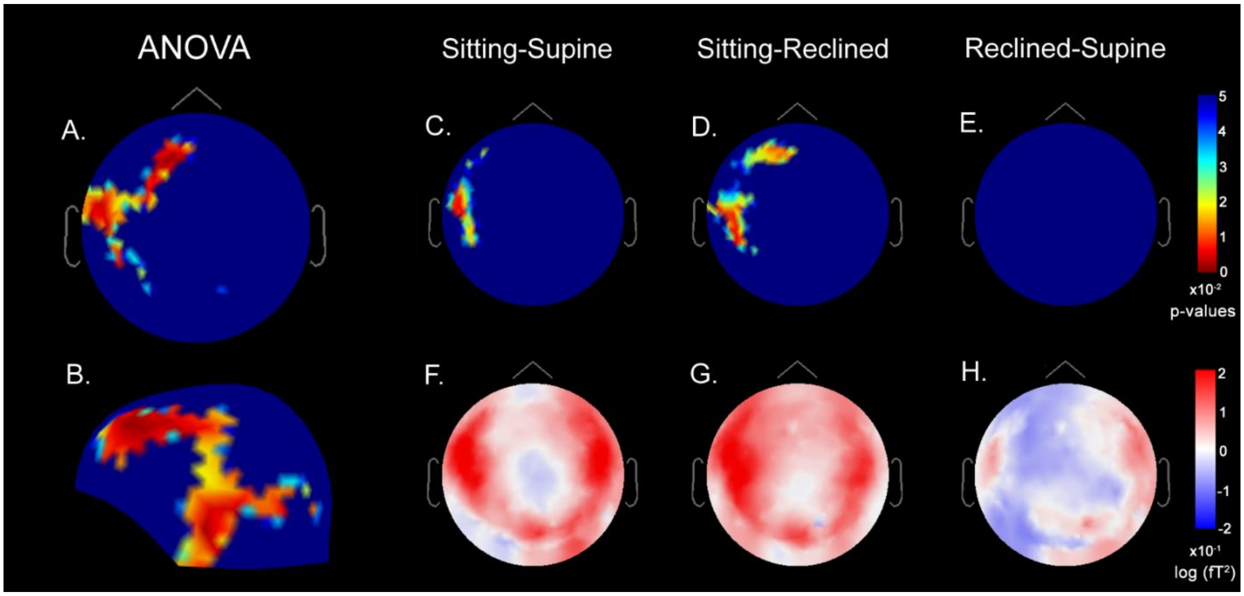

Figure. 5 High-gamma activity differs across postures

A. *Color map depicting scalp regions where two-way ANOVAs yielded statistically significant (red: $p < .01$ to light blue: $p < .05$) and non-significant changes (dark blue: $p > .05$) across postures.* ***B.*** *The same ANOVA results mapped onto a 3-dimensional depiction of the MEG helmet (viewed from the left side).* ***C-E.*** *Heat maps shows Tukey-corrected pairwise comparisons between specific postures. Any color other than dark-blue represents an increase in power while sitting upright.* ***F-H.*** *Maps depicts the average power differences between specific postures. Red indicates an increase in power when more upright whereas blue indicates a decrease in power when more upright.*

In the empty-room recordings, ANOVAs revealed a main effect of dewar position on seven of the 275 sensors in the high-gamma range only (Fig. 6). Two of the sensors displaying significant changes between postures in the empty-room recordings also showed significance in the participant analysis. However, pairwise Tukey-comparisons revealed that in the case of empty-room recordings, statistically significant differences arose between supine and reclined postures only, whereas in the participant analysis changes occurred between sitting and supine or sitting and reclined, but not between supine and reclined.

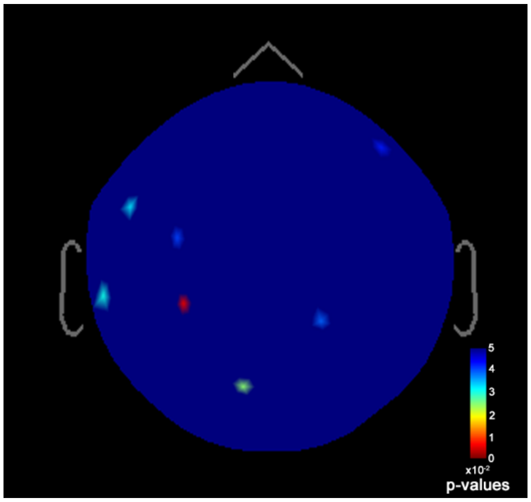

Figure 6. Empty-room ANOVA results

This figure shows the seven sensors that differed in high-gamma power across dewar positions in the empty-room recordings.

Discussion

We present the first demonstration of using MEG to compare resting-state brain activity in multiple postures. Our results suggest that variations in posture perturb resting-state neurophysiology. High-gamma (62-90 Hz) activity increased over left frontal and left temporal regions when participants sat upright compared to when sitting reclined or lying horizontal (Fig. 5). The first and second runs were comparable, suggesting a change in baseline activity rather than a transient event-mediated effect. These findings have direct relevance for comparisons between upright EEG recordings and supine fMRI scans. EEG experiments have implicated gamma band activity in a host of cognitive processes including attention and memory (Jensen, Kaiser, &

Lachaux, 2007). The BOLD signal, which serves as a proxy for neural activity, as ascertained by fMRI measurements, correlates tightly with synchronized gamma activity (Niessing et al., 2005; Nir et al., 2007; Shmuel & Leopold, 2008). Our demonstration that postural manipulation is sufficient to amplify spontaneous neural activity warrants caution in interpreting results between imaging modalities that tend to employ different postures (i.e., EEG and fMRI). In particular, these results likely bear on studies examining resting state recordings of neural activity. Researchers might uncover distinct RSNs based on the posture assumed in a given experiment. To overcome this potential caveat, researchers attempting to compare EEG, MEG, and fMRI data could conduct simultaneous recordings with an MRI compatible EEG system or record MEG in the supine posture. Complementing previous accounts from EEG (L.-J. Chang et al., 2011; Thibault et al., 2014) and PET (Ouchi et al., 2005, 2001), the present findings indicate that resting-state neuroimaging data differs when sitting upright compared to when lying down supine.

Of the various physiological mechanisms contributing to high-gamma activity, our data suggest that changes in local cortical activity may account for the posture-mediated differences recorded at the sensors. In addition, contamination due to muscle activity might also contribute to our recordings because it pervades EEG and MEG signals in the gamma range (Muthukumaraswamy, 2013). Frontalis muscles peak around 20-30 Hz and temporalis muscles at 40-80 Hz (Goncharova, McFarland, Vaughan, & Wolpaw, 2003). Based on the unilaterality of our results, however, it appears unlikely that muscle contamination accounts for the present results. Examining the differences in high-gamma activity between postures at the individual level reveals that bilateral frontal, temporal, and occipital activity typical of muscles artifacts (Goncharova et al., 2003) is largely absent (Fig. 7). Nonetheless, unilateral significance does not imply significance of unilaterality. Thus, we cannot completely rule out muscle contamination as a contributing factor. Indeed, visual inspection of Figure 5 (F-G) intimates that high-gamma increased in both hemispheres when more upright; yet, this effect was smaller and statistically non-significant in the right hemisphere. We recently ran a comparable experiment using EEG and EMGs and found that posture influenced neither lateral neck and superior jaw muscles (sternocleidomastoid and masseter) nor muscles superior, lateral, and inferior to the eye (frontalis and orbicularis oculi) (Thibault et al., 2014). While in that previous study an EMG placed on the trapezius recorded an increase in muscle activity when sitting upright, we would not expect frontal and temporal artifacts to originate from the trapezius. Instead we would expect such potential muscle contamination to generate a gradient of postural EEG effects—greatest around occipital regions and diminishing further away, weakest towards frontal areas. However, our data are inconsistent with this pattern (Fig. 5).

One recent EEG study (Rice et al., 2013) postulated that posture-mediated changes in CSF thickness may be the key mechanism underlying alterations in gamma oscillations. In the present experiment, however, we observed significant MEG changes over the left hemisphere only; yet, body-tilt is unlikely to prompt unilateral changes in CSF thickness across participants. Indeed, heat maps comparing postures within individual participants lack a clear bilateral effect we might have expected if differences in CSF influenced the MEG signal (Fig. 7). As we discuss above, nonetheless, unilateral significance does not necessarily imply significance of unilaterality.

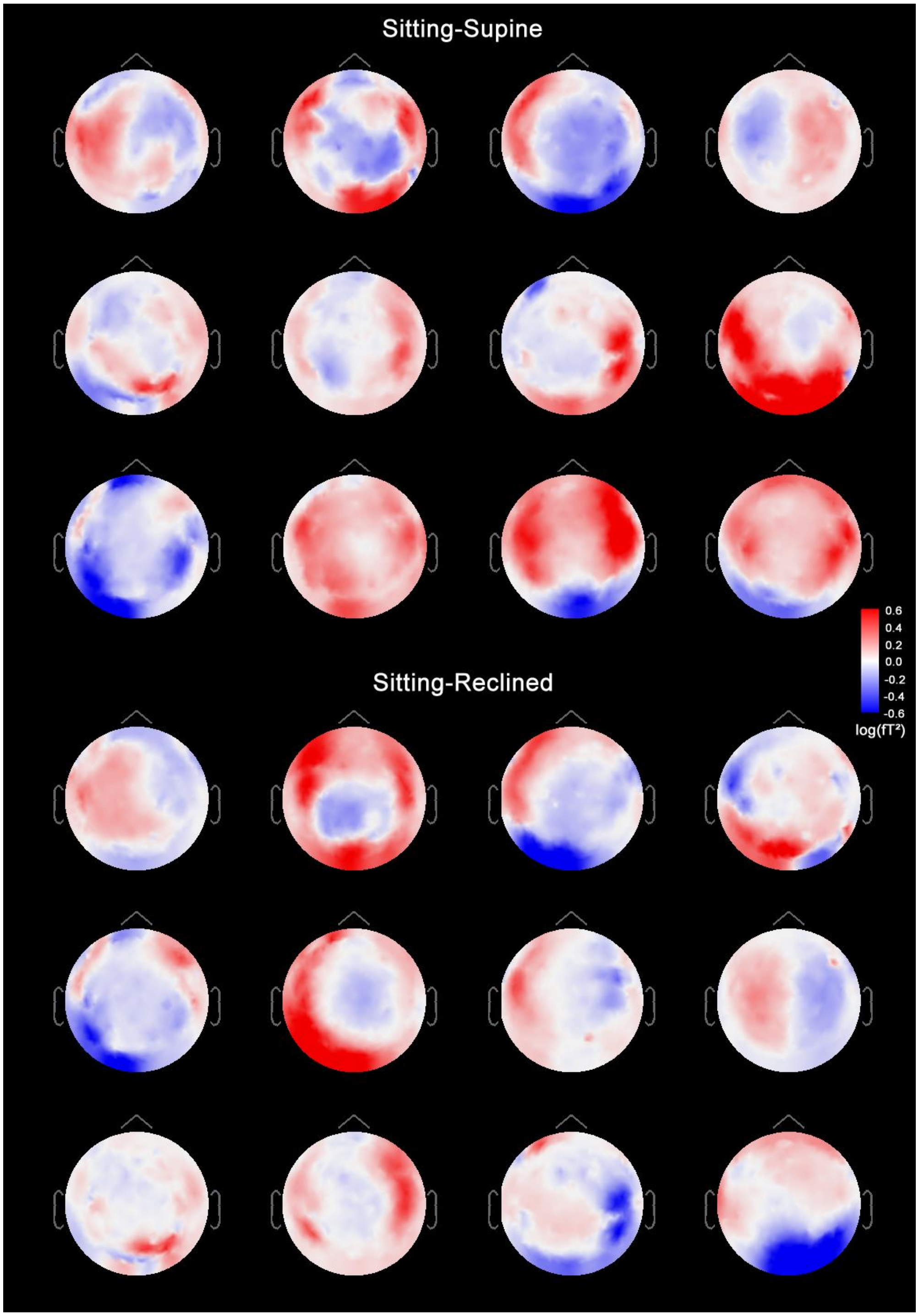

Figure 7. Individual differences in high-gamma

Heat maps depict the difference in high-gamma power for each of the 12 participants between sitting and supine postures and sitting and reclined postures.

The relationship between CSF thickness and multi-posture MEG is poorly understood. While CSF thickness distorts the topography of electric and magnetic signals comparably, this cephalic fluid increases the magnitude of MEG data only slightly while decreasing the magnitude of EEG data substantially (Vorwerk et al., 2014). One experiment leveraged upright and recumbent MRI scanners to demonstrate that total intracranial CSF decreases when upright compared to when supine as gravity draws fluids downward into the spinal canal (Alperin et al., 2005). Given these previous findings, we might expect a widespread decrease in MEG gamma activity when upright, paralleling the decrease in total intracranial CSF. However, our results diverge from this pattern (Fig. 5). Another recent study highlighted the spatial specificity of posture-related CSF thinning. This account demonstrated that, when supine, occipital CSF thins by up to 30% compared to when prone (Rice et al., 2013). However, this study did not include an upright condition, likely due to the sparse availability of erect MRI scanners. Thus, the relative thickness of frontal and occipital CSF between upright and supine postures remains elusive. Multi-posture simultaneous EEG/MEG recordings could shed light on how body position and CSF shifting differently affect magnetic and electric brain signals.

We observed postural effects over the inferior and dorsolateral frontal gyri, the lateral sulcus, and the supramarginal gyrus of the left hemisphere across participants (Fig. 5B) and within almost all individuals (Fig. 7). These cortical regions contain major speech centers, including Broca’s and Wernicke’s areas, as well as auditory cortex. As all our participants were right-handed, lateralized results may suggest that posture influenced language faculties. Yet, the precise locus of activity change remains undetermined as sensors lateral to, rather than above, the neuronal source measure the field maxima (Bastiaansen & Knösche, 2000).

Future experiments incorporating source-level analysis, phenomenological experience-sampling, or behavioral tasks, will likely further unravel the intricacies underlying multi-postural brain data. We hope to report on such efforts before long. Taken together, our multi-posture MEG findings corroborate previous EEG and PET reports and highlight posture as a determinant of neuroimaging data.

Caveats

The present MEG results differ from previous EEG data collected from similar experiments. While EEG efforts demonstrated high-gamma, low-gamma, and beta modulation, our MEG analysis revealed high-gamma alterations only. Whereas EEG electrodes rest directly on the scalp and thus limit variations in brain-to-electrode distance across participants, MEG brain-to-sensor distances range widely depending on head size and position in the helmet. As the magnetic field decays exponentially with distance from the source, brain-to-sensor distance may encourage large inter-subject and inter-run variance, potentially masking posture-mediated power modulation. Thus, the present MEG results may depict only the most salient effects observed in previous multi-postural EEG experiments. We attempted to control for this variable by co-registering head placement relative to helmet position for all 72 runs (12 participants x 3 postures x 2 runs). We found that current software, however, is unable to effectively transform data with notable variations in brain-to-sensor distance across 72 runs. Nonetheless, differences in brain-to-sensor distance across postures are unlikely to account for our findings because we observed largely unilateral changes. Decreased brain-to-sensor distance for the left hemisphere would correspond to increased brain-to-sensor distance for the right hemisphere. Under such circumstances we would expect opposing directions of high-gamma modulation between hemispheres, a pattern incongruent with our group level results (Fig. 5 F-G). At the individual level, however, a few heat maps show opposing differences in high-frequency power between postures in the right and left hemispheres (Fig. 7). A slightly lateralized head position between postures may have contributed to these participant heat maps. Between-subject variations in brain-to-sensor distance likely decreased statistical power and may have masked potential difference in magnetic activity. In the future, more advanced helmet co-registration algorithms would likely permit explorations of sensor-level effects. Source analyses, which register data from multiple runs to a common source-space referential, would also serve to reveal additional spatial information.

Head motion might also affect our results. To account for this possibility, we excluded epochs with head positions greater than 5 mm from the initial position. Notably, excessive head displacement occurred in only three sitting runs and one reclined run. Some participants may slouch during recording in upright and reclined positions, thus causing a substantial shift in head position (Gross et al., 2013). This finding suggests the supine posture may best serve researchers aiming to minimize head movements. Moreover, whereas in certain neuroimaging contexts small head movements, even those that survive standard motion correction, can generate spurious resting-state findings (e.g., fMRI functional connectivity; Power et al. 2012), in the present MEG context head movements likely increased variance in the topography and amplitude of the MEG signal and decreased statistical sensitivity (Stolk, Todorovic, Schoffelen, & Oostenveld, 2013). Such minor head movements may have obfuscated the effects we previously reported in an EEG context wherein electrodes retain a consistent position directly against the scalp (Thibault et al., 2014).

The angle of the head compared to the MEG helmet may have differed slightly across postures. Variation in head orientation can alter the geometric relationship between a specific sensor and the underlying anatomy (i.e., the position of a specific sulcus relative to the sensor) and consequently impact the amplitude of the measured signals (Okamoto et al., 2004). In future efforts, standardizing head position across postures and across participants using head localizer coils may help obviate this potential caveat.

Finally, as all our participants were right handed, muscle contamination and head position may have introduced different artifacts at sensors above the right and left hemispheres. Yet, any effect of handedness on the laterality of muscle activity or head position would likely persist within a given participant across all postures. Such an effect would have had a negligible impact on our results because we analyzed MEG differences across postures, not between hemispheres. However, if right-handed people consistently increase unilateral muscle tension, or tilt their heads to one side, when lying down but not when sitting upright, this would present a potential confound. We are not familiar with any research supporting this possibility.

Conclusion

Our present effort demonstrates how MEG can illuminate the influence posture wields on the resting human brain. MEG affords a powerful means of comparing multiple body positions in the same imaging modality. Our piece addresses the methodological issues inherent to neuroimaging studies of posture and highlights the benefits of our approach. Furthermore, we present a sensor-level analysis, laying the foundation for follow-up analytic efforts to further probe how body position alters fine-grained oscillatory dynamics within the resting brain. Unlocking the influence of posture on neural processing would account for the orthostatic parameters associated with distinct scanning environments and pave the road to a more scientific understanding of this pervasive, albeit little acknowledged, procedural nuance.

Article Four

Preface. This experiment took additional measures to extend our sensor-level MEG and EEG findings. To overcome differences in head-to-sensor distance in MEG research, we acquired anatomical MRI scans, digitized each participant’s head shape with hundreds of sample points in relation to a few head-positioning electrodes, and conducted analyses at the source-level, which use information from all the magnetometers and incorporates the relative distance from each sensor to each digitized head point. We replicate the main high frequency findings from our EEG experiment and find additional changes in low frequency activity—potentially associated with the longer time participants held each posture. The source analysis further allowed us to identify more specific brain regions that may hold responsible for the sensor-level differences seen in our EEG experiment. Two EEG studies, which were published after we submitted our results for this article, support both our low frequency (Spironelli et al., 2016) and high frequency findings (Spironelli & Angrilli, 2017).

Source-localization of brain states associated with canonical neuroimaging postures

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Abstract

Cognitive neuroscientists rarely consider the influence that body position exerts on brain activity; yet, postural variation holds important implications for the acquisition and interpretation of neuroimaging data. Whereas participants in most behavioral and electroencephalography (EEG) experiments sit upright, many prominent brain imaging techniques—e.g., functional magnetic resonance imaging (fMRI)—require participants to lie supine. Here we demonstrate that physical comportment profoundly alters baseline brain activity as measured by magnetoencephalography (MEG)—an imaging modality that permits multi-postural acquisition. We collected resting-state MEG data from 12 healthy participants in three postures (lying supine, reclining at 45°, and sitting upright). Source-modeling analysis revealed a broadly distributed influence of posture on resting brain function. Sitting upright versus lying supine was associated with greater high-frequency (i.e., beta and gamma) activity in widespread parieto-occipital cortex. Moreover, sitting upright and reclined postures correlated with dampened activity in prefrontal regions across a range of bandwidths (i.e., from delta to low gamma). The observed effects were large, with a mean Cohen's *d* of .95 (SD = .23). In addition to neural activity, physiological parameters such as muscle tension and eye blinks may have contributed to these posture-dependent changes in brain signal. Regardless of the underlying mechanisms, however, the present results have important implications for the acquisition and interpretation of multimodal imaging data (e.g., studies combining fMRI or PET with EEG or MEG). More broadly, our findings indicate that generalizing results—from supine neuroimaging measurements to erect positions typical of ecological human behavior—would call for considering the influence that posture wields on brain dynamics.

Introduction

Neuroimaging researchers typically assume that body position has a negligible impact on human brain activity. However, postural discrepancies may hold important implications for brain function in general and for specific imaging methodologies in particular (Raz et al., 2005; Thibault & Raz, 2016). Behavioral findings intimate that body posture alters perceptual thresholds and cognitive processing (Lipnicki & Byrne, 2008; Lundström et al., 2008). Moreover, converging evidence demonstrates that posture regulates physiological factors, including hemodynamics, and influences concomitant neurocognitive function (Ouchi et al., 1999; Chang et al., 2011; Fardo, Spironelli, & Angrilli, 2013; Rice et al., 2013; Cole, 1989; Thibault et al., 2014, 2016; Spironelli & Angrilli, 2011; Spironelli et al., 2016; Benvenuti, Bianchin, & Angrilli, 2013). Comparing postures using a stance-adjustable position emission tomography (PET) gantry, one study reported signal differences across a range of cortical and subcortical regions (Ouchi et al., 1999). In addition, a few studies have found changes in electroencephalography (EEG) signals as a function of posture (Chang et al., 2011; Rice et al., 2013; Fardo et al., 2013; Cole, 1989; Spironelli & Angrilli, 2011; Spironelli et al., 2016; Benvenuti et al., 2013). An EEG effort from our group indicated that orthostatic condition rapidly influences high-frequency electrical activity across the cortex (Thibault et al., 2014). In addition, we recently published a proof-of-concept analysis based on the present multi-postural magnetoencephalography (MEG) data-set (Thibault, Lifshitz, & Raz, 2016). However, this preliminary sensor-level analysis could hardly elucidate how body position influences neural activity in specific anatomical areas. Thus, here we used a source-localization approach to further examine the effects of posture at the level of regional brain function.

Body posture may impact neural function through a variety of physiological mechanisms. Gravity in the supine position stimulates baroreceptors that reduce sympathetic system activation (Mohrman, 2003), decreasing noradrenergic output from the locus coeruleus (Berridge & Waterhouse, 2003) and consequently dampening cortical excitability (Rau & Elbert, 2001). In addition, supine posture modulates respiration, regardless of age, by altering diaphragm function (Rehder, 1998). This caveat holds special import for independent component analysis (ICA)-based measures of resting-state functional connectivity, which show substantial respiratory confounds (Birn et al., 2008). Such postural nuances come to the fore as researchers increasingly compare supine functional magnetic resonance imaging (fMRI) findings with resting-state electrophysiological data from EEG and intracranial recordings, often acquired in the upright position (Agam et al., 2011; Lei et al., 2012; Lei et al., 2011).

MEG is advantageous for studying the effects of posture on brain activity because certain MEG systems offer scanning capabilities across a range of body positions (see Fig. 4). In contrast, although upright MRI scanners for humans exist, they tend to employ low magnetic fields, and often preclude functional sequences. Moreover, whereas previous studies of posture used either PET or EEG, these methodologies lack integration of high-resolution spatial and temporal signals. On the one hand, PET provides reasonable spatial resolution but crude temporal resolution via an indirect measure of neural activity. On the other hand, EEG directly measures brain oscillations with millisecond precision but offers poorer signal localization due to smearing of electrical signals when passing through the cranial fluids and tissues (Vorwerk et al., 2014). Here we leveraged MEG localization analysis, which offers a direct measure of oscillatory activity with high spatiotemporal accuracy, to unravel the influence of body position on regional activity throughout the cortex.

Materials and methods

Participants

Twelve participants (mean age = 26.4 ± 4.2 years; six females) provided written informed consent in accordance with the Research Ethics Board at the Montreal Neurological Institute and in compliance with the Declaration of Helsinki. Participants were right-handed, reported normal or corrected-to-normal vision, and received customary monetary compensation for their involvement.

Procedure

All sessions began with a two-minute empty-room MEG recording. We then tested participants for magnetic artefacts in a brief preliminary MEG scan. For the main portion of the experiment, participants transitioned among three postures (sitting upright, reclining at 45°, and lying supine) in a counterbalanced fashion. For each posture, participants underwent two 8-minute resting-state MEG scans, separated by a brief (1 - 2 minute) break in the scanner. Throughout the MEG acquisitions, we instructed participants to relax, remain still, and fixate on a point directly ahead while keeping their eyes open. We standardized the visual environment by draping a white sheet around their visual field.

Magnetoencephalography

We acquired MEG data using the VSM/CTF system (MEG International Services Ltd.) at the Montreal Neurological Institute. The sensor array consisted of 270 axial gradiometers plus an additional nine reference magnetometers and 17 reference gradiometers farther from the helmet to remove environmental noise. We recorded using a sampling rate of 2400 Hz inside a dedicated scanning room with full 3-layer passive magnetic shielding, while head-positioning coils and a 3-D digitizer system (Polhemus Isotrack) registered cephalic position throughout. In line with standard guidelines, we recorded electrocardiograms (ECG) and electrooculograms (EOG) to capture heartbeat and eye-blink artifacts (Gross et al., 2013). Between postures participants left the scanning room while an experimenter adjusted the angle of the MEG dewar. We then waited for 15 minutes, followed by a two-minute empty-room recording, to ensure that the liquid helium level outside the helmet and the temperature at the sensors had stabilized. Based on tests of our MEG system at the Montreal Neurological Institute, we determined that noise contamination from the sensors levels off within 15 minutes (Figure 8 displays empty room and participant-scan noise spectra for all dewar positions and body postures). Whereas the helium boil-off rate increases when the dewar is in the supine recording position, all sensors remain submerged in liquid helium and the temperature at each sensor remains constant.

Before the scans we placed foam blocks between the helmet and the forehead of participants to help reduce head motion, if needed. The exact placement of these foam blocks depended on the size and shape of the individual head. We instructed participants to position their head such that they were touching but not pressing against the top of the helmet. Recently acquired T1-weighted anatomical MRI volumes helped map head position relative to the helmet. To facilitate the analysis, we down-sampled the high-resolution triangulated cortical surfaces to 15,000 vertices in line with standard protocol (Baillet et al., 2001).

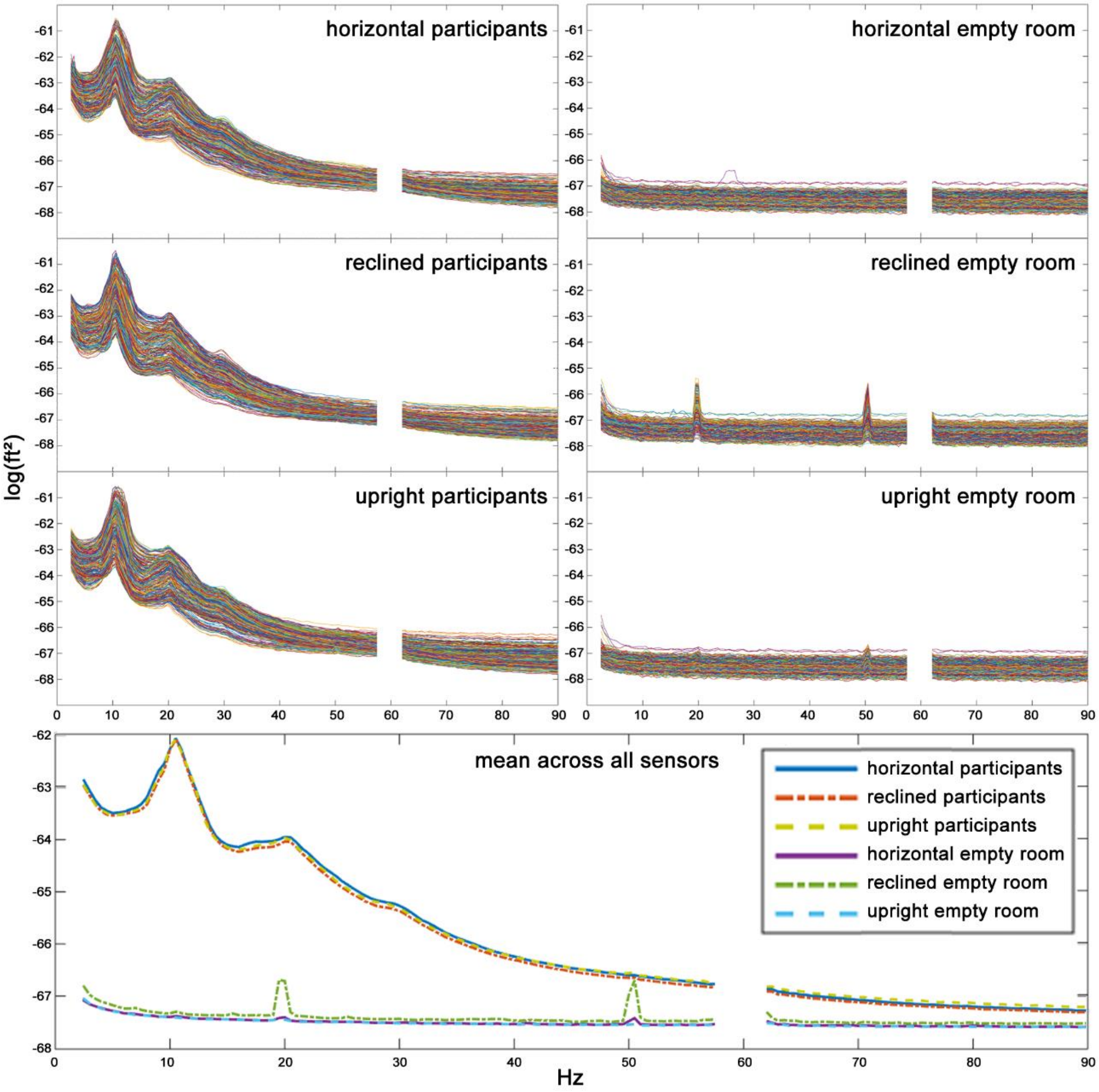

Figure 8. Noise spectra for participant and empty room recordings

The top six graphs depict the power spectrum densities for each of the 270 gradiometers averaged across all runs for each posture (for participant recordings, on the left) and each dewar position (for empty room recordings, on the right). The bottom graph depicts the average across all 270 gradiometers for each of the above six conditions. As in our analysis, in this graph we removed frequencies below 2 Hz as well as electrical contamination from 58-62 Hz. When performing our source analysis we removed the environmental noise detected prior to each participant recording by accounting for an empty-room noise covariance matrix. For example, this analysis regressed out the two blips around 20 Hz and 50 Hz in the reclined empty room condition.

Data processing

We processed and analyzed MEG data using *Brainstorm* (Tadel et al., 2011). We applied a high-pass filter at 0.1 Hz and removed potential electrical contamination using a sinusoidal (notch) filter at 60, 120, 180, and 240 Hz. We then removed cardiac sources and contamination from eye blinks and eye movements by designing signal-space projectors (SSPs). Each SSP was specific to a particular run. We removed one cardiac and one blink SSP from each run in order to maintain comparable cleaning procedures and levels of background data subtracted between postures. We then visually inspected all data and discarded segments with any lingering ocular or cardiac contamination as well as high-amplitude muscle artefacts. We discarded data segments in which either of the two head localizer coils (left and right pre-auricular points) was farther than five millimeters from its position at the beginning of the recording; on average, participants moved their head less than two millimeters by the end of the recording (see Fig. 9). We calculated a noise covariance matrix from each of the 36 empty-room recordings (i.e., 12 participants by three postures). Each baseline noise recording was then applied to the corresponding participant recording to tease apart fluctuations in instrumental and environmental dynamics that the sensors detected in the empty room (Tadel et al., 2011). This procedure minimizes the potential influence of noise differences associated with different dewar positions.

We computed a head model of the cortex surface for each run using overlapping spheres, and proceeded to compute sources using the whitened and depth-weighted linear L2-minimum norm estimates (wMNE) algorithm implemented in *Brainstorm*. To normalize sources across participants, we projected (warped) the sources from each participant onto the *MNI/Colin27* template brain (Collins et al., 1998). The algorithms responsible for this transformation from sensor-level data to source-space activity take into account head placement in relation to sensor location and thus compensate for differences in head size between participants and head placement across runs. We then calculated the power-spectrum density (PSD) for each run at all 15,000 vertices on the template brain for delta (δ) 2-4 Hz, theta (θ) 4-8 Hz, alpha (α) 8-14 Hz, beta (β) 14-30 Hz, low-gamma (γ1) 30-58, and high-gamma (γ2) 62-90 Hz using 50% overlapping windows of two-second epochs. We then divided these 15,000 vertices into 68 cortical regions as per the Desikan-Killiany neuroanatomical atlas (Desikan et al., 2006). We averaged the PSDs across all the vertices in each scout to obtain 68 averaged PSDs.

Statistical analysis

We first calculated the average of the two runs for each participant in each posture. Using the R statistics package, we conducted two-tailed paired sample t-tests on the logarithm of the power of the current density for each Desikan-Killiany region (Desikan et al., 2006) for each bandwidth, for a total of 408 (68 regions by six bandwidths) p-values per contrast (i.e., sitting upright vs. lying supine, sitting upright vs. reclining at 45°, reclining at 45° vs. lying supine). To account for multiple comparisons, we calculated adjusted *p*-values (*q*-values) using the false discovery rate function from the *qvalue* package available in R (Storey et al., 2015) for each of the three contrasts. For the empty-room recordings, we repeated this analysis for the PSD values obtained from each magnetic sensor, rather than from the Desikan-Killiany regions used for the participant recordings (due to the absence of a head in the dewar), and found no statistical difference between postures. We also performed one-tailed paired sample t-tests on heart rate for each contrast.

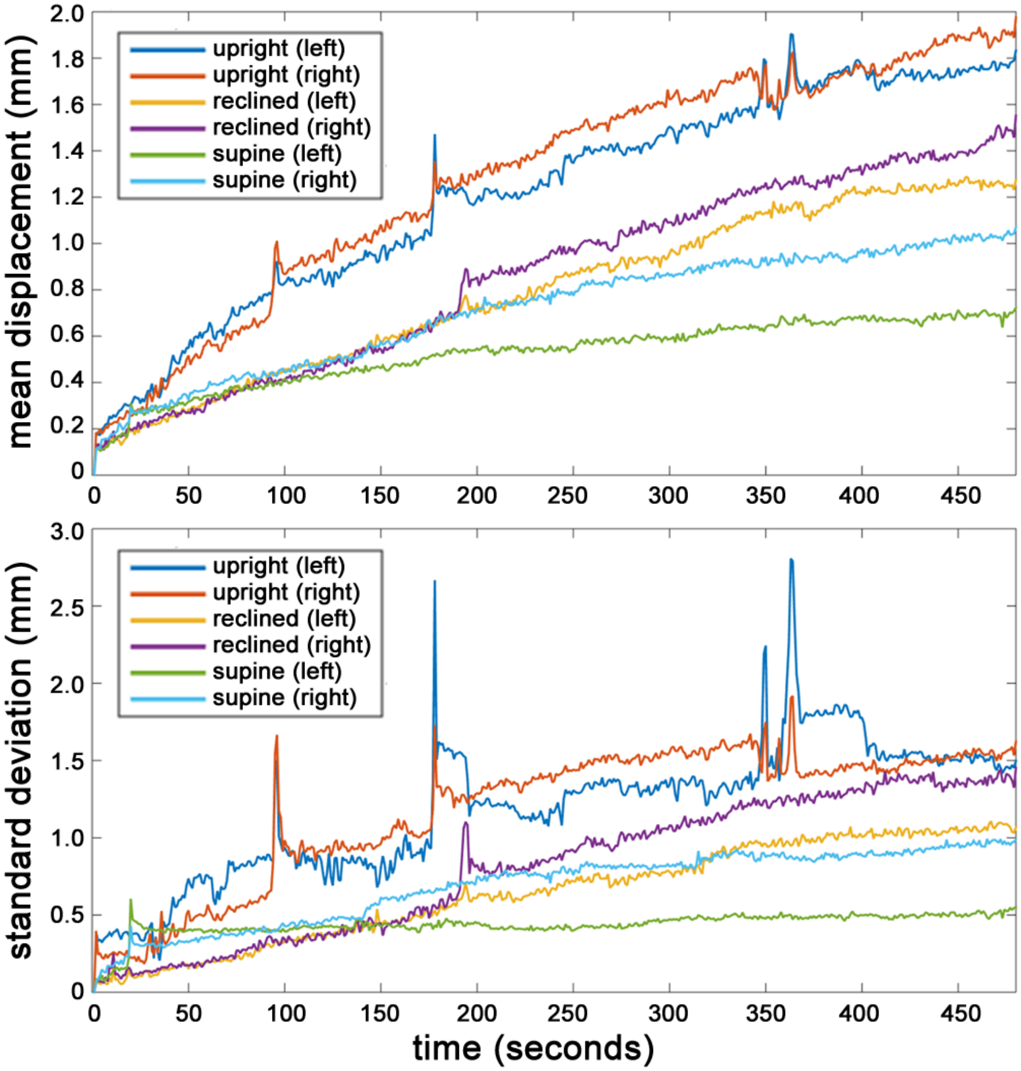

Figure 9. Head displacement in upright and supine postures

This figure displays, as a function of posture, the means and standard deviations in head displacement of the left and right auricular head localizer units at every second of the 480 second (eight-minute) recordings. On average, participants displaced their head by about twice as much when sitting upright (left: 1.7 mm, right: 2.0 mm) compared to when lying supine (left: 0.7 mm, right: 1.1 mm). However, mean head displacements in all postures remained well below the threshold (~5 mm) that would call for repositioning the head or initiating a new head position file in standard MEG analysis practice (Gross et al., 2013; Whalen et al., 2008). Longer recordings and particular populations (e.g., children: Wehner et al., 2008) increase the likelihood of greater *head displacement. In such experiments, posture may prove especially pertinent with respect to head movement.*

Results

Our main contrast of interest investigated differences in oscillatory power across the whole brain between sitting upright and lying supine. For this contrast, we conducted 408 t-tests (68 scout regions by six bandwidths). Of these tests, 76 yielded significant differences in brain signal (corrected for multiple comparisons, $q < .05$). Figure 10 displays the significant brain regions and frequency bands for the contrast between sitting upright and lying supine. Table 1 further lists the anatomical label, effect size, and amplitude difference for each of the significant regions at each bandwidth. The mean Cohen's d for these significant effects was .87 (SD = .28), indicating large effect sizes.

In addition to our primary analysis, we also investigated power differences associated with reclining by conducting two contrasts (408 t-tests for each): (1) reclining vs. lying supine, and (2) reclining vs. sitting upright. In the reclined vs. supine contrast, 16 of the 408 t-tests yielded significant changes in brain signal (corrected for multiple comparisons, $q < .05$; see Table 2). The effects were large, with a mean Cohen's *d* of 1.33 (SD = .28). Although this mean effect size was notably larger than in the sitting upright vs. lying supine contrast, the amplitude of the changes was similar (compare Tables 1 and 2). Thus, the difference in effect size likely reflects a difference in variance. When comparing between sitting upright and reclining we found a significant difference in only one region at one bandwidth.

Heart rate was greater in more upright postures (sitting upright: 70.7 beats per minute; reclining: 68.8 bpm; lying supine: 64.6 bpm). Using a Bonferroni corrected $\alpha = .017$, only the difference between sitting upright and lying supine ($p < .001$, $d = 1.33$) and reclining and lying supine ($p = .015$, $d = .72$) met significance (sitting upright vs. reclining: $p = .05$, $d = .52$). As an exploratory post-hoc analysis, we tested whether between-posture differences in heart rate correlated with between-posture differences in oscillatory power (using Pearson's correlation coefficients at each neuroanatomical region and bandwidth). These analyses yielded no significant correlations, yet the results remain inconclusive because the relationship between heart rate and brain activity may be non-linear and our analysis underpowered.

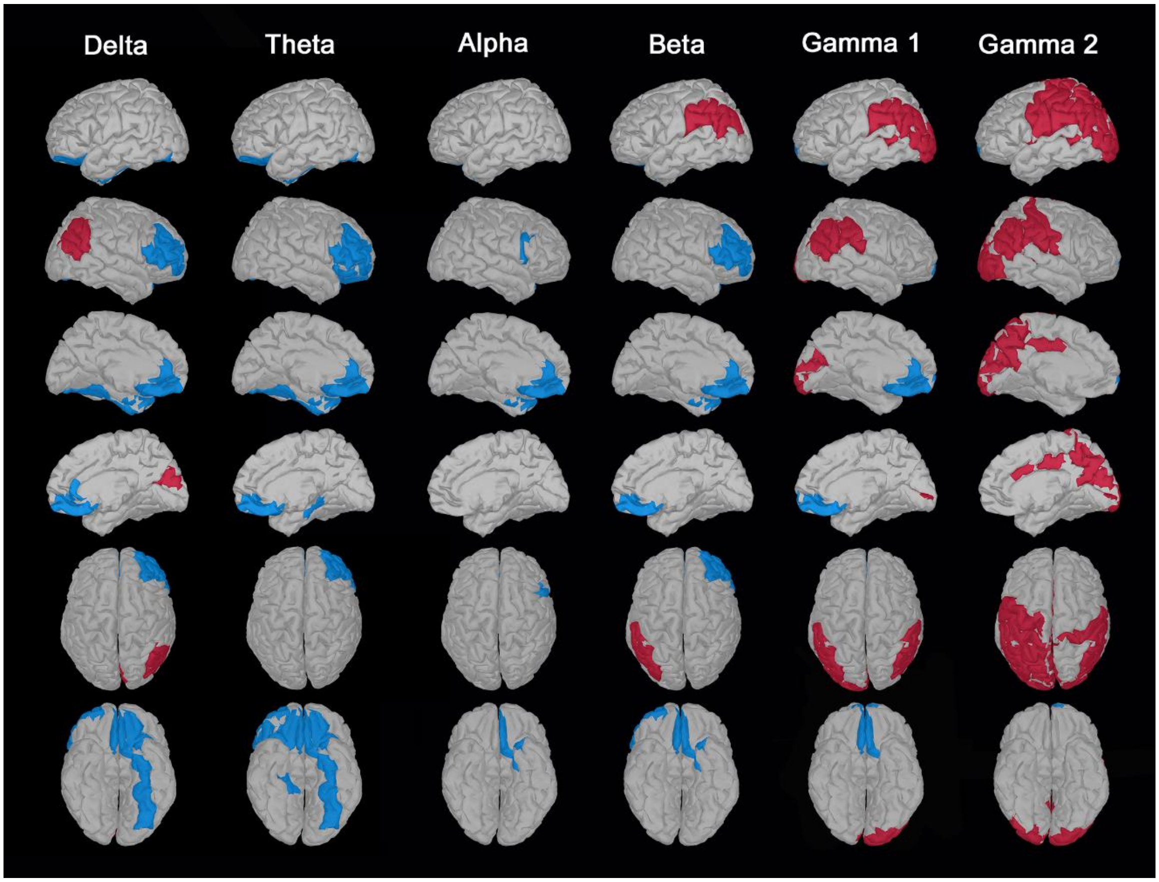

Figure 10. Posture-dependent changes in regional brain activity

Colored brain regions show areas where t-tests revealed source-level power differences when contrasting sitting upright against lying supine (mapped on the Desikan-Killiany neuroanatomical atlas). Red ($q < .05$) signifies greater oscillatory activity when sitting upright, whereas blue ($q < .05$) signifies lower activity when sitting upright. Each column presents one brain map viewed from six different angles.

	Delta		Theta		Alpha		Beta		Gamma 1		Gamma 2	
Desikan-Killiany Region	*d*	Δ	*d*	Δ	*d*	Δ	*d*	Δ	*d*	Δ	*d*	Δ
LT temporalpole	0.92	-0.50	1.08	-0.41	0.74	-0.32	0.75	-0.32				
LL rostralanteriorcingulate	0.91	-0.49	0.88	-0.34	0.80	-0.33	0.77	-0.31	0.73	-0.09		
LPF medialorbitofrontal	0.90	-0.54	1.17	-0.43	0.98	-0.39	0.97	-0.39	0.76	-0.12		
LT fusiform	0.88	-0.34	0.79	-0.26								
RF parstriangularis	0.86	-0.33	1.24	-0.31			1.16	-0.21				
RP inferiorparietal	0.86	0.29							0.82	0.16	0.99	0.14
LT entorhinal	0.85	-0.44	0.79	-0.35	0.90	-0.28	0.85	-0.28				
RPF medialorbitofrontal	0.80	-0.41	0.94	-0.31			0.83	-0.27	0.73	-0.11		
LPF lateralorbitofrontal	0.79	-0.47	0.95	-0.30								
RO cuneus	0.78	0.42									0.74	0.18
RL rostralanteriorcingulate	0.76	-0.37										
RF rostralmiddlefrontal	0.76	-0.36	0.91	-0.31			0.76	-0.29				
RT parahippocampal			0.82	-0.20								
RPF parsorbitalis			0.81	-0.24								
RPF lateralorbitofrontal			0.76	-0.25								
RF parsopercularis					0.78	-0.24						
LP inferiorparietal							0.80	0.31	0.85	0.24	1.22	0.20
LP supramarginal							0.72	0.20	0.90	0.25	1.04	0.28
RPF frontalpole									1.33	-0.24		
LPF frontalpole									1.11	-0.26	0.71	-0.18
RP supramarginal									1.06	0.12	1.22	0.15
LT transversetemporal									0.88	0.24	0.92	0.29
LT bankssts									0.80	0.22	0.99	0.24
LO lateraloccipital									0.78	0.28	0.94	0.27
LO pericalcarine									0.76	0.28	0.85	0.27
RO pericalcarine									0.74	0.26	0.80	0.24
LO cuneus									0.72	0.26	0.80	0.20
LC postcentral											0.94	0.21
LL posteriorcingulate											0.92	0.12
RL posteriorcingulate											0.79	0.09
LC precentral											0.77	0.19
RL caudalanteriorcingulate											0.77	0.09
RP precuneus											0.76	0.17
RC postcentral											0.75	0.09
LP superiorparietal											0.74	0.14
RT bankssts											0.74	0.17
RO lateraloccipital											0.71	0.23
LP precuneus											0.71	0.16

Table 3. *This table lists Desikan-Killiany neuroanatomical regions where $q < .05$ between sitting upright and lying supine. Each result includes effect size (Cohen's d) and the amplitude of the difference (Δ).*

	Delta		Theta		Alpha		Beta		Gamma 1		Gamma 2	
Desikan-Killiany Region	*d*	Δ	*d*	Δ	*d*	Δ	*d*	Δ	*d*	Δ	*d*	Δ
LT temporalpole	1.15	-0.48										
RPF medialorbitofrontal	1.20	-0.44										
RL rostralanteriorcingulate	1.20	-0.47										
LPF lateralorbitofrontal	1.25	-0.48	1.14	-0.26								
LPF medialorbitofrontal	1.28	-0.65	1.67	-0.44	1.58	-0.37						
LT insula	1.26	-0.27										
LO lingual	1.27	-0.25										
LL rostralanteriorcingulate	1.41	-0.53										
LT inferiortemporal	1.48	-0.36										
LT fusiform	1.85	-0.35	1.27	-0.26								
LT parahippocampal			1.13	-0.22								
RPF frontalpole									1.10	-0.23		

Table 4. *This table lists Desikan-Killiany neuroanatomical regions where q < .05 between reclined and supine postures. Each result includes effect size (Cohen's d) and the amplitude of the difference (Δ).*

Discussion

The present study leverages multi-postural MEG to unravel how body orientations associated with prevalent imaging procedures (e.g., sitting upright in EEG vs. lying supine in fMRI) impact resting-state brain activity. Extending previous sensor-level findings (Chang et al., 2011; Rice et al., 2013; Cole, 1989; Fardo et al., 2013; Benvenuti, Bianchin, & Angrilli, 2013; Spironelli & Angrilli, 2011; Spironelli et al., 2016; Thibault et al., 2014; Thibault et al., 2016), here we report a source-level MEG analysis revealing that sitting upright, compared to lying supine, was associated with greater power in high-frequency bands (i.e., extending from beta to high gamma) in a wide swath of parieto-occipital cortex. Furthermore, prefrontal oscillatory power was dampened in the upright-seated position to varying degrees depending on the bandwidth (with effects ranging from delta to low gamma bands). Beyond our primary analysis contrasting sitting upright vs. lying supine, we also investigated brain activity associated with reclining at 45°. When comparing reclined to supine posture, we found power differences in frontal regions, which largely overlapped with the effects from the lying supine vs. sitting upright contrast. On the other hand, we hardly found any significant brain changes between reclining and sitting upright. Effect sizes were large across all significant tests, with a mean Cohen's *d* of .95 (SD = .23). This overarching pattern of results indicates that the oscillatory dynamics of the resting brain differ dramatically between supine posture and more upright body positions.

EEG studies have associated high-frequency activity with cognitive processing (e.g., alert mental states) (Kaiser & Lutzenberger, 2005), and lower-frequency activity with relaxation (e.g., drowsy states) (Strijkstra et al., 2003). Thus, the present findings suggest that the brain may linger in a mode of decreased vigilance when supine compared to when upright. In line with this interpretation and related accounts (e.g., Jones & Dean, 2004), our ECG data showed lower heart rate in the supine posture.

Our present findings accord with previous reports investigating the influence of posture on resting-state brain function. The collective evidence indicates that upright postures are associated with greater power in high-frequency bands (Thibault et al., 2014; Chang et al., 2011; Cole et al., 1989) and reduced power in low-frequency bands (Chang et al., 2011; Spironelli et al., 2016). Our earlier sensor-level analysis of the current dataset also showed high-gamma increases in more upright postures, but these effects were restricted to smaller regions of the left hemisphere (Thibault et al., 2016). In sensor-level MEG analysis, however, variation in head distance from the sensors presents a substantial confound (see discussion in Thibault et al., 2016). This methodological caveat may explain why our earlier sensor-level analysis was unable to pick up the more robust, distributed effects we observed here using a source-localization approach.

In terms of regional brain activity, our present observations coalesce with the findings of an earlier account using multi-postural PET (Ouchi et al., 1999). Congruent with our observation of greater upright gamma power in parieto-occipital areas, this PET study reported increased cerebral blood flow to visual areas when standing upright compared to when lying down. Yet, here we observed a more distributed pattern of high-frequency activity—extending beyond the visual areas to a large portion of posterior cortex. In addition, we found differences in low-frequency bands among frontal regions, which were absent from our previous EEG results (Thibault et al., 2014). In that EEG study, however, participants assumed body positions for shorter time periods and received instructions from experimenters every 30 s to change behavioral condition (e.g., to open or close their eyes for the next block). Thus, participants may have had less time to settle into a relaxed state during the supine position, which may have limited the differences in low-frequency power between postures. Of particular interest, the present source analysis revealed alterations in core regions of the default-mode network (e.g., posterior cingulate, precuneus, inferior parietal lobule, parahippocampus, rostral anterior cingulate), which has been proposed as a central hub of anatomical and functional organization in the human brain (ven den Heuvel & Sporns, 2013).

Certain physiological parameters may have played a role in shaping our results. Muscle activity exerts an influence on signals in the gamma range (Muthukumaraswamy, 2013) and thus might have contributed to the posterior high frequency activity. In addition, persistent eye-blink artefacts might have survived our standard data cleaning procedures and thus contributed to the orbital activity. On the other hand, systematic differences in head position are unlikely to explain the present results. Although the back of the head might have been closer to the sensors in the supine position, our source-space analysis accounts for variations in head placement using participant-specific 3-D digitization of cranium size and shape, head localizer coils, and MRI-guided anatomy per individual. Moreover, we would expect opposing results in frontal versus parieto-occipital regions if a consistent shift toward occipital head placement drove neural difference. In particular, we would expect higher occipital signal in the supine posture because these regions would be closer to the sensors. Instead, our results show lower parieto-occipital power in the supine posture. Regardless of the underlying causes, the alterations we observed hold broad implications for the field of neuroimaging.

Orthostatic caveats take on particular importance as the domain of cognitive neuroscience moves toward triangulating data from multiple imaging modalities involving different body stances (Agam et al., 2011; Calhoun & Sui, 2016; Lei et al., 2011; Garcés et al., 2016). Even within the realm of MEG, posture varies from study to study: whereas upright positions are most typical, supine measurements are also common in multimodal imaging contexts (e.g., Larson-Prior et al., 2013; Carhart-Harris et al., 2016) and when investigating specific clinical populations (e.g., epilepsy: Pellegrino et al., 2016; multiple sclerosis: Schoonheim et al., 2013). Unfortunately, many a MEG report neglects to specify the acquisition posture. In addition, our main finding that upright posture is associated with higher parieto-occipital gamma power has direct relevance for comparisons between upright EEG/MEG data and supine fMRI scans. Intracranial, EEG, and MEG recordings have implicated gamma band activity in a host of cognitive functions including attention, memory, and sensory processing (Jensen et al., 2007). Moreover, our MEG data are relevant for fMRI studies because the BOLD signal, which serves as a proxy for neural activity in fMRI, correlates with gamma activity (Niessing et al., 2005; Nir et al., 2007). Our findings thus highlight how sitting upright or lying down—body positions associated with common imaging modalities—impact the resultant data acquired via those technologies. The current account paves the road to a more scientific understanding of posture as a ubiquitous, albeit little acknowledged, procedural caveat in cognitive neuroscience research.

Article Five

Preface. This article builds on our empirical work and explores a potential application of our main findings. To account for the differences between everyday contexts and neuroimaging environments (including postural discrepancies), some scientists propose to conduct research with simple, portable EEG systems. Popular among these devices are the *Insight* from Emotiv, the *Mindwave* from NeuroSky, and the *Muse* from InteraXon. These inexpensive, basic, and easy-to-use EEG devices have drawn a new crowd to EEG research. A community of citizen neuro-technology enthusiasts use these devices for research on topics including emotion, meditation, sleep, and cognitive enhancement. This user group holds the potential to conduct valuable *citizen science* (i.e., where a large distributed base of members of the general public collect and share data that would be difficult and time-consuming for scientists to collect themselves). Brain scientists, however, have been more reluctant to adopt these consumer EEG devices. In this article, we evaluate the claims consumer EEG companies make and the usefulness of the devices they sell. In a second section of this article (which I exclude from this thesis), my co-author Anna Wexler delves into the regulatory and ethical implications of my evaluation of these EEG devices. This article demonstrates that there is too little research to justify the use of consumer EEG devices for most research purposes, even if they allow for ecological postures and environments.

Notably, the subject of this article overlaps largely with another domain of research I became highly involved with during my doctoral studies: neurofeedback. I briefly touch on my neurofeedback work before the *General Discussion* of this thesis. Neurofeedback aims to train individuals to gain control over their brain activity by providing them with a live EEG readout, or more recently, fMRI data. Many of the consumer EEG devices we discuss in this article are marketed as neurofeedback devices. They mostly lack data to support relevant neurofeedback claims.

Excerpt from: **Mind-Reading or Misleading? Assessing Direct-to-Consumer Electroencephalography (EEG) Devices Marketed for Wellness and Their Ethical and Regulatory Implications**

Anna Wexler, Robert Thibault

Journal of Cognitive Enhancement 1-7, (2018)

Assessing the evidence

In this paper we focus on assessing the evidence for the wellness-related claims shown in Table 5. Although the marketing approaches taken by consumer EEG companies differed in tone, they all relied on the assumption that observing one's own brainwaves can improve well-being in relation to concentration, stress, performance and other behaviors. However, for consumer EEG to improve well-being beyond the benefits derived from placebo effects, at least three assumptions would need to hold true. First, the device would need to validly and reliably record the brain signals that companies claim to measure. Second, the measured brain signal would need to accurately reflect a given behavior or mental state. Third, providing individuals with their brainwave data would need to help them alter a behavior or mental state. Here, we analyze the evidence base for each of these three assumptions.

Table 5. *Number of direct-to consumer EEG devices, out of the 18 included in our dataset*, making claims relating to improving behavior, mental states, or well-being.*

	n
Improves focus/concentration	12
Reduces stress & promotes relaxation	12
Improves meditation	9
Improves sleep	9
Optimizes cognitive performance	8
Improves athletic performance	6
Optimizes learning	5
Improves memory	3

** Devices included in our dataset include Aurora Dreamband from iWinks LLC, Aware from United Sciences, Dreem from Rythm, Insight from EMOTIV, FocusBand from T 2 Green Pty Ltd, iBand+ from Arenar, Kokoon from Kokoon Technology Limited, Mindball from Interactive Productline, MindWave from NeuroSky, Mindset from Mindset, Melomind from myBrain Technologies, Muse from InteraXon, SenzeBand from Neeuro, Neuroon Open from Inteliclinic, Neuroplus from NeuroPlus, Inc., Sleep Shepherd from Sleep Shepherd, Super Brain II from REX, and Versus by NeuroTherapeutics.*

(1) The device validly records brain activity.

If consumer EEG devices were substantially equivalent to research grade EEG systems it could be comfortably assumed that they measure brain waves. However, consumer EEG devices differ from research systems in many regards. Their hardware generally includes only a few electrodes compared to the 32-128 commonly used in research; they utilize dry rather than wet electrodes, which have greater impedances and noise levels (Mathewson et al., 2017); and they employ passive rather than active electrodes, which are not designed to amplify the EEG signal at the site of acquisition before transmitting it through the wires. Their software for online artifact removal and source localization, which are two complex tasks that companies and an open source EEG community have been working on for decades, generally differs from the tried-and-tested programs commonly used in research. In the context of consumer EEG, moreover, there is no experienced technician to ensure low impedance, remove sweat from the scalp, minimize muscle and eye artifacts, and avoid contamination from electrical appliances. These differences may compound, resulting in considerably different outputs from consumer and research grade devices. Notably, many consumer EEG devices employ only a few electrodes placed directly over facial muscles (forehead and temporalis) that can contaminate the EEG signal wit muscle activity orders of magnitude greater than brain waves (Whitham et al., 2007). Thus, before accepting that a consumer EEG device validly records brain activity, data from a given device would need to be compared to that from a method known to validly record brainwaves—for example, a research grade EEG system.

To attempt to validate consumer EEG devices, researchers could either (a) simultaneously record from a consumer and research-grade device; (b) compare recordings from consumer and research-grade devices taken at different times; or (c) run a standard EEG protocol with the consumer device and examine whether the results reflect established findings. Of the 18 devices assessed, we could identify only one company that took the first approach and simultaneously recorded from two EEG systems. They found that recordings from their device, Versus, correlated highly with those taken with a five-sensor wet-electrode system (Wyckoff et al., 2015). In another study, researchers utilized the second approach, and found that the two consumer EEG devices tested—Mindwave and Muse—were susceptible to artifacts, and the latter showed poor test-retest reliability (Ratti et al., 2017). At least one company used the third approach, and collaborated with academic researchers to show that their device, Muse, can identify age-related changes in the EEG that are partially consistent with the literature (Hashemi et al., 2016). However, appended to that study are comments from one reviewer who criticized the lack of validation of the analysis protocols, and recommended that even the revised version not be published. A second study conducted by academic researchers showed that Muse could detect event-related potentials (Krigolson et al., 2017); however, it is unclear how well these results would translate to consumer use as the authors found that data quality was only “sufficient” after research assistants had become experienced in setting up participants with the Muse headset.

For the remaining 15 devices, after browsing through the company websites and using online search engines, we were unable to identify any publicly available research that tested validity via one of the methods outlined above. We acknowledge that such evidence may be proprietary. However, without this data, the public has little reason to believe that most consumer EEG devices validly and reliably record brain activity.

(2) Brain waves derived from EEG accurately reflect certain behaviors or mental states.

Scientists can leverage EEG data in at least two ways to attempt to identify mental states and behaviors: by using pre-specified bandwidths or applying machine learning algorithms. The first and historically more common approach parcels EEG data into five bandwidths—delta, theta, alpha, beta, gamma—and can generally provide the information necessary to distinguish between two widely diverging states, such as sleep and wakefulness. On the one hand, these bandwidths were defined almost a hundred years ago and continue to effectively serve as a tool for analyzing brain data across a range of disciplines including neurobiology, medicine, and research on cognition. On the other hand, in the consumer EEG context, these bandwidths seem to be employed in the overly-simplistic manner commonly used in neurofeedback practice—where the amplitude of certain bandwidths not only correlates with, but is assumed to drive a particular behavior or mental state (e.g., increasing the amplitude of one's alpha waves will cause a meditative state). This belief rests on a shaky foundation (Thibault and Raz, 2017). For one, while expert meditators may have high levels of alpha activity, individuals can also achieve a meditative state while producing little alpha activity, and high amplitude alpha waves can also be produced when individuals are anxious (Beyerstein, 1990). Thus, alpha amplitude remains unconvincing as a marker for meditation. In a similar manner, neurofeedback practitioners often attempt to increase beta activity (~13-30 Hz) because a number of studies correlate this frequency with heightened attention. And yet, beta amplitude also correlates with alcoholism (Rangaswamy et al., 2002) and *poor* attention in children with ADHD (Ogrim et al., 2012). Moreover, some of the most robust neurofeedback studies show that attention can improve substantially (Cohen's d=1.5) without any significant change in underlying EEG activity (Schönenberg et al., 2017). Behavior can also remain objectively unchanged when individuals nonetheless learn to increase a pre-specified bandwidth of brain activity (Schabus et al., 2017). Thus, most mental states and behaviors cannot be clearly inferred by parceling brain waves into standard frequency bins. Although sleep can be inferred from EEG data, it remains unclear how gaining access to this data can help improve sleep.

Increasingly, researchers are turning to the second approach and using machine learning to derive mental and behavioral states from EEG data. In the general EEG literature, this method has shown moderate success at identifying more specific states than is possible using only pre-specified bandwidths (e.g., distinguishing workload intensities and vigilance levels). With regard to consumer EEG, we identified a number of studies that applied machine learning to data collected with Muse and Mindwave. Some of these experiments, for example, could identify better than chance alone, lapses in attention (Armanfard et al., 2016) and whether individuals were watching "emotional" versus "logical" videos (Bashivan et al., 2016). Even when consumer EEG devices successfully distinguish between mental states, however, they likely do so based on the electrical activity produced by facial muscles, which contaminates the EEG signal. When individuals are resting, their muscle activity can continue to produce high-frequency electrical signals 10-200 times greater in amplitude than brain waves (Whitham et al., 2007). These signals can dominate parts of the EEG recording and are difficult to remove even from data collected with research-grade EEG systems. Thus, it remains unlikely that consumer EEG devices—which utilize fewer electrodes and simpler components—would rely primarily on brain activity to distinguish mental states. With these considerations in mind, consumer EEG devices nonetheless maintain the potential to one day serve as drowsiness detectors (even if relying on data from muscles), for example, to alert drivers when they appear fatigued. Beyond drowsiness, there is currently little evidence to suggest that these devices, regardless of the methods used, can track the brain signatures associated with other consumer EEG promises such as optimal performance and improved learning or memory capacity.

(3) Providing individuals with EEG brainwave data can help them improve the behavior or mental state in question.

Rather than conducting research, the majority of consumer EEG companies implicitly or explicitly rely on findings from the neurofeedback literature. This reliance remains problematic because not only do consumer-grade and research-grade devices differ substantially, but the neurofeedback literature itself is hardly convincing. Of over 3,000 publications claiming that neurofeedback using EEG can improve attention, cognitive performance, insomnia, and a range of other behaviors, only eleven experiments employ a double-blind and leverage a sham-control group (e.g., who receive data from a previously recorded participant; Thibault and Raz, 2017). Ten of these studies demonstrate equivalence between sham and genuine neurofeedback. Thus, the use of consumer EEG largely rests on a body of literature that has yet to establish the benefit of receiving genuine brainwave data.

Participants in neurofeedback studies likely improve their behavior not because they viewed their brain activity, but because of salient psychosocial influences (e.g., placebo effects: Kirsch et al., 2016) and the benefits of cognitive training in general. Indeed, participants in the neurofeedback context interact with practitioners over multiple sessions (Margo, 1999), are immersed in a clinical environment with flashy technology (Ali et al., 2014; Olson et al., 2016), and receive an expensive treatment (Waber et al., 2008). These influences likely increase expectation and motivation, which in turn alter the behavior or mental state in question (Nichols and Maner, 2008). Moreover, because consumer EEG companies target behaviors and mental states that are highly amenable to psychological factors (see Table 5), placebo effects likely play a large role (Wampold et al., 2005). In some experiments, these psychosocial influences are large enough to match the efficacy of standard-of-care treatments (e.g., Fuchs et al., 2003). If participants in neurofeedback studies are indeed improving due to psychosocial and cognitive mechanisms it is far from clear that these same effects would replicate in the consumer context (without the clinical setting, expert treatment, etc.).

If consumer EEG devices do indeed help improve aspects of well-being, data would be needed from studies using consumer devices. At least three consumer EEG companies have conducted such studies. One experiment showed that when individuals used Muse rather than participate in 10 minutes of online high school math lessons they improved reaction time on a Stroop task (Bhayee et al., 2016). Based on the substantial difference between the experimental groups alongside the impossibility of a double-blind, placebo effects may explain the findings. Another device, Versus, has a few in-house case studies and at least one peer-reviewed experiment (Sherlin et al., 2012) on sports performance—none employed a control group and independent replication is lacking. Finally, NeuroPlus has one non-peer-reviewed in-house experiment with a control group that received no treatment. While this study suggests that their device improves attention, due to the weak research design, it may have been that psychosocial influences drove the improvement. Although these companies may be commended for publicly sharing research conducted with their own devices, the experimental designs conflate EEG effects with placebo responses. Taken together, there is little evidence to support the marketing claims of consumer EEG companies regarding altering mental states and behavior.

From Posture to Neurofeedback (an interlude)

Beyond a common interest in consumer EEG devices, my work on body posture brought me to neurofeedback through an additional path. In recent years, it has become clear that individuals can use fMRI to modulate the BOLD signal much more reliably than EEG to modulate electrical brain activity. Posture is one among a host of differences between EEG and fMRI neurofeedback. In the *Introduction*, I explained how emotion researchers found that posture accounts for observed difference in brain activity lateralization between EEG and fMRI studies. Similar to that group's line of thought, I was initially curious if posture held partially responsible for the difference between learning in EEG neurofeedback and fMRI neurofeedback.

Upon delving into the neurofeedback literature, I discovered a complex movement that involved academic researchers, practitioners, business people, and the general public. The EEG neurofeedback literature suffered from publication bias that seems to be partially upheld by ideological and financial conflicts of interest (Thibault, Lifshitz, & Raz, 2017). I could find very few critical appraisals of this set of techniques. The fMRI neurofeedback literature was distinct from its EEG counterpart and generally employed more robust methods and clearer reporting. I discovered that the two fields differed in much more than posture and imaging device. With colleagues, I published a critical field-wide review and demonstrated that lore often outweighs the available evidence (Thibault et al., 2016). In a follow-up article, we proposed three basic criteria for EEG neurofeedback researchers to strive for if they want clinicians to consider their technique (Thibault & Raz, 2016b). I also led a systematic review of 99 fMRI neurofeedback experiments (Thibault, MacPherson, Lifshitz, Roth, & Raz, 2018). Together these contributions helped challenge neurofeedback research towards stronger methods. I am now working with dozens of leaders in the field to devise a best-practices checklist for neurofeedback research (inspired by the CONSORT—Consolidated Standards of Reporting Trials—and PRISMA—Preferred reporting items for systematic reviews and meta-analyses—guidelines). Similar to how cognitive neuroscience can benefit from considering imaging postures, neurofeedback research can benefit from considering a number of imaging related nuances.

General Discussion

Summary of findings

The main body of this thesis consists of three published experiments. Each attempts to answer a similar question with slightly different methodologies. Article 2 uses high-density EEG for short recording sessions in a variety of conditions. Article 3 and 4 recorded resting state MEG for longer sessions and looked at both sensor-level and source-level neural activity. With these three different methodologies we obtained partially overlapping results. Our findings converge and triangulate with data from the wider literature to suggest that body posture alters neuroimaging data by increasing high-frequency brain activity and reducing low-frequency oscillations when upright compared to supine.

When combining various experimental findings to draw an overarching conclusion, we must consider the problem of *generality* (e.g., where combining the general results across studies may arrive at a different conclusion compared to interpreting the specific results of each study). In our edited volume, Jared Cooney Horvath discusses how the field of brain training can suffer from the problem of generality. In some experiments, participants may increase the speed at which they perform; in others, their accuracy; in others yet again, their sustained attention. Yet, in the experiment where speed improved, measures of accuracy and sustained attention may have remained unchanged; in the study where accuracy improved, speed and sustained attention may have remained unchanged; and so on. If we speak of the findings in *general* terms, we can conclude that in each experiments brain training improved performance. However, if take a more systematic (and scientific) approach, we would evaluate each element of performance individually. Using this outlook we would find that there is more evidence against brain training to improve performance, than for it.

The effect of posture on brain activity does not suffer from the problem of generality. The effects are often specific, have been replicated, and triangulate well with other fields of knowledge. In Article 2 and 4, we demonstrate an increase in high frequency posterior oscillations when upright compared to supine. Article 3 failed to identify this change, likely due the imperfect nature of sensor-level analysis on multi-posture MEG data. Our finding was later replicated by an independent group (Spironelli & Angrilli, 2017) and converges with PET findings that document increases in posterior brain activity when upright (Ouchi et al., 1999), and the literature on increased visual engagement when upright (e.g., Guterman et al., 2012).

We might expect to see similar postural difference in fMRI data in parieto-occipital regions because the BOLD signal correlates closely with synchronized gamma oscillations (Niessing et al., 2005; Nir et al., 2007; Shmuel & Leopold, 2008). Gamma activity plays an important role in sensory processing and is associated with working and long-term memory (Jensen et al., 2007). Gamma oscillations are further related to attention in both sensory and non-sensory brain regions (Jensen et al., 2007). Computational models further suggest that gamma activity may accompany states of preparatory attention or vigilance and help single out stimuli and amplify the neural response to them (Borgers, Epstein, & Kopell, 2005). Taken together, our findings that the supine posture pairs with lesser amplitude gamma activity suggest that the brain is less prepared for action when lying down; and, moreover, that this effect is significant enough to alter neuroimaging data.

In Article 4 we also discovered greater low-frequency frontal activity when lying supine compared to sitting upright. Article 3 likely missed this findings based on the caveats surrounding sensor-level multi-posture MEG analyses; Article 2, because participants alternated between tasks frequently and never held a position for more than a few minutes, which inhibited drowsy states. Our low-frequency findings in Article 4 converge with those from a two-electrode EEG study that found increased delta and theta when participants lay supine for 15 minutes (L.-J. Chang et al., 2011), and a recent study showing an increase in frontal delta after lying supine for two hours (Spironelli et al., 2016). Higher amplitudes of low-frequency neural activity have been associated with relaxed and drowsy states (Strijkstra, Beersma, Drayer, Halbesma, & Daan, 2003). In young adults in particular, which formed our study sample, fontal delta activity is linked to drowsiness (Münch et al., 2004). Our low-frequency findings also triangulate with cognitive research showing increased drowsiness (Caldwell et al., 2003), faster sleep onset (Cole, 1989), and impaired task performance when supine (Lundström et al., 2008).

In Article 5, we were the first group to systematically identify all portable EEG devices targeted directly to consumers and evaluate their claims. Given the divergence between everyday environments and the laboratory EEG context (e.g. posture), some scientists have begun using these more crude devices to conduct their research. We found an absence of evidence to justify using these devices to research the human brain.

Together, our findings support the concept of the *embodied brain*. In other words, that our brain activity and the associated neuroimaging data, rely heavily on our body and surrounding environment.

Underlying mechanisms by which posture operates

"At least two physiological and one cognitive mechanism contribute to the influence of posture on brain data: (1) changes in noradrenalin output, (2) altered CSF thickness, and (3) a preparatory cognitive state based on the subset of interactions possible with the environment" (p. 4).[2]

"**(1)** The supine position hampers cortical excitability (Lipnicki, 2009; Spironelli et al., 2016). When lying horizontally, compared to upright, gravitational loads redistribute and stimulate arterial and cardiopulmonary baroreceptors, and in turn, lead to a reduction in sympathetic nervous system activity (Mohrman & Heller, 2003). This process appears to impede noradrenergic release from neurons in the locus coeruleus (Berridge & Waterhouse, 2003; Murase, Inui, & Nosaka, 1994) and drives downstream cortical inhibition (Rau & Elbert, 2001). A cleverly designed experiment supports this theory (Cole, 1989). The researcher applied leg pressure via anti-shock trousers (normally used to treat severe blood loss) to maintain levels of baroreceptor activity between lying horizontally and lying head-up on a 40° incline. They found less high-frequency EEG activity only in the condition with reduced baroreceptor firing (i.e., 40° incline without leg pressure). Further theoretical (Lipnicki, 2009) and experimental reports (Schneider et al., 2008; Vaitl & Gruppe, 1992) support the idea that gravity initiates a physiological cascade that leads to cortical inhibition.

(2) Slight shifts in CSF thickness can drastically alter EEG data (Ramon et al., 2006; Ramon et al., 2004; Wendel et al., 2008) and, to a lesser extent, MEG data (Vorwerk et al., 2014). Strong evidence for this interaction comes from a unique two-part multi-posture MRI and EEG

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[2] All quoted text in the general discussion comes from a review I published (Thibault & Raz, 2016a). This practice follows the McGill thesis guidelines.

study (Rice et al., 2013). The researchers found that when supine compared to prone, gravity draws the brain downwards, thins out the highly conductive CSF in occipital regions by 30%, brings the brain slightly closer to posterior scalp electrodes, and in turn, amplifies high-frequency occipital EEG power by an average of 80% (Rice et al., 2013). While this study provides a wealth of information, the scarcity of erect MRI scanners likely precluded an upright condition. And yet, a complementary low-field (0.5 T) MRI study scanned participants in the seated and supine positions and found that gravity draws fluids downward into the spinal canal when upright, decreases intracranial CSF and cerebral blood flow, and amplifies intracranial compliance (Alperin et al., 2005). Measures of CSF thickness in circumscribed cortical regions, however, were not reported. Thus, the quantitative differences in CSF thickness between supine and upright postures remains largely elusive. The finding that CSF not only distorts electromagnetic brain signals, but also varies in thickness among postures, raises particular concern regarding the standard practice of using anatomical MRI data acquired in the supine posture to construct head models for EEG and MEG analyses. Whereas postural CSF discrepancies may correlate well with brain imaging data, a clear story hardly emerges relating CSF thickness to behavioral observations. This insight suggests that factors beyond CSF likely contribute to the influence of posture on human functioning.

(3) A preparatory cognitive state, set to act on the subset of possible interactions between the current position of a participant and their surrounding environment, may partially account for the influence of posture on brain activity. For example, when lying down, the brain may be poorly prepared for locomotion (de Lange, Helmich, & Toni, 2006), to observe a moving visual field (Kano, 1991), or to socially and physically interact with our environment (Hari & Kujala, 2009). Motor plans depend on ongoing limb configuration (de Lange et al., 2006), the excitability of motor cortex increases in free-standing compared to supported postures (Tokuno, Taube, & Cresswell, 2009), and when sitting, compared to supine, people react more quickly to moving visual fields (Kano, 1991) and are more likely to perceive themselves as moving when exposed to a moving visual field (Guterman et al., 2012). Moreover, the supine posture decreases social behaviors (Harmon-Jones & Peterson, 2009; Price et al., 2012) and hardly invites typical social interactions known to modulate brain activity, such as eye contact (Ferri et al., 2014). These posture-dependent cognitive states may manifest in both resting-state brain oscillations (L.-J. Chang et al., 2011; Spironelli et al., 2016; Thibault et al., 2014) and neural responses to stimuli (i.e., ERPs: Fardo et al., 2013; Price et al., 2012; Spironelli and Angrilli, 2011). The causality of interactions between cognition and brain activity may always remain elusive; cognitive states propel physiological change (i.e., top-down processes) and physiological parameters also weigh on cognitive states (i.e., bottom-up effects).

Taken together, physiological cascades, cranial fluids, and cognitive set all exert varying influences on brain imaging data across postures. Whereas noradrenergic output and cognitive processing may directly influence cortical activity measured at the neuronal level, CSF shunts the transmission of electromagnetic activity from neurons to sensors and exerts little influence on neuronal activity itself. Adopting experimental designs that evaluate and integrate these three mechanisms can only help to better understand ecological human functioning" (p. 4-5).

Correcting and accounting for the effects of posture

"Two paths emerge to overcome postural caveats in neuroimaging. First, we can rework standard experimental designs to minimize the influence of posture on brain activity; and second, we can embrace new imaging technologies conducive to everyday human behavior.

Accounting for the three aforementioned postural mechanisms would require a combination of innovative experimental designs, computational expertise, and a new body of research to draw upon. For example, to maintain cortical excitability in the supine posture, researchers could entertain the possibility of applying pressure to the body via anti-shock trousers to maintain baroreceptor firing (Cole, 1989), pharmacologically sustaining noradrenalin levels, or providing periodic stimulation via conversation or sensory input to sustain participant alertness. Overcoming variation in CSF thickness may require anatomical brain scans from each participant plus compensatory algorithms to calculate the standard redistribution of CSF as a function of posture. Such algorithms do not yet exist and would demand further head modeling research that taps into a database of posture-induced CSF perturbations across individuals (e.g., see Rice et al., 2013).

Novel research on posture and cognition, moreover, could help future experimental designs minimize variations in cognitive state among postures. For example, research already demonstrates that poor sleep impedes working memory when supine compared to sitting (Muehlhan, Marxen, Landsiedel, Malberg, & Zaunseder, 2014) and hampers psychomotor performance when sitting compared to standing (Caldwell et al., 2003). These findings suggest that weeding out sleep-deprived participants from supine imaging experiments could help researchers collect brain data that better reflect upright human functioning. Neuroimagers could further benefit from extending similar screening procedures to participants with mood and hormonal disturbances in response to MRI environments (Muehlhan, Lueken, Wittchen, & Kirschbaum, 2011) and mental performance problems in response to scanner noise (Pripfl, Robinson, Leodolter, Moser, & Bauer, 2006). With diligence, neuroimagers can improve current research paradigms to account for a number of these postural discrepancies.

Imaging the human brain increasingly relies on smaller, lighter, and more mobile hardware. These devices hold the potential to thrust brain imaging toward investigating everyday interactive and social cognition. With the use of overhead gantries, participants undergoing EEG and fNIRS can now move and interact in a laboratory environment (Gramann et al., 2011; Mahoney et al., 2016). Recent developments, moreover, permit individuals to connect EEG electrodes to their smartphone and record brain activity in everyday contexts (Stopczynski, Stahlhut, Larsen, Petersen, & Hansen, 2014). Moving while recording EEG, however, comes with caveats. Muscle activity, eye movement, and head motion all contaminate the EEG signal, especially in high-frequency bandwidths (Muthukumaraswamy, 2013). One potential concern is that researchers who are not careful may mistake these artifacts for brain oscillations themselves. The fNIRS signal also remains sensitive to motion artifacts, but responds less to muscle contamination. These portable devices sacrifice signal quality for ecological human functioning. The use of these technologies, however, is not an “either-or” dilemma. In a single experiment, we can combine data from the more precise and static imaging modalities with data from ecological yet coarser devices. Similar to how portable devices revolutionized the field of eye-tracking (Hayhoe & Ballard, 2005), wearable neuroimaging technologies hold promise to revolutionize how we study the living human brain” (p. 5-6).

Future Directions

Our finding that posture affects brain activity is, in itself, of little surprise. Our everyday experience and the literature on cognition point in this direction. What is significant, however, is that posture alters the brain enough to impact the neuroimaging experiments which much of cognitive neuroscience relies on. To more fully understand the relation between posture and brain activity, scientists can conduct further experiments and additional analyses. More recent M/EEG investigation often go beyond observing common bandwidths of oscillatory activity alone and move toward analyzing cross-frequency coupling (CFC) and more specifically, phase-amplitude coupling (PAC) (Canolty & Knight, 2010; Voytek et al., 2010). Coherence between brain regions (e.g., visuo-motor alpha coherence: Rilk, Soekadar, Sauseng, & Plewnia, 2011) is another more advanced measure which requires careful analysis to avoid mistaking volume conduction for genuine source coherence (Srinivasan, Winter, Ding, & Nunez, 2007). Analyzing these measures may provide a more complete understanding of the neural differences, especially in relation to functional connectivity and RSNs, between body comportments.

Leveraging upright MRI scanners for functional sequences and multi-posture imaging would help make leaps forward in our understanding of posture and the brain. There exists one vertical 3.0 Tesla MRI scanner capable of recorded high-quality functional sequences in Japan (Nakada & Tasaka, 2001). However, this machine is mostly used for clinical and anatomical purposes. Lower strength vertical MRI scanners, of which there are many more, could be used to investigate alterations in CSF distribution and thickness between sitting and supine postures. Data from this type of study could be used to create algorithms that compensate for postural difference in CSF when employing head models from supine MRI scans for upright EEG and MEG analyses. Creating compensatory algorithms for functional data (rather than anatomical difference) presents a much more daunting task.

Electrocorticography (ECoG) and intracortical recordings, while invasive and difficult to find patients to record, would provide deep insights about the mechanisms behind the findings of this thesis. We acknowledge that a benefit-risk evaluation precludes such an experiment. CSF has little effect on ECoG recordings because the electrodes are placed directly on the cortex. Intracortical recordings, moreover, would provide even more precise information about cortical sources. TMS and tES experiments generally employ the upright posture. Testing these technologies in various posture could also help elucidate how posture alters the preparatory set of the brain. With recent advances in combined stimulation and brain imaging (e.g., Thut et al., 2017; Witkowski et al., 2016), researchers could also directly observe whether TMS and tES impact neural activity differently depending on posture. Brain stimulation experiments, as with neuroimaging and cognitive studies, could consider which posture to use based on their research question.

As with any field of scientific investigation, the future of embodied cognition, body posture, and brain imaging will benefit from more rigorous and reproducible research practices. Future studies could pre-register their protocols, analyses, and hypotheses (Nosek, 2015). Pre-registration is an effective way to avoid p-hacking (i.e., taking unreasonable analytical choices to achieve statistically significant results), hypothesizing after the results are known (HARKing), and other questionable research practices that fuel publication bias and reduce replicability (Munafò et al., 2017). Uploading data to an open access repository would allow for re-analyses and additional studies from independent research groups (Choudhury, Fishman, McGowan, & Juengst, 2014). The MEG lab at the Montreal Neurological Institute has initiated an open access repository called OMEGA (Niso et al., 2016). Along with more reproducible methods, researchers across disciplines that use neuroimaging could clearly document which posture their participants assumed during their experiment. Together, these practices can only help to advance research in any field.

General conclusion

The present findings indicate that body posture influences brain activity enough that it alters neuroimaging recordings. This finding raises a caveat that has been largely overlooked across cognitive neuroscience research. Additional data from other cognitive experiments and neuroimaging studies support our conclusion. “Whereas, ecological comportments such as standing and moving recruit a host of additional brain processes and represent the base from which we perform our largest diversity of interactions, few brain imaging studies ask participants to stand or move. A pillar of neuroimaging, MRI, confines participants to a supine position seldom assumed during common wakefulness. This state of affairs brings into question the practice of using neuroimaging findings to inform our ecological behavior of everyday life. Bridging the lacuna between imaging context and ecological posture would further unveil the neural processes giving rise to the living human brain” (p. 6).

Our postural findings merge with our upcoming edited volume, and our work on neurofeedback, to suggest that brain imaging, like any other nascent field, is transitioning through a phase of critique and improvement. Many scientists are exploring this set of techniques and an appreciation for nuance and critical appraisals is increasing. As neuroimaging research continues to advance, and scientists overcome more and more relevant shortcomings, we are sure to further unravel the link between brain and behavior.

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