Title
A Collection of Works in Neuroergonomics

Author
Gougelet, Robert Joseph

Publication Date
2020

UNIVERSITY OF CALIFORNIA SAN DIEGO

A Collection of Works in Neuroergonomics

A dissertation submitted in partial satisfaction of the
requirements for the degree Doctor of Philosophy

in

Cognitive Science

by

Robert J. Gougelet

Committee in charge:

Bradley Voytek, Chair
Seana Coulson
Scott Klemmer
Scott Makeig
Lara Rangel
John Serences

2020

The Dissertation of Robert J. Gougelet is approved, and it is acceptable in quality and form for publication on microfilm and electronically:

Chair

University of California San Diego

2020

DEDICATION

To my parents
and to those who so freely offered
their guidance and support
along the way

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

ACKNOWLEDGEMENTS

Thanks to Brad Voytek for your commitment, guidance, and advisement.

Thanks to my committee for your openness, willingness, and participation.

Chapter 1, as it appears in Neuroergonomics: The brain in the workplace and everyday life. The dissertation author was the primary author of this paper.

Chapter 2, as it appears in Frontiers in Human Neuroscience, 2020, Gougelet, Robert J.; Terzibas, Cengiz; & Callan, Daniel E. The dissertation author is the primary investigator and author of this paper.

Chapter 3, in part, was submitted for publication of the material as it may appear in European Journal of Neuroscience, 2020, Gougelet, Robert J. & Miyakoshi, Makoto. Bradley Voytek was also acknowledged in the acknowledgement section of the publication as it may appear. The dissertation author is the primary investigator and author of this paper.

VITA

2010	Bachelor of Arts, Psychology, New College of Florida
2012	Bachelor of Arts, Mathematics, University of South Florida
2020	Doctor of Philosophy, Cognitive Science, University of California San Diego

2012-2019	Teaching Assistant, University of California San Diego
2012-2014	Research Assistant, Cognitive Neuroscience Laboratory
2014-2019	Research Assistant, Neural and Data Analytics Laboratory
2012-2019	Research Associate, Swartz Center for Computational Neuroscience
2019-2020	Research Scientist, Naval Health Research Center

PUBLICATIONS

Gougelet, R. J., Terzibas, C., Callan, D. E. (2020) Cerebellum, basal ganglia, and cortex mediate performance of an aerial pursuit task. *Frontiers in Human Neuroscience, 14,* 29.

Gougelet, R. J. (2018). Neural oscillation dynamics of emerging interest in neuroergonomics. Invited chapter for Elsevier book Neuroergonomics: The Brain at Work in Everyday Life.

Datko, M., **Gougelet, R. J.,** Huang, M. X., & Pineda, J. A. (2016). Resting state functional connectivity MRI among spectral MEG current sources in children on the autism spectrum. *Frontiers in Neuroscience, 10,* 258.

POSTERS AND PRESENTATIONS

Gougelet, R. J., Miyakoshi, M., Voytek, B., Makeig, S. (2018). Oscillatory mechanisms of planning vs. memory. Poster presented at Society for Neuroscience, San Diego, CA.

Gougelet, R. J., Terzibas, C., Callan, D. E. (2018). Functional network activity mediates shift of attention during inattentional deafness in an aviation pursuit task. Talk presented at International Neuroergonomics Conference, Philadelphia, PA.

Gougelet, R. J., Ouyang, A. C., Patel, R. D., Wang, X., Voytek, B. (2016). Evaluating high-resolution frequency spectral estimation approaches to real-time frequency modulation neurofeedback. Poster presented at Society for Neuroscience, San Diego, CA.

Gougelet, R. J., Terzibas, C., Callan, D. E. (2016). Neuroergonomic multimodal neuroimaging during a simulated aviation pursuit task. Talk presented at International Neuroergonomics Conference, Paris, FR.

Gougelet, R. J., Donoghue, T., Piper, M., Althoff, A., Urbach, T. P., Voytek, B. (2015). Influencing visual target detection with oscillatory phase-specific stimulus presentation. Poster presented at Society for Neuroscience, Chicago, IL.

Goodman, S., Sharma, R., Datko, M., **Gougelet, R. J.,** Donoghue, T., Castro, N., Sloan, M., Gomez, D., Courelli, A., Onder, Y., Pineda, J. A. (2015) Paving the way for real-time functional imaging in autism: Preliminary results from a combined neurofeedback and biofeedback intervention. Poster presented at the Real-Time Functional Imaging and Neurofeedback Conference, Gainesville, FL.

Scheiner, G. K., Soghoyan, G. Z., **Gougelet, R. J.,** Vahid, A. M., Pineda, J. A. (2015). Changes in EEG, mindfulness, and self-experiential state through Guided Subtraction Meditation. Poster presented at Society for Neuroscience, Chicago, IL.

Soghoyan, G. Z., Scheiner, G. K., **Gougelet, R. J.,** Vahid, A. M., Pineda, J. A. (2015). EEG-mediated perceived stress reduction through Guided Subtraction Meditation. Poster presented at Society for Neuroscience, Chicago, IL.

Datko, M., **Gougelet, R. J.,** Metke, M., Donoghue, T., Kirchgessner, M., Castro, N., Huang, M. X., Pineda, J. A. (2015). MEG source modeling during imitation, observation, and resting state in children on the autism spectrum. Talk presented at Society for Neuroscience, Chicago, IL.

Gougelet, R. J., Miyakoshi, M., Makeig, S. (2014). EEG and kinematic temporal dynamics during a dart throwing visuospatial working memory task. Poster presented at Cognitive Neuroscience Society, San Francisco, CA.

Gougelet, R. J., Miyakoshi, M., Birger, A., Cummins, C., Le, J., Wooten, A., Makeig, S. (2014). Mobile Brain/Body Imaging: Combined EEG and motion capture during a dart throwing visuospatial working memory task. Poster presented at Society for Neuroscience, Washington D.C..

Bylsma, L. M., White, K. E., **Gougelet, R. J.,** Salomon, K. & Rottenberg, J. (2012). Attenuated cardiovascular reactivity in depression is mood-state dependent. Poster presented at the Annual Meeting of the Society for Psychophysiological Research, New Orleans, LA.

Gougelet, R. J. (2010) The Mu rhythm: An electrophysiological measure of motor, emotional, and cognitive empathy. Thesis defense before committee, New College of Florida, Sarasota, FL.

Gougelet, R. J. (2008) Using biocybernetics to create adaptive cognitive-based learning environments. Poster presented at the USRP Poster Session, NASA Langley Research Center

AWARDS AND INTERNSHIPS

2017 **Summer Graduate Teaching Scholar**, UCSD
Group and personalized training for teaching at the college level
Advisor: Dr. Erilynn Heinrichsen

2015 **NSF EAPSI Fellowship**, Center for Information and Neural Networks, Osaka University. Neuroergonomic multimodal neuroimaging during an aviation pursuit task
Advisor: Dr. Daniel Callan

2013 **JPLSIP Intern,** NASA Jet Propulsion Laboratory
Microwave biosensing for emergency and disaster response
Advisor: Dr. James P. Lux

2008 **USRP Intern,** NASA Langley Research Center
Using biocybernetics to create adaptive cognitive-based learning environments
Advisors: Dr. Alan Pope, Dr. Thomas Pinelli, Robert Starr, M.A.

TEACHING

2019 **Graduate TA**, Introduction to Data Science, UCSD, Dr. Shannon Ellis

2018 **Graduate TA**, Introduction to Data Science, UCSD, Dr. Bradley Voytek
Graduate TA, Cognitive Design Studio, UCSD, Dr. Mary Boyle
Instructor of Record, Introduction to Statistical Analysis, Cognitive Science Department, UCSD
Graduate TA, Prototyping, UCSD, Dr. Steven Dow
Instructor of Record, Introduction to Statistical Analysis, Cognitive Science Department, UCSD

2017 **Instructor of Record**, Introduction to Statistical Analysis, Cognitive Science Department, UCSD
Graduate TA, Cognitive Design Studio, UCSD, Dr. Nan Renner

2016 **Graduate TA**, Intro to Human-Computer Interaction, UCSD, Dr. Scott Klemmer
Graduate TA, Intro to Human-Computer Interaction, UCSD, Dr. Philip Guo
Graduate TA, Modeling and Data Analysis, UCSD, Dr. Jake Olson
Graduate TA, Intro to Data Science, UCSD, Dr. Bradley Voytek
Graduate TA, Intro to Human-Computer Interaction, UCSD, Dr. Scott Klemmer

2015 **Graduate TA**, Intro to Human-Computer Interaction, UCSD, Dr. Scott Klemmer

2014 **Massive Online Open Course TA**, Learning How to Learn, Coursera, Dr. Barbara Oakley, Dr. Terrence Sejnowski
Graduate TA, Neuroanatomy and Physiology, UCSD, Dr. Jaime Pineda
Graduate TA, Psychopharmacology, UCSD, Dr. Michael Datko
Graduate TA, Cognitive Ethnography, UCSD, Dr. Edwin Hutchins

2013 **Graduate TA,** Distributed Cognition, UCSD, Dr. Edwin Hutchins
Graduate TA, Introduction to Statistical Analysis, UCSD,
Dr. Raphael Nunez
Graduate TA, Psychopharmacology, UCSD, Dr. Matthew Schalles

2009 **Undergraduate TA**, Developmental Psychology, NCF,
Dr. Michelle Barton

2008 **Undergraduate TA**, Calculus II, NCF, Dr. David Mullins

WORK, VOLUNTEERING, AND CERTIFICATIONS

2019 **Research Scientist**, Naval Health Research Center, San Diego, CA. EEG data analysis.

2018 **Cognitive Science Department Senior TA**, UCSD. Overseeing course evaluations, faculty/TA cooperation, and training of new TA's in the department

2017 **Center for the Integration of Research, Teaching, and Learning Associate**, UCSD. NSF funded certification course for implementing and advancing effective teaching practices

Cognitive Science Department Senior TA, UCSD. Overseeing course evaluations, faculty/TA cooperation, and training of new TA's in the department

2016 **Cognitive Science Department Graduate Student Association Representative,** UCSD. Representing graduate student constituents of the department in student government proceedings

University Centers Advisory Board, UCSD
Representing graduate students in designing university center spaces and services

2015 **GrAdvantage Leadership and Teamwork Certification,** UCSD
Year-long leadership and project management training for academia and industry, culminating in a project on equality, diversity, and inclusion at UCSD presented to Vice Chancellor Becky Petitt

Cognitive Science Department Graduate Student Association Representative, UCSD
Representing graduate student constituents of the department in student government proceedings

2014 **Cognitive Science Department Graduate Outreach Coordinator,** UCSD
Organizing outreach and volunteer events for the department

Cognitive Science Department Graduate Representative, UCSD
Representing graduate student constituents of the department in intradepartmental affairs

ABSTRACT OF THE DISSERTATION

A Collection of Works in Neuroergonomics

by

Robert J. Gougelet

Doctor of Philosophy in Cognitive Science

University of California San Diego, 2020

Professor Bradley Voytek, Chair

Neuroergonomics is a nascent field of study that seeks to apply knowledge and tools from neuroscience to better optimize the tracking and regulation of human factors in the everyday and working environments. Neuroergonomics emphasizes the use of naturalistic and ecologically relevant experimental tasks to make important advancements from sterile experimental settings to useful real-world scenarios. This dissertation offers two naturalistic and ecologically relevant experimental tasks, as well as innovative neuroimaging and statistical analysis techniques, to contribute to, and demonstrate the feasibility of, the growing field of neuroergonomics. For the first experimental task, we designed a three-dimensional and first-person fMRI task during which human subjects maneuvered a simulated airplane in pursuit of a target airplane along constantly changing headings. The second experiment involves recording mobile EEG from human subjects performing a working memory adaptation of the everyday task of dart throwing. We find encouraging neuroimaging results from both experiments and relate them to important cognitive neuroscience theories on human action and working memory. In so doing, we demonstrate the feasibility of neuroergonomics and how knowledge and tools from neuroscience can indeed help us understand the brain at work and in everyday life.

CHAPTER ONE
Neural Oscillation Dynamics of Emerging Interest in Neuroergonomics

Neuroergonomists Should Know About Neural Oscillations

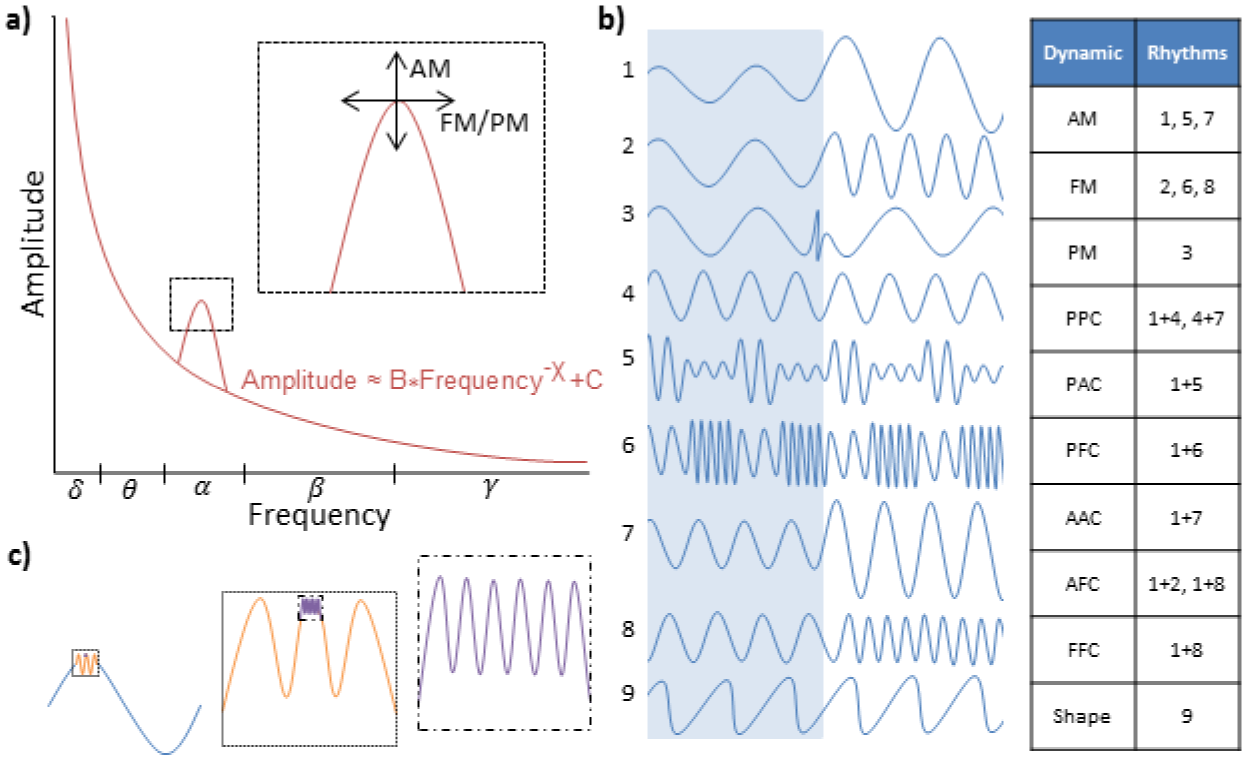
Neuroergonomists seek to apply knowledge and tools from neuroscience to better optimize the tracking and regulation of human factors in the everyday and working environments, e.g. assessing and tracking mental workload using electroencephalography (EEG; Gevins & Smith, 2006). The study of neural oscillations in neuroscience using electrophysiology continues to generate notable interest, knowledge, and tools that Neuroergonomists should attend to. Problematically, one finds little discussion on the application of what we know about neural oscillations in this nascent field of neuroergonomics. Pioneers such as Gevins and Smith (2006) have provided a solid foundation that needs building upon, especially since new tools and interpretations have arisen since their work. Thus, the next section of this chapter introduces neural oscillations and relates neural oscillation dynamics of emerging interest to neuroergonomic states of interest; particularly mental workload (Tsang & Vidulich, 2006), decision making, vigilance (Warm, Parasuraman, & Matthews, 2008), fatigue, situational awareness (Tsang & Vidulich, 2006), skill retention, and user error. The subsequent section concludes with a practical vision of how neural oscillations might be leveraged in neuroergonomics, suggesting methodology and next steps to interested neuroergonomists.

Neural Oscillation Dynamics of Emerging Interest

What are neural oscillations? Simply put, when few to millions of neurons fire together in rhythm, they change their surrounding electromagnetic field. This electromagnetic field change is proportionate to the number of neurons involved and how well-coordinated they fire. Electrophysiologists call these rhythmic changes in the electromagnetic field *neural oscillations* and use voltmeters or magnetometers to measure them (Buzsáki, Anastassiou, & Koch, 2012).

Neural oscillations have wide theoretical implications, as they may be a fundamental computational mechanism in the brain (Buzsáki & Draguhn, 2004; Siegel, Donner, & Engel, 2012). They reflect rhythmic fluctuations of underlying neural excitation and inhibition, corresponding to precise and well-regulated time windows of communication. This precisely timed communication supports preferential routing of information in the brain (Fries, 2005), and better coordinates more fundamental neural processing such as spike synchrony (Singer, 1999). This coordination can occur across large and distant brain regions, potentially mediating top-down sensorimotor processing more generally (Engel, Fries, & Singer, 2001). The precise time coordination of neural oscillations could also support bottom-up temporal binding together of features of internal representations, as well (Engel & Singer, 2001).

Electrophysiologists transform time-varying electrophysiology signals into their frequency domain, or spectral, representations to study neural oscillations (see Figure 1.1a). The Fourier transform does this by breaking down a signal into a spectrum of frequency components, each with a respective amplitude and phase. In practice, the spectrum of frequencies is broken down into normatively defined bands: delta (less than 4 Hz), theta (4 to 8 Hz), alpha (8 to 12 Hz), beta (12 to 30 Hz), and gamma (greater than 30 Hz). When a sinusoidal-like neural oscillation is presumed embedded in the time-varying signal, it is verified as a peak in amplitude on the spectrum with its own frequency and phase. Electrophysiologists identify neural oscillations by the band in which their peaks fall, e.g. calling an oscillation or rhythm in the gamma band a “gamma rhythm.” Changes in spectral properties of neural oscillations, defined here as amplitude, frequency, and phase modulation, could have broad neuroergonomic consequences.



Dynamic	Rhythms
AM	1, 5, 7
FM	2, 6, 8
PM	3
PPC	1+4, 4+7
PAC	1+5
PFC	1+6
AAC	1+7
AFC	1+2, 1+8
FFC	1+8
Shape	9

Figure 1.1. Spectral representation and dynamics of neural oscillations. AM: amplitude modulation; FM: frequency modulation; PPC: phase-phase coupling; PAC: phase-amplitude coupling; PFC: phase-frequency coupling; AAC: amplitude-amplitude coupling; AFC: amplitude-frequency coupling; FFC: frequency-frequency coupling; Shape: non-sinusoidal shape of the time-domain waveform. a) The frequency spectrum representation of an electrophysiological signal. Alpha oscillation embedded as a peak in the alpha frequency band. This oscillation can be subject to amplitude, frequency, and phase modulation. b) Modulation and coupling dynamics of different oscillations/rhythms in the time domain. Note that coupling cannot occur without modulation. c) Hierarchical PAC embedding of higher frequency oscillations in lower frequency oscillations.

Amplitude, Frequency, and Phase Modulation of Neural Oscillations

Amplitude modulation (see Figure 1.1ab), sometimes known as event-related synchronization or desynchronization (Pfurtscheller & da Silva, 1999), has been well studied and summarized elsewhere regarding neuroergonomics (Gevins & Smith, 2006), and neuroscience more generally (Klimesch, 1999). Briefly, increased amplitude of alpha oscillations is suggested to reflect increased top-down rhythmic inhibitory control of processing (Klimesch, Sauseng, & Hanslmayr, 2007). Increased inhibitory control might be used to suppress distracting external or internal information, potentially indexing mental workload, decision making, vigilance, skill retention, and user error. Engel and Fries (2010) suggest beta band amplitude increases are associated with motor control, particularly the top-down maintenance of the “status quo” of active sensorimotor processes. Beta band amplitude modulation might therefore index user error, sensorimotor skill acquisition, and decision making. In addition, frontal theta amplitude increases correspond to greater working memory load and attentional demands, as well as greater long-term learning (Gevins & Smith, 2006), and is therefore suitable for measuring mental workload and skill retention. Increased alpha and delta amplitude canonically index sleepiness and fatigue, as well.

Frequency modulation refers to the changing of frequency of the peak amplitude of a frequency band (see Figure 1.1ab), presumably reflecting an embedded oscillation (see Figure 1.1a). Frequency modulation research predominantly focuses on peak alpha frequency (PAF) (Klimesch, Schimke, & Pfurtscheller, 1993; Angelakis, Lubar, Stathopoulou, & Kounios, 2004). Higher trait-level PAF in individuals indicates higher intelligence, reading and verbal ability, and cognitive preparedness, whereas decreasing PAF parallels age-related declines in memory. Frequency modulation as an index of long-term learning and cognitive preparedness might then index skill retention and situational awareness. During task performance, transient increases in PAF reflect accurate working memory retrieval and span, whereas decreases in PAF reflect task difficulty, reaction time, and physical fatigue. Therefore, transient changes in PAF could index transient changes in mental workload, vigilance, and fatigue. Users who volitionally increase their transient PAF actually enhance their cognitive performance (Angelakis et al., 2007). Little frequency modulation results exist outside the alpha band, but there is a potential relationship between theta peak frequency and working memory load (Moran et al., 2010).

Phase modulation of a neural oscillation has been primarily studied as phase resetting (see Figure 1.1ab). Klimesch, Sauseng, and Hanslmayr (2007) suggest that phase resetting reflects early top-down influences on sensory-semantic processing and is actually the evoked phase reset of alpha oscillations, though this issue is contentious (cf. Makeig et al., 2004). Theta phase resetting has been implicated in user error (Yeung, Bogacz, Holroyd, Nieuwenhuis, & Cohen, 2007), trait intelligence (Thatcher, North, & Biver, 2008), and auditory decision making (Barry, 2009). Notably, phase and frequency modulation are mathematically related, since the slope of the phase representation of a sinusoidal signal is shallower or steeper if the frequency is slower or faster, respectively, i.e. frequency is the temporal derivative of phase. Therefore, findings regarding frequency modulation might extend to phase modulation.

Amplitude, Frequency, and Phase Coupling of Neural Oscillations

Cross-frequency coupling is a generic term for when multiple neural oscillations within or between brain regions mutually drive the spectral properties of each other and may provide profound computational affordances in the brain (Jensen & Colgin, 2007), with broad neuroergonomic consequences. Assuming only two oscillations are involved, coupling can occur in the form of phase-phase; phase-amplitude; phase-frequency; amplitude-amplitude; amplitude-frequency; or frequency-frequency interactions; all discussed below (see Figure 1.1b). Notably, all forms of coupling cannot occur without some form of modulation, implying the underlying physiological mechanisms may be the same.

Phase-phase coupling, a near-zero difference between the phases of two oscillations, is widely studied as phase synchrony, a posited fundamental mechanism of integration in the brain (Varela, Lachaux, Rodriguez, & Martinerie, 2001). Phase synchrony potentially mediates attention, multisensory integration, as well as learning and memory at multiple spatial and temporal scales (Fell & Axmacher, 2011). It could therefore be relevant to those interested in measuring mental workload, decision making, vigilance, situational awareness, and skill retention. It has also been related to user error (Cavanagh, Cohen, & Allen, 2009).

Phase-amplitude coupling provides a potentially robust, versatile, and multiscale mechanism for a nested multiplexing, or hierarchical structure, of neural oscillations (Lakatos et al., 2005). In this hierarchical structure, higher frequency oscillations increase in amplitude along the peak phases of lower frequency oscillations (see Figure 1c). Generally, large-scale network level activity is indexed by slow and low-frequency oscillations, whereas small-scale local level activity is indexed by fast and high-frequency oscillations. Phase-amplitude coupling could therefore support the transformation of information across temporal and spatial scales through this nesting of higher frequency oscillations in lower frequency oscillations (Canolty & Knight, 2010). The phase of low-frequency oscillations could then rhythmically entrain to external and internal stimuli, aligning bursts of increased gamma amplitude along the low-frequency phases, supporting well-timed learning, attention, and memory. Considering the potential role of phase-amplitude coupling in transformation of information at different scales, it could be particularly pertinent to situational awareness and decision making but could also be useful as an indicator for general information processing, relevant for mental workload, vigilance, fatigue, skill retention, and user error.

Amplitude-amplitude coupling might play an important role in large-scale neuronal interactions subserving sensorimotor decision making and top-down attention (Siegel, Donner, & Engel, 2012). This form of coupling may therefore index mental workload, decision making, vigilance, and situational awareness. Gamma amplitude comodulation could occur as the result of multiple brain regions coupling to the phase of a lower frequency, more widespread, oscillation (Buzsáki & Wang, 2012). Considering that traditional phase-phase coupling, or coherence, measures include an amplitude-amplitude component (Bruns, 2004), many phase-phase coupling findings are worth dissociating from amplitude-amplitude coupling.

Phase-frequency, amplitude-frequency, and frequency-frequency coupling seem to be understudied, perhaps due to the minimal study of frequency modulation of unitary neural oscillations. These exact terms may not emerge in the literature, as many of the other forms of modulation and coupling have arisen with different names, e.g. phase synchrony as phase-phase coupling. Therefore, standardization of terms regarding modulation and property-property coupling is suggested here, in order to emphasize the fundamental spectral properties of oscillations: amplitude, frequency, and phase.

Waveform Shape and Neural Noise

Non-synchronous, or non-oscillatory, properties of the electrophysiological signal, such as waveform shape and wideband shape of the frequency spectrum, might change with potential neuroergonomic consequences, but are understudied. Phase-amplitude and phase-phase coupling might actually be conflated with waveform shape (Cole & Voytek, 2017), so findings regarding them may actually be a consequence of waveform shape. In addition, the shape of the overall spectrum, parameterized by its fit to a broadband power law relationship between frequency and amplitude, $Amplitude \sim B * Frequency^{-\chi} + C$, could reflect the non-oscillatory "asynchronous," or scale-free, changes in cortical potentials (see Figure 1.1a). This 1/f "neural noise," in turn, could reflect the balance of excitation and inhibition across the human cortex, interdependently interacting with neural oscillations (Gao, Peterson, & Voytek, 2016). Having such a measure of excitation and inhibition through parameterization of the frequency spectrum is important, considering the critical roles excitation and inhibition play in cortical processing (Yizhar et al., 2011). The chi parameter in the power law relationship between frequency and amplitude as an index for global excitation and inhibition might therefore index mental workload, vigilance, fatigue, and situational awareness.

Leveraging Neural Oscillations in Neuroergonomics

Table 1.1 summarizes how neuroergonomists might measure and manipulate neuroergonomic states by measuring and manipulating neural oscillations. Applying the knowledge and tools of neural oscillations could take many forms. Applications in research settings could take the form of interface, workspace, or workflow redesign by measuring neural oscillation modulation and coupling dynamics during user testing. Fieldwork interventions could be done via measurement and adaptive interface response to, or active manipulation of, neural oscillation modulation and coupling.

Another form of leveraging neural oscillations could take the form of simple neurofeedback (Heinrich, Gevensleben, & Strehl, 2007). An interface readout of the user's state could be enough to significantly affect task performance. Yet another form could involve enhanced timing of the presentation of important interface and situational information. Indexing optimal brain information processing windows, e.g. particular amplitudes or phases of ongoing oscillations, could inform when adaptive interfaces present information. Lastly, real-time neurostimulation using "brain pacemakers" could affect the spectral modulation and coupling of the user's oscillations as a potential (albeit challenging) means to create optimal neuroergonomic states (Huang, Edwards, Rounis, Bhatia, & Rothwell, 2005).

Table 1.1. Measuring ergonomic/human factors via neural oscillation dynamics. An X indicates that the ergonomic/human factor could be measured by the neural oscillation dynamic, a query mark indicates no association has been widely reported. AM: amplitude modulation; FM: frequency modulation; PPC: phase-phase coupling; PAC: phase-amplitude coupling; PFC: phase-frequency coupling; AAC: amplitude-amplitude coupling; AFC: amplitude-frequency coupling; FFC: frequency-frequency coupling; 1/f: power law shape of Fourier spectrum; Shape: shape of the time-domain waveform.

	AM	FM	PM	PPC	PAC	AAC	PFC	AFC	FFC	1/f	Shape
Mental workload	X	X	?	X	X	X	?	?	?	X	?
Decision Making	X	X	X	X	X	X	?	?	?	?	?
Vigilance	X	X	X	X	X	X	?	?	?	X	?
Fatigue	X	X	?	?	X	?	?	?	?	X	?
Situational Awareness	X	X	X	X	X	X	?	?	?	X	?
Skill Retention	X	X	X	X	X	?	?	?	?	?	?
User error	X	?	X	X	X	?	?	?	?	?	?

How do we measure neural oscillations in research settings? For an excellent introduction to time-series analysis of electrophysiology signals, and how to extract amplitude, frequency, and phase information from unitary oscillations see Cohen (2014). Phase-phase coupling can be measured using phase-locking statistics (Lachaux, Rodriguez, Martinerie, & Varela, 1999). Phase-amplitude coupling has a variety of methods of measurement (Tort, Komorowski, Eichenbaum, & Kopell, 2010). Amplitude-amplitude coupling has been measured using amplitude envelope correlation (Bruns, 2004). Unfortunately, methods for measuring amplitude-frequency, phase-frequency, and frequency-frequency coupling have not been thoroughly developed.

How do we measure neural oscillations in the field? EEG is likely best. One suggested method is the use of independent components analysis (Delorme & Makeig, 2004) to decompose EEG data into oscillatory and non-oscillatory brain activity (e.g. Onton & Makeig, 2009). Next, one discards noisy independent components and non-brain components identified using well-constrained inverse models (Baillet, Mosher, & Leahy, 2001). Processing data in this way could overcome many noise issues.

What can neuroergonomists do? Firstly, they can explore the understudied domains of knowledge in neural oscillation research: frequency and phase modulation; phase-frequency, amplitude-frequency, and frequency-frequency coupling; waveform shape; and broadband asynchronous activity. Neuroergonomists can also conduct multimodal studies relating less tractable tools to more tractable tools, e.g. magnetoencephalography to EEG, or functional magnetic resonance imaging to EEG. Because they have the vision to extend the knowledge and tools of neuroscience into the everyday and working environments, neuroergonomists are poised to make much needed strides in the application of neural oscillation research.

Acknowledgements

Chapter 1, as it appears in Neuroergonomics: The brain in the workplace and everyday life. The dissertation author was the primary author of this paper.

References

Angelakis, E., Lubar, J. F., Stathopoulou, S., & Kounios, J. (2004). Peak alpha frequency: an electroencephalographic measure of cognitive preparedness. Clinical Neurophysiology, 115(4), 887-897.

Angelakis, E., Stathopoulou, S., Frymiare, J. L., Green, D. L., Lubar, J. F., & Kounios, J. (2007). EEG neurofeedback: a brief overview and an example of peak alpha frequency training for cognitive enhancement in the elderly. The Clinical Neuropsychologist, 21(1), 110-129.

Barry, R. J. (2009). Evoked activity and EEG phase resetting in the genesis of auditory Go/NoGo ERPs. Biological Psychology, 80(3), 292-299.

Baillet, S., Mosher, J. C., & Leahy, R. M. (2001). Electromagnetic brain mapping. IEEE Signal Processing Magazine, 18(6), 14-30.

Bruns, A. (2004). Fourier-, Hilbert-and wavelet-based signal analysis: are they really different approaches?. Journal of neuroscience methods, 137(2), 321-332.

Buzsáki, G., Anastassiou, C. A., & Koch, C. (2012). The origin of extracellular fields and currents—EEG, ECoG, LFP and spikes. Nature Reviews Neuroscience, 13(6), 407-420.

Buzsáki, G., & Draguhn, A. (2004). Neuronal oscillations in cortical networks. Science, 304(5679), 1926-1929.

Buzsáki, G., & Wang, X. J. (2012). Mechanisms of gamma oscillations. Annual review of neuroscience, 35, 203-225.

Canolty, R. T., & Knight, R. T. (2010). The functional role of cross-frequency coupling. Trends in Cognitive Sciences, 14(11), 506-515.

Cavanagh, J. F., Cohen, M. X., & Allen, J. J. (2009). Prelude to and resolution of an error: EEG phase synchrony reveals cognitive control dynamics during action monitoring. Journal of Neuroscience, 29(1), 98-105.

Cohen, M. X. (2014). Analyzing neural time series data: Theory and practice. Boston, MA: MIT Press.

Cole, S. R., & Voytek, B. (2017). Brain oscillations and the importance of waveform shape. Trends in Cognitive Sciences.

Delorme, A., & Makeig, S. (2004). EEGLAB: an open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. Journal of Neuroscience Methods, 134(1), 9-21.

Engel, A. K., Fries, P., & Singer, W. (2001). Dynamic predictions: oscillations and synchrony in top–down processing. Nature Reviews Neuroscience, 2(10), 704-716.

Engel, A. K., & Fries, P. (2010). Beta-band oscillations—signalling the status quo?. Current Opinion in Neurobiology, 20(2), 156-165.

Engel, A. K., & Singer, W. (2001). Temporal binding and the neural correlates of sensory awareness. Trends in Cognitive Sciences, 5(1), 16-25.

Fell, J., & Axmacher, N. (2011). The role of phase synchronization in memory processes. Nature Reviews Neuroscience, 12(2), 105-118.

Fries, P. (2005). A mechanism for cognitive dynamics: neuronal communication through neuronal coherence. Trends in Cognitive Sciences, 9(10), 474-480.

Gao, R. D., Peterson, E. J., & Voytek, B. (2016). Inferring synaptic excitation/inhibition balance from field potentials. bioRxiv, 081125.

Gevins, A., & Smith, M. E. (2006). Electroencephalography (EEG) in neuroergonomics. Neuroergonomics: The brain at work, 15-31.

Heinrich, H., Gevensleben, H., & Strehl, U. (2007). Annotation: Neurofeedback–train your brain to train behaviour. Journal of Child Psychology and Psychiatry, 48(1), 3-16.

Huang, Y. Z., Edwards, M. J., Rounis, E., Bhatia, K. P., & Rothwell, J. C. (2005). Theta burst stimulation of the human motor cortex. Neuron, 45(2), 201-206.

Jensen, O., & Colgin, L. L. (2007). Cross-frequency coupling between neuronal oscillations. Trends in Cognitive Sciences, 11(7), 267-269.

Klimesch, W. (1999). EEG alpha and theta oscillations reflect cognitive and memory performance: a review and analysis. Brain Research Reviews, 29(2), 169-195.

Klimesch, W., Sauseng, P., & Hanslmayr, S. (2007). EEG alpha oscillations: the inhibition–timing hypothesis. Brain Research Reviews, 53(1), 63-88.

Klimesch, W., Schimke, H. & Pfurtscheller, G. (1993). Alpha frequency, cognitive load and memory performance. Brain Topography, 5(3), 241-251.

Lachaux, J. P., Rodriguez, E., Martinerie, J., & Varela, F. J. (1999). Measuring phase synchrony in brain signals. Human Brain Mapping, 8(4), 194-208.

Lakatos, P., Shah, A. S., Knuth, K. H., Ulbert, I., Karmos, G., & Schroeder, C. E. (2005). An oscillatory hierarchy controlling neuronal excitability and stimulus processing in the auditory cortex. Journal of Neurophysiology, 94(3), 1904-1911.

Onton, J. A., & Makeig, S. (2009). High-frequency broadband modulation of electroencephalographic spectra. Frontiers in Human Neuroscience, 3, 61.

Makeig, S., Debener, S., Onton, J., & Delorme, A. (2004). Mining event-related brain dynamics. Trends in Cognitive Sciences, 8(5), 204-210.

Moran, R. J., Campo, P., Maestu, F., Reilly, R. B., Dolan, R. J., & Strange, B. A. (2010). Peak frequency in the theta and alpha bands correlates with human working memory capacity. Frontiers in Human Neuroscience, 4, 200.

Pfurtscheller, G., & Da Silva, F. L. (1999). Event-related EEG/MEG synchronization and desynchronization: basic principles. Clinical Neurophysiology, 110(11), 1842-1857.

Siegel, M., Donner, T. H., & Engel, A. K. (2012). Spectral fingerprints of large-scale neuronal interactions. Nature Reviews Neuroscience, 13(2), 121-134.

Singer, W. (1999). Neuronal synchrony: a versatile code for the definition of relations?. Neuron, 24(1), 49-65.

Thatcher, R. W., North, D. M., & Biver, C. J. (2008). Intelligence and EEG phase reset: a two compartmental model of phase shift and lock. NeuroImage, 42(4), 1639-1653.

Tort, A. B., Komorowski, R., Eichenbaum, H., & Kopell, N. (2010). Measuring phase-amplitude coupling between neuronal oscillations of different frequencies. Journal of Neurophysiology, 104(2), 1195-1210.

Tsang, P. S., & Vidulich, M. A. (2006). Mental workload and situation awareness. In Salvendy, G. (Ed.), Handbook of human factors and ergonomics (pp. 243-268), (3rd ed.). Retrieved from http://dx.doi.org/10.1002/0470048204.ch9

Varela, F., Lachaux, J. P., Rodriguez, E., & Martinerie, J. (2001). The brainweb: phase synchronization and large-scale integration. Nature Reviews Neuroscience, 2(4), 229-239.

Warm, J. S., Parasuraman, R., & Matthews, G. (2008). Vigilance requires hard mental work and is stressful. Human Factors: The Journal of the Human Factors and Ergonomics Society, 50(3), 433-441.

Yeung, N., Bogacz, R., Holroyd, C. B., Nieuwenhuis, S., & Cohen, J. D. (2007). Theta phase resetting and the error-related negativity. Psychophysiology, 44(1), 39-49.

Yizhar, O., Fenno, L. E., Prigge, M., Schneider, F., Davidson, T. J., O’Shea, D. J., ... & Stehfest, K. (2011). Neocortical excitation/inhibition balance in information processing and social dysfunction. Nature, 477(7363), 171-178.

CHAPTER TWO
Cerebellum, Basal Ganglia, and Cortex Mediate Performance of an Aerial Pursuit Task

Abstract

The affordance competition hypothesis is an ethologically inspired theory from cognitive neuroscience that provides an integrative neural account of continuous, real-time behavior, and will likely become increasingly relevant to the growing field of neuroergonomics. In the spirit of neuroergonomics in aviation, we designed a three-dimensional, first-person, continuous, and real-time fMRI task during which human subjects maneuvered a simulated airplane in pursuit of a target airplane along constantly changing headings. We introduce a pseudo-event-related, parametric fMRI analysis approach to begin testing the affordance competition hypothesis in neuroergonomic contexts and attempt to identify regions of the brain that exhibit a linear metabolic relationship with the continuous variables of task performance and distance-from-target. In line with the affordance competition hypothesis, our results implicate the cooperation of the cerebellum, basal ganglia, and cortex in such a task, with greater involvement of the basal ganglia during good performance, and greater involvement of cortex and cerebellum during poor performance and when distance-from-target closes. We briefly review the somatic marker and dysmetria of thought hypotheses, in addition to the affordance competition hypothesis, to speculate on the intricacies of the cooperation of these brain regions in a task such as ours. In doing so, we demonstrate how the affordance competition hypothesis and other cognitive neuroscience theories are ready for testing in continuous, real-time tasks such as ours and in other neuroergonomic settings more generally.

Introduction

For catching dinner, a mate, or a baseball, the visual tracking and interception of moving targets is a pertinent task to many creatures. Brain-imaging studies that examine this task often operationalize it in an overly simplistic and reductionist manner, using only basic shapes and simple movement, which are far removed from real world experience. The nascent field of neuroergonomics attempts to address this oversimplification by bringing neuroscience into everyday life and the workplace (Parasuraman, 2003). Moreover, recent invocations of ethology in cognitive neuroscience have emphasized consideration of naturalistic real-time behavior and suggest new interpretations of neural data in ethological and ecological contexts (Cisek, 2007; Cisek & Kalaska, 2010), like those of interest in neuroergonomics. In this experiment, we adopt a neuroergonomic and ethological framework and use a robust real-world aviation task with continuous, real-time interactivity to identify brain regions underlying the visual tracking and interception of a moving object.

Previous research on visual tracking and interception of moving targets have identified numerous brain regions involved in visual perception, motor control, prediction, planning, and execution. These brain regions include middle temporal/V5, lateral occipital cortex, inferior parietal lobule, superior parietal lobule, frontal eye field, sensorimotor cortex, supplementary motor area, cerebellum, and basal ganglia (Fautrelle et al., 2011; Field and Wann 2005; Lencer and Trillenberg, 2008; Lungu et al., 2016; Nagel et al., 2006; Ohlendorf et al., 2007; Senot et al., 2008). While identifying the metabolic activity of specific brain regions in the performance of our task is important, the "affordance competition hypothesis" offers an appealing systems-level and integrative account of how the brain might perform continuous and real-time actions in tasks such as ours and in the world. We believe the affordance competition hypothesis will become increasingly relevant in neuroergonomic contexts for this reason.

The affordance competition hypothesis emphasizes a pragmatic and parallelized role of the brain in the performance of real-time and interactive behavior (for a review, see Cisek, 2007;

Cisek & Kalaska, 2010). The affordance competition hypothesis posits that ongoing action selection, i.e. "what to do", and action specification, i.e. "how to do it", occurs in a highly distributed and simultaneous manner, with the cerebellum, basal ganglia, and cortex specifically implicated as important network nodes. More specifically, peaks of tuned neural activity pertinent to multiple potential actions in visual, parietal, and premotor cortex are competitively biased by recurrent connections with basal ganglia and prefrontal cortical regions that collect information for action selection, cerebellar attunement, and execution. The integrative and cooperative function of the cerebellum, basal ganglia, and cortex seems evident elsewhere in the literature (Bostan & Strick, 2018, Caligiore et al., 2017).

Concurrent to new interpretations of neural data, the affordance competition hypothesis emphasizes continuous, real-world, real-time, and interactive tasks, in consideration of the evolution of the brain and its naturally time-pressured, complex, and risky ethological circumstances. Recent theory on grounded and embodied cognition echo these sentiments (Wilson, 2002; Barsalou, 2008). It stands to reason that simultaneous action selection and specification, especially among many multiple potential actions, has ethological advantages over the serial processing of complete internal representations and abstractions of the world, as is suggested by contrasting prominent information processing accounts of cognition.

With these ethological considerations of the affordance competition hypothesis in mind, and in an attempt to apply it in a neuroergonomic setting, we designed a three-dimensional and first-person fMRI task during which human subjects maneuvered a simulated airplane in pursuit of a target airplane along constantly changing headings; see Figure 2.1 for details. This task was originally inspired to be a three-dimensional and more realistic version of the traditional smooth pursuit (Krauzlis, 2004) and shape-tracing tasks (Gowen & Miall, 2007). This task might be imagined as a formation-flying task, wherein the subjects are "following the leader" or it might also be imagined as a non-violent version of a simulated aerial "dog-fight".

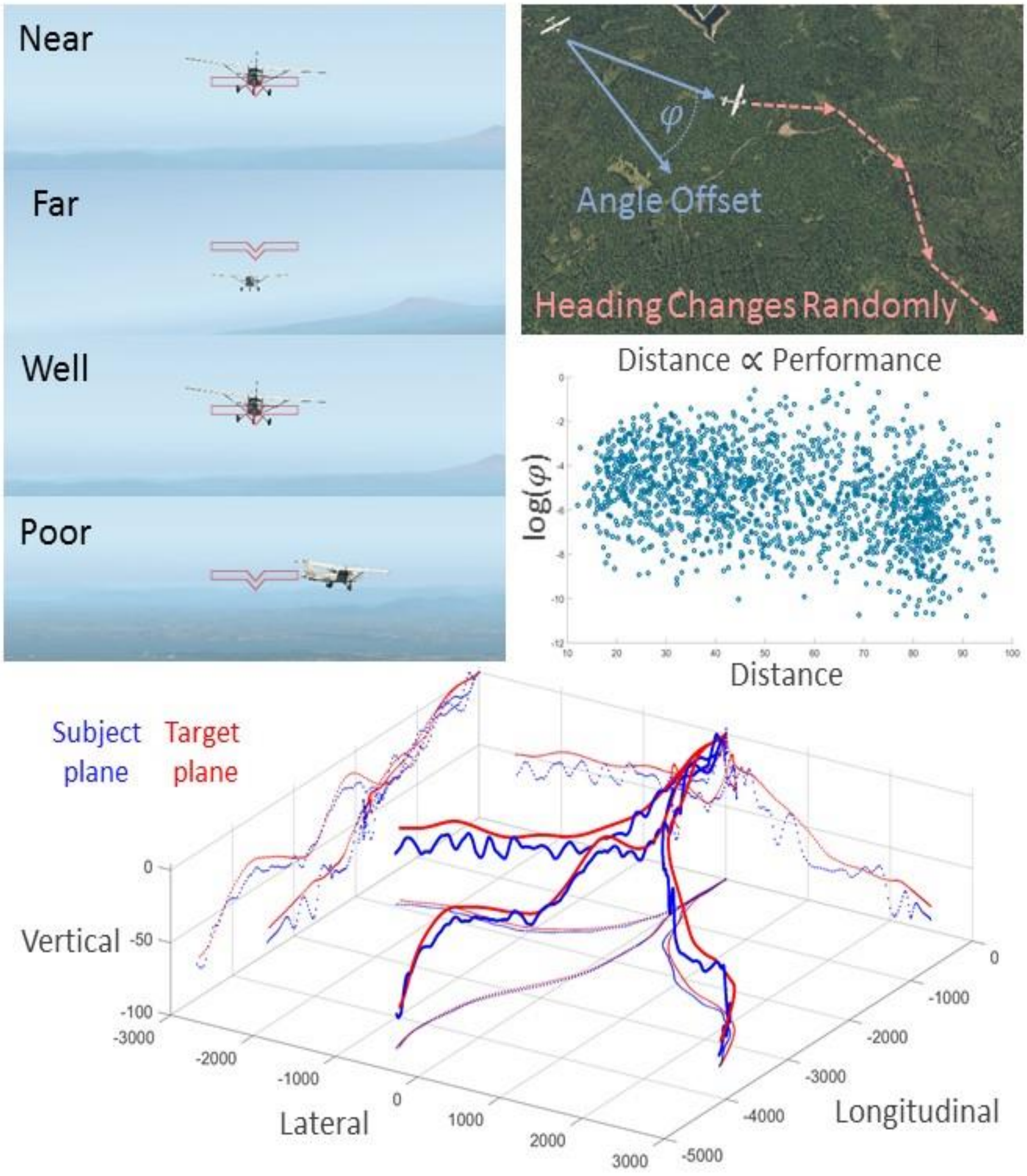


Figure 2.1. Description of the experimental task conducted in the fMRI scanner. (A) First-person depiction of two behavioral variables of interest: experimentally manipulated distance (top two) and performance (bottom two). (B) Subjects were tasked with training a crosshair on the target airplane, which changed headings randomly. Performance was measured as log of three-dimensional angle offset; negative is better. (C) Behavioral results showed a strong relationship between distance and performance; flying farther away was easier. (D) Three-dimensional depiction of three runs of subject and target plane trajectories; note the constant course correction of the subject.

We quantified subject performance of this task as how well the subjects could keep the target airplane in the center of their visual field, measured by the logarithm of the angle offset (in radians) between the three-dimensional vector projected outward from the center of their visual field and the vector projected from the three-dimensional location of the subject airplane to the target airplane (Figure 2.1A and 2.1B). This task was made particularly challenging by imposing smooth but unpredictable heading changes of the leading airplane, as well as imposing smooth changes in both airplanes' velocities to vary the distance between the two airplanes in an oscillating pattern. See Figure 2.1D for example traces of the location of both airplanes during three runs of the task.

Under the affordance competition hypothesis, we predict this task, and others like it, will exhibit highly distributed brain activity, with the cerebellum, basal ganglia, and cortex as important network nodes, and as continuous action selection and specification co-occur. An open question under the affordance competition hypothesis is the extent to which ongoing performance and time pressures of the task influence network activity. We compared brain activity when subjects were performing poorly on the task vs. when they were performing well. We also manipulated the ongoing distances between the airplanes and predict that greater time pressure, i.e. closer proximity, will elicit greater network activity as action selection and specification are forced to occur with greater simultaneity. Since both task performance and distance-from-target are continuous variables with no discernible events to time-lock to, we introduce a pseudo-event-related, parametric fMRI analysis approach to test these predictions. Lastly, we briefly review the somatic marker and dysmetria of thought hypotheses, in addition to the affordance competition hypothesis, to speculate on the intricacies of the cooperation of these brain regions in a task such as ours.

Methods

Subjects

24 Japanese subjects from Osaka University and neighboring areas had an average age of 24.4 (SE = 1.35) years, five of which were female, and all were right-handed. Fourteen of the subjects identified themselves as pilots and were recruited from nearby glider clubs. The other subjects reported experience with first-person video games, e.g. driving games. All subjects had normal or corrected visual acuity using MRI-compatible eyeglasses. All subjects had previously trained extensively on the experimental task, having completed the same task as part of a larger study prior to entering the scanner.

Procedures

The flying task.

The flying task was designed in X-Plane 9, a versatile and programmable flight simulation software. Subjects flew behind a target plane at experimentally manipulated headings, speeds, and distances, and were tasked to maintain pursuit of the target plane and train a crosshair on the target plane by maneuvering their own plane (Figure 2.1A). Subjects controlled a fiber-optic flight stick with only pitch and roll axes enabled. Subject and target plane throttles were experimentally manipulated to vary the distance between them. The heads-up display for the subjects was limited to a simple crosshair. Each flying block was 90 seconds long, followed by a 60 second passive period. Subjects flew four flying blocks. See the following articles for further information regarding the fMRI and MEG compatible flight simulation system utilizing X-Plane (Callan et al., 2012; Callan et al., 2013; Callan et al., 2016a; 2016b; Durantin et al., 2017). Subjects also performed an auditory task simultaneous to the flying task, results from which showed no statistical significance and are not presented here.

In the scanner.

Audio and video stimuli for the flying task were presented to the subject within the MRI scanner. Video was projected to a mirror behind the head coil that could be viewed by a mirror mounted on the head coil. MR-compatible headphones were used to present audio (Hitachi Advanced Systems' ceramic transducer headphones; frequency range 30 – 40,000 Hz; approximately 20 dB SPL passive attenuation). The engine, propeller, and wind sounds of the airplane were constantly playing in the background. This background sound was presented at approximately 85 dBA with the greatest power at 120 Hz with some reduced power at 100 Hz, 155 Hz, 206 Hz, 236 Hz, 275Hz, 310 Hz, 350 Hz, and 466 Hz (recorded using Bruel & Kjaer sound level meter type 2250-S).

Scanner noise.

The maximum sound pressure level recorded inside the bore for the multiband EPI sequence used in this study was 95 dBA with a dominant peak at 700 Hz and a lesser one at 2200 Hz (recorded using a microphone on Opto Acoustics MRI compatible noise canceling headphones). The Hitachi Advanced Systems' headphones used in this study provide approximately 20 dB of passive attenuation. This places the scanner noise at approximately 75 dBA, about 10 dBA lower than the level at which the background noise was presented.

fMRI

Scanning.

This fMRI experiment was conducted at the Center for Information and Neural Networks using a Siemens Trio 3T scanner using similar procedures as those reported in Durantin et al. (2017). We used a multiband (factor = 2) gradient-echo EPI sequence employing the blipped CAIPI algorithm (Setsompop et al., 2012). The scanning parameters were the following: Coil =

32 Channel head coil; FOV = 192x192mm; Matrix 64x64; TR = 1700 ms; TE = 30 ms; FA = 70 degrees; Slice thickness = 3.0 mm no gap (3x3x3 mm voxel resolution across the entire brain); Number of slices = 50; Series = Interleaved). Given the low multiband factor of 2 (Preibisch et al., 2015; Todd et al., 2016) combined with the 8mm smoothing preprocessing step it is unlikely that our multiband scanning procedures adversely affect our results. An entire experimental session consisted of one fMRI session of around 11.5 minutes (approximately 400 scans). Some of the subjects had a resting state 8-minute session (283 scans) and/or a T1 anatomical MRI scan with 1x1x1 mm voxel resolution before and/or after the experimental session. The resting state scans were not used in the fMRI analysis. Dummy scans were automatically collected by the Siemens Trio 3T Scanner. Fieldmaps were not collected.

The subjects were instructed to keep their body as still as possible to reduce the degree of head and body movement artifacts. The use of a strap on the forehead and cushions around the head were also used to immobilize the head. The joystick was placed next to the subject in a manner such that minimal movement of the hand and wrist was required to control the continuous movement of the airplane, in order to reduce potential body movement related artifacts.

Preprocessing.

The fMRI scans were preprocessed using functions within SPM8 (Wellcome Department of Cognitive Neurology, UCL). Images from the experimental session were realigned, unwarped, and spatially normalized to a standard space using a template EPI image (2x2x2 mm voxels) provided in SPM, and were smoothed using an 8x8x8 mm FWHM Gaussian kernel. Spatial normalization was conducted by using the mean EPI image (after realignment and unwarping preprocessing steps) as the source image, and the SPM MNI EPI image (given with the SPM software) as the template image to normalize to. One advantage of using the mean EPI image rather than an anatomical T1 or T2 image for normalization is that it avoids the necessary extra step of having to co-register the T1 (or T2) image to the same space as the acquired EPI images (which could result in some degree of error) in order to apply the normalization parameters to the entire set of EPI used for further SPM analysis. No subjects were excluded because of excessive head motion. All subjects had less than 3 mm translation and 5 degrees rotation deviations between scans. The realignment parameters were used as regressors of non-interest to account for small deviations in head movement across scans. Auto-regression was used to correct for serial correlations. High pass filtering (cutoff period 240 seconds; twice the maximum duration between identical condition stimuli) was carried out to reduce the effects of extraneous variables (scanner drift, low frequency noise, etc.).

Analysis.

Regional brain activity for each subject for the various conditions was assessed using a general linear model (GLM) employing a pseudo-event-related design. Given the continuous nature of the two variables of interest, flying performance and flying distance, there were no overt experimental events to time-lock the analysis to. Meanwhile, a block design would not provide much temporal precision below the 90 s flying blocks. Instead, randomly time-jittered pseudo-events were generated throughout the time course of the task. To prevent temporal dependence effects, the interval between pseudo-events was randomly generated from an exponential distribution with a minimum of three seconds and a maximum of fifteen seconds. In order to investigate a linear relationship between the time-varying values of the two variables of interest and brain activity, a parametric modulator approach was employed (for an example, see Negel et al., 2006).

Parametric modulation is implemented as amplitude weighting of the impulse functions corresponding to pseudo-event onset by the values of the continuous “parametric modulators” performance and distance. Flying performance took continuous values between 1 and 2 radians corresponding to the angle offset between the center of the visual field and the location of the center of the target airplane. Flying distance took continuous values between approximately 10 and 150 meters. These values were intrinsically normalized relative to each subject’s average performance and distance. The canonical hemodynamic response function (HRF) was convolved with the parametrically modulated pseudo-event onset impulse functions and represented in the GLM to account for lag in the Blood Oxygenation Level Dependent (BOLD) response.

Two experimental regressors (flying performance and distance) were included in the GLM as parametric modulators. Including both parametric modulators in the same GLM allows for the contribution for each parameter to be determined while removing the effect of the other. This is because the parameter that is not being used for the contrast under investigation will be treated as a regressor of non-interest and its variance will be removed from the signal (Keibel and Holmes, 2004). For two contrasts, the parametric modulators were made negative to identify metabolic activity that exhibits the opposite relationship with the parametric modulators, i.e. identify regions that are more active when performance worsens or when distance decreases. Six head-realignment parameters were also included in the GLM for all analyses as regressors of non-interest to account for artifacts in head movement correlations. An additional regressor corresponding to an unrelated auditory task was used to regress out potential effects of this task. Fixed effects analyses were conducted for each subject. Random effects analyses were conducted across subjects for the contrasts of interest given below using t-tests within SPM8.

Results

Behavior

Flying performance was quantified as a three-dimensional angle offset, in radians, and was transformed logarithmically in preparation for a parametric statistical test, and showed a statistical correlation with experimentally manipulated distance; r(1526) = -0.33, p = 7.39 x 10-41 (Figure 2.1C). Subjects performed better when farther away from the target. This relationship survives with similarly strong results after detrending to remove time-series dependence effects r(1525) = -0.31, p = 2.53 x 10-36.

fMRI

As can be seen in Figure 2.1C, there is a small (r = -0.33) but significant correlation between performance and distance. By including these two parametric modulators in the same GLM it is possible to treat the variance of one parametric modulator as an effect of non-interest and remove it from the signal to better determine the unique contribution of the other parametric modulator for each contrast of interest. The results reported in Figures 2.2 and 2.3, and Table 2.1 report contributions for each parametric modulator and contrast of interest.

The first contrast (Figure 2.2A) shows the parametric modulation of brain activity by poor task performance. Large areas of the frontal and visual cortices and cerebellum were activated. The second contrast (Figure 2.2B) shows the parametric modulation of brain activity relative to good task performance. The basal ganglia are clearly identified, together with visual and insular cortices. The third contrast (Figure 2.3) shows an *increase* in parametric modulated activity by distance. The results are similar to that of the flying contrasts; except less frontal activity, and greater activity in the parietal and somatosensory cortices. No significant voxels were found showing a *decrease* in parametric modulated activity by distance. A separate event-related analysis design targeting the events of the secondary auditory task produced no significant voxels of activation. Contrasts testing the interaction between the secondary auditory task and both performance and distance of the current model also produced no significant results that survived corrections for multiple comparisons.

Discussion

Activity concurrent with poor performance (Figure 2.2A) on the task was found primarily in cortical and cerebellar regions. Activity concurrent with performing well (Figure 2.2B) on the task was found primarily in the basal ganglia, as well as in primary visual and motor cortices. As time-pressure increased, and distance-to-target closed, widespread cortical and cerebellar activity, particularly in parietal and somatosensory cortices, increased (Figure 2.3). The results of our experiment seem to support the affordance competition hypothesis (Cisek, 2007; Cisek & Kalaska, 2010), which claims that the cerebellum, basal ganglia, and cortex are involved in ethological and ecologically relevant continuous, real-time tasks such as ours.

One striking result is the isolated involvement of the basal ganglia when flying well. Encouragingly, Durantin, Dehais, Gonthier, Terzibas, and Callan (2017) found similar results to ours for flying well; the basal ganglia, namely the putamen and caudate, were active when their subjects were performing their flying task well. Durantin et al. (2017) also found similar results to ours for poor flying performance; with widespread posterior and cerebellar activity and notable activity in the right prefrontal regions, though orbitofrontal activity is absent in their results. On the other hand, brain activity regarding first-person flying in Callan et al. (2012) showed similar right (and left) prefrontal activity together with orbitofrontal activity and widespread posterior and cerebellar activity. Our results are also very similar to the involvement of the cerebellum, basal ganglia, and cortex in maintaining a safe driving distance (Uchiyama, Ebe, Kozato, Okada, & Sadato, 2003). While our results reproduce previous findings and generally confirm the affordance competition hypothesis, future work is necessary to elucidate the intricacies of the cooperation of these brain regions, but we provide some speculation below.

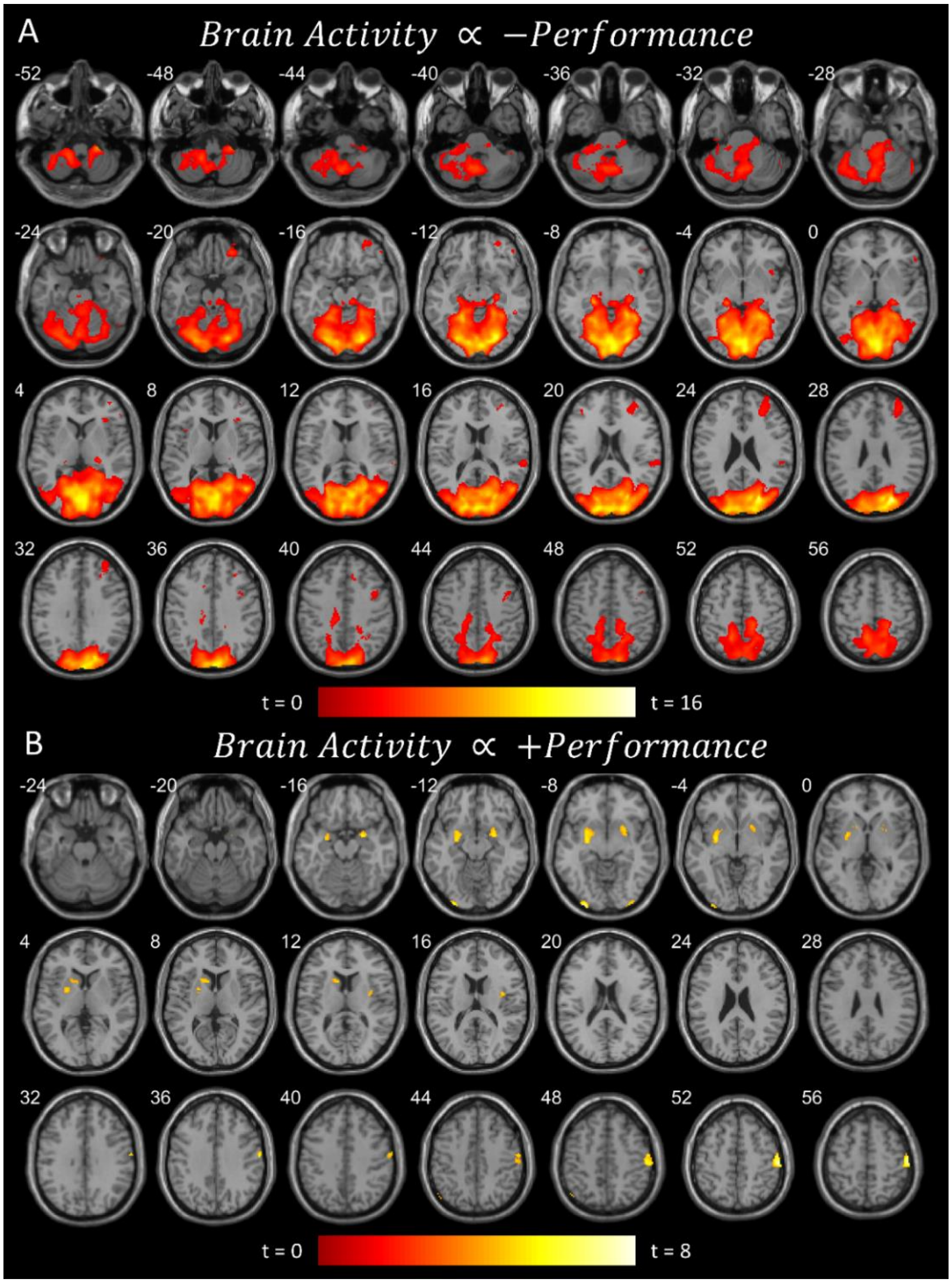


Figure 2.2 (A) Brain areas that become more active when performance worsens, or less active when performance improves (pFDR < 0.05 peak level corrected across entire brain) rendered on anatomical MRI slices using xjView toolbox (https://www.alivelearn.net/xjview). Note cerebellar and cortical activity. (B) Brain areas that become more active when performance improves, or less active when performance worsens. Same rendering as (A). Note basal ganglia activity.

Cerebellum and Dysmetria of Thought

The cerebellum is often understood as a clock or “time machine” (Bareš et al., 2019). The cerebellum is comprised of a unique and specialized neuronal architecture that provides a mechanism by which neuronal signals can be temporally manipulated and synchronized (Ivry & Keele, 1989), offering a neural substrate dedicated to temporal information processing. In particular, the cerebellum appears to encode signal predictability, receiving gated input dependent upon whether such input is expected (Lawrenson, Watson, & Apps, 2016), thereby reflecting its important role as a mechanism of signal comparison and feedback control, especially in motor timing (Eccles, 2013).

Indeed, the cerebellum appears highly involved in the process of the perception of time, itself (Ivry & Schlerf, 2008). Moreover, neural disorders such as Parkinson’s and spinocerebellar ataxia can disrupt the cerebellum’s timing functionality, leading to deficits in motor timing (Bareš et al., 2010; Bareš et al., 2011). These deficits might also occur at a network level, namely in cervical dystonia, potentially interfering with the cooperation between the cerebellum and basal ganglia (Filip et al., 2017).

Under the "dysmetria of thought" hypothesis, the unique neural architecture of the cerebellum appears to support a non-conscious "harmonizing" among converging neural signals of internal representations, external stimuli, and self-generated responses (Schmahmann, 2010). Such a "universal cerebellar computation" is useful in not just motor, but cognitive and autonomic/emotional contexts as well (Buckner, 2011, Schmahmann, 1996), wherein a dysfunctional cerebellum can lead to broad yet selective pathologies (Schmahmann, 2004). In line with the dysmetria of thought hypothesis, the cerebellum therefore seems perhaps relevant to our task as a hub for the harmonizing of eye and hand motor decision-making, internal and external representations of self, target, and environment, and perhaps motivational priorities and emotional states as well.

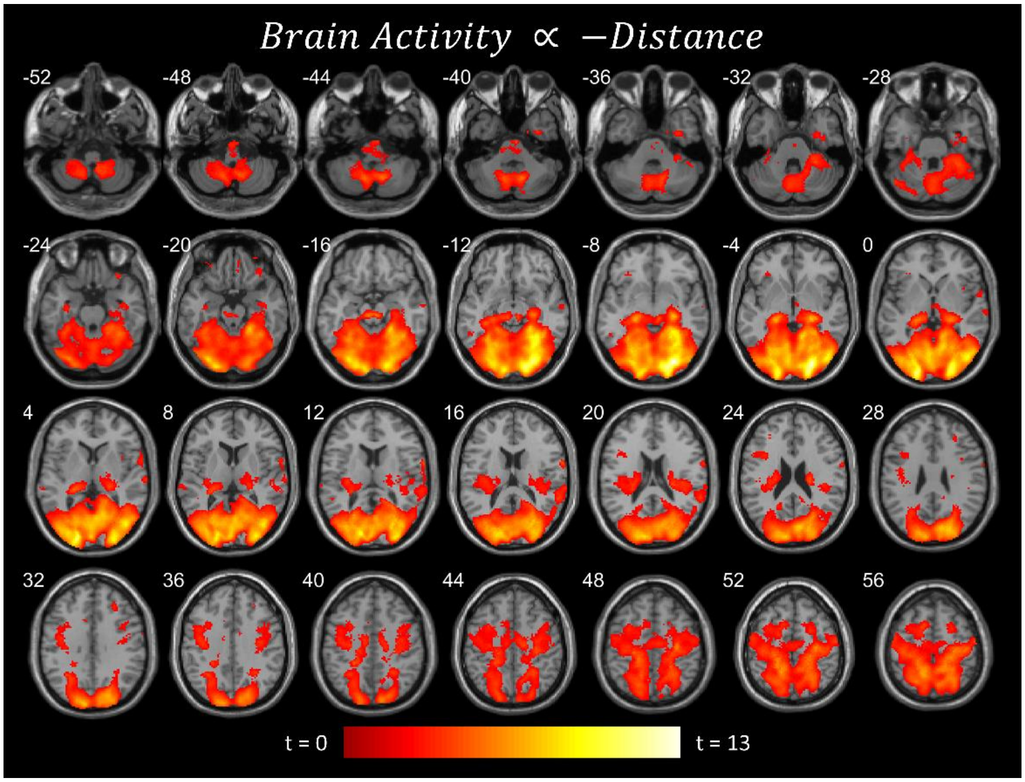


Figure 2.3. Brain areas that become more active when near the target. Significant parametric modulation (pFDR < 0.05 peak level corrected across entire brain) rendered on anatomical MRI slices using xjView toolbox (https://www.alivelearn.net/xjview). Note widespread, distributed activity, particularly in cerebellum and cortex.

Cortex and Somatic Markers

We observed widespread cortical activity during poor performance and near distance-from-target. The prefrontal cortex is suggested to be responsible for the maintenance of task-relevant information over time (Miller & Cohen, 2001). While inaccessible via the current task and analysis design, we speculate the activity we observed in the dorsolateral prefrontal cortex, as well as in the visual, orbitofrontal, and insular cortices, mediates the organization of task-relevant internal and external representations for input into the activated cerebellum, wherein its inputs are "harmonized" for subsequent output to premotor and motor cortices.

Under the “somatic marker hypothesis”, the ventromedial cortex is a frontal cortical region suggested to use its relationship with the amygdala and insular/somatosensory cortices to guide somatic state-dependent decision making (Bechara, Damasio, & Damasio, 2000). We found significant metabolic activity in these regions. Our first-person task, with lifelike continuous responsiveness and engagement, likely invokes somatic markers that guide action, perhaps indicating how the airplane becomes an "extension" of the body (Callan et al., 2012). Moreover, Menon and Uddin (2010) have proposed an important role for the insular cortex as facilitating access to attentional and working memory resources of large-scale cortical networks, as well. We suspect that the insular cortex activity we found during poor performance is concurrent with the aversive state of being out of control of the airplane, creating an aforementioned somatic marker (Bechara, Damasio, & Damasio, 2000) that instigates widespread cerebellar and cortical network reorganization (Menon & Uddin, 2010).

Basal Ganglia

The basal ganglia are best known for their involvement in the performance and acquisition of goal-directed behavior and reward processing, involving large networks of functionally parallel cortical and subcortical circuits (Haber, 2003; Haber & Knutson, 2010). The basal ganglia have also been broadly implicated in the inhibition of competing, and disinhibition of goal-directed, motor programs (Mink, 1996). Current suggestions of the mechanism by which the basal ganglia perform these functions is through the selection and inhibition of cortical and subcortical signals via internal reentrant loops across mainly parallel circuits (Lanciego, Luquin, & Obeso, 2012).

From the above, we therefore believe the basal ganglia is in the position to balance motivational and arousal decision factors in the performance of neuroergonomic tasks such as ours. We also speculate that under improved flying performance, the basal ganglia might be creating a rewarding somatic marker together with a well-harmonized state of cooperation between visual and motor cortices. At the least, the cooperation between the basal ganglia and cerebellum regarding motor timing and coordination is evident in the literature (Middleton & Strick, 2000), and basal ganglia activity in a fine motor control task such as ours is reasonable.

Other Findings

Regarding behavior, Figure 1C shows that the distance between the subject plane and target plane is related to performance on the task. Since distance was experimentally manipulated, flying farther away from the target seems to make the task easier. Our explanation is that subjects have less time to respond to directional changes of the target plane when the target plane is nearer to them. We also suggest that the continuously changing distance between the two planes elicits a continuously changing degree of how “offline” or “online” the task is. When the distance between the two planes is large, the subjects revert to a more “offline” and relaxed mental state, whereas when the distance is small the subjects become more engaged and “online”. We think this explains why we found no significant fMRI activity when the subjects were far from the target plane but vast activity when the subjects were near. This is also further evidence for the affordance competition hypothesis, such that distributed network activity and action selection and specification are most prominent when distances are near and the greatest time pressures, as found in ethological contexts, are imposed.

To supplement our results, we obtained NeuroSynth (Yarkoni, Poldrack, Nichols, Van Essen, & Wager, 2011) keywords associated with the locations of SPM cluster maxima we list in

Table 1 to help indicate the potential brain region and/or related cognitive phenomena. Most of the keyword matches are as expected. One oddity is the activation of brain regions often implicated in the processing of noxious stimuli and pain; mainly originating in the insular cortex. This motivates our speculation that such insular activity may act as a somatic marker, and we suggest that the insula might play a more prominent role in neuroergonomic contexts in general.

Another oddity is the orthographic and reading-like phenomenology that the NeuroSynth keywords suggest when the two planes are far apart (Table 1; Figure 3). The subjects are perhaps scanning and projecting small trajectories upon the airplane, treating it as a distant object with some agency. There also seems to be a shift in activity to auditory regions, perhaps indicating a shift of attention toward the unrelated auditory task that subjects were simultaneously performing, though additional analyses focusing on the auditory task produced no significant results after correction for multiple comparisons.

Future Directions in Neuroergonomics

Our above results and discussion have implications toward the field of neuroergonomics. We believe the application of the various cognitive neuroscience theories such as affordance competition hypothesis (Cisek & Kalaska, 2010), dysmetria of thought and its universal cerebellar computation (Schmahmann, 2010), and the somatic marker hypothesis (Bechara, Damasio, & Damasio, 2000), could provide a richer understanding of more ethological and ecologically relevant neuroergonomic tasks, such as ours. Future work in aviation, and neuroergonomics more generally, will likely benefit from the testing and application of these theories.

We also believe that the pseudo-event-related parametric fMRI design we suggest here will be an important method for future work in neuroergonomics, which will likely have continuous, real-time tasks with continuously fluctuating environmental or human factors like performance, workload, or fatigue. To encourage the engineering and design component of neuroergonomics and human factors, we hope these results and discussion can be applied toward new trainings, interventions, or interface designs. An objective measure of flying performance would provide a new dimension for distinguishing otherwise equally performing pilots/operators (Kane & Engel, 2002). As suggested elsewhere (Gougelet, 2019), future work might also involve the translation of less tractable to more tractable measures (e.g. fMRI to MEG, MEG to EEG, MEG to fNIRS) for eventual integration into everyday situations; thereby supporting the aims of neuroergonomics as a field of study.

Acknowledgements

Chapter 2, in part, as submitted for publication of the material as it may appear in Frontiers in Human Neuroscience, 2020, Gougelet, Robert J.; Terzibas, Cengiz; & Callan, Daniel E. The dissertation author is the primary investigator and author of this paper.

Table 2.1. MNI coordinates for selected cluster maxima (>8mm apart) of brain activity in figures.

Figure	Neurosynth Keywords (Yarkoni et al., 2011)	MNI			T-value	# of Voxels
Figure 2A - Performance		x	y	z		
	vision, occipital cortex, motion	22	-82	28	15.72	42797
	occipital, visual, fusiform	26	-78	-12	12.39	
	early visual, v1, lingual gyrus	4	-90	-2	12.10	
	orbitofrontal cortex, cognitive control	32	38	-22	5.26	184
	orbitofrontal cortex	30	54	-16	3.65	
	dorsolateral prefrontal, tasks	30	40	26	4.19	460
	noxious, prefrontal	34	54	22	2.98	
	dorsolateral prefrontal, memory tasks	32	46	16	2.88	
	shapes, shifting, frontostrial, occipital temporal	52	-60	-28	4.11	48
	fusiform face, cortex cerebellum	50	-50	-28	3.08	
	cerebellar, passive viewing, finger movement	50	-68	-26	3.02	
	premotor, motor	64	-30	18	3.90	121
	somatosensory, secondary somatosensory, pain, tactile	54	-30	24	2.87	
	temporoparietal junction, tasks, middle frontal gyrus	40	8	40	3.17	112
	frontal eye field, action, eye movements	38	0	44	3.07	
	anterior insula, temporal difference learning, pain	34	30	8	3.13	36
	motor cortex, primary motor, hand	-32	-26	70	2.91	54
	insula, pain, response inhibition	40	14	-6	2.90	37
Figure 2B + Performance		x	y	z		
	finger somatosensory cortex	58	-22	52	7.97	393
	hand somatosesory cortex	54	-26	60	6.99	
	primary somatosensory cortex	56	-14	52	6.05	
	visual motion	-30	-100	-8	7.26	66
	amygdala, fear	24	0	-14	6.07	212
	putamen, losses, striatum, reward	26	8	-10	4.87	
	putamen, motor, basal ganglia	26	6	0	4.21	
	amygdala, fear, putamen	-26	-6	-8	5.62	346
	striatum, putamen, reward	-28	4	-6	5.49	
	putamen, basal ganglia, motor	-26	0	4	5.03	
	caudate, dorsal striatum	-12	14	10	5.37	87
	striatum, putamen, ventral striatum	-20	12	-2	4.15	
	insular cortex, noxious, nociception	36	-6	14	4.96	41
Figure 3 - Distance		x	y	z		
	occipital, visual, ventral visual, object	26	-82	-8	12.62	70194
	reading, visually presented, orthographic	22	-94	-4	11.09	
	early visual, visual, word form	-22	-98	0	10.78	
	visual cortex, v1	-20	-96	4	10.38	
	fusiform, navigation, objects	32	-50	-10	9.87	
	fusiform, objects, parahippocampal	28	-52	-10	9.29	
	visual, objects, fusiform	46	-78	-2	9.27	
	disgust, occipitotemporal, agent	-10	-94	-12	9.07	
	serotonin, negative emotion, noxious, dorsolateral	28	34	32	3.36	71
	temporal pole, mentalizing, neutral	-34	-14	-24	3.32	55
	auditory cortex, superior temporal	-66	-26	8	2.92	43
	listening, middle cortex, auditory	66	-12	-12	2.86	30

References

Bareš, M., Lungu, O. V., Husárová, I., & Gescheidt, T. (2010). Predictive motor timing performance dissociates between early diseases of the cerebellum and Parkinson's disease. The Cerebellum, 9(1), 124-135.

Bareš, M., Lungu, O. V., Liu, T., Waechter, T., Gomez, C. M., & Ashe, J. (2011). The neural substrate of predictive motor timing in spinocerebellar ataxia. The cerebellum, 10(2), 233-244.

Bareš, M., Apps, R., Avanzino, L., Breska, A., D’Angelo, E., Filip, P., ... & Lusk, N. A. (2019). Consensus paper: decoding the contributions of the cerebellum as a time machine. From neurons to clinical applications. The Cerebellum, 18(2), 266-286.

Barsalou, L. W. (2008). Grounded cognition. Annu. Rev. Psychol., 59, 617-645.

Bechara, A., Damasio, H., & Damasio, A. R. (2000). Emotion, decision making and the orbitofrontal cortex. Cerebral cortex, 10(3), 295-307.

Bostan, A. C., & Strick, P. L. (2018). The basal ganglia and the cerebellum: nodes in an integrated network. Nature Reviews Neuroscience, 1.

Buckner, R. L. (2013). The cerebellum and cognitive function: 25 years of insight from anatomy and neuroimaging. Neuron, 80(3), 807-815.

Caligiore, D., Pezzulo, G., Baldassarre, G., Bostan, A. C., Strick, P. L., Doya, K., ... & Lago-Rodriguez, A. (2017). Consensus paper: towards a systems-level view of cerebellar function: the interplay between cerebellum, basal ganglia, and cortex. The Cerebellum, 16(1), 203-229.

Callan, D., Falcone, B., Wada, A., Parasuraman, R. (2016a). Simultaneous tDCS-fMRI identifies resting state networks correlated with visual search enhancement. Frontiers in Human Neuroscience 10(72), 1-12. Doi: 10.3389/fnhum.2016.00072.

Callan, D., Gamez, M., Cassel, D., Terzibas, C., Callan, A., Kawato, M., Sato, M. (2012). Dynamic visuomotor transformation involved with remote flying of a plane utilizes the ‘Mirror Neuron’ system. PLoS ONE 7(4), 1-14.

Callan, D., Terzibas, C., Cassel, D., Callan, A., Kawato, M., Sato, M. (2013). Differential activation of brain regions involved with error-feedback and imitation based motor simulation when observing self and an expert's actions in pilots and non-pilots on a complex glider landing task. NeuroImage 72, 55-68.

Callan, D., Terzibas, C., Cassel, D., Sato, M., Parasuraman, R. (2016b). The brain is faster than the hand in split-second intentions to respond to an impending hazard: A simulation of neuroadpative automation to speed recovery to perturbation in flight attitude. Frontiers in Human Neuroscience 10(187), 1-21. Doi: 10.3389/fnhum.2016.00187.

Cisek, P. (2007). Cortical mechanisms of action selection: the affordance competition hypothesis. Philosophical Transactions of the Royal Society B: Biological Sciences, 362(1485), 1585-1599.

Cisek, P., & Kalaska, J. F. (2010). Neural mechanisms for interacting with a world full of action choices. Annual review of neuroscience, 33, 269-298.

Durantin G., Dehais F., Gonthier N., Terzibas C., & Callan D. (2017). Neural signature of inattentional deafness. Human Brain Mapping 38(11), 5440-5455. Doi 10.1002/hbm.23735.

Eccles, J. C. (2013). The cerebellum as a neuronal machine. Springer Science & Business Media.

Fautrelle, L., Pichat, C., Ricolfi, F.., Peyrin, C., and Bonnetblanc, F. (2011). Catching falling objects: The role of the cerebellum in processing sensory-motor errors that may influence updating of feedforward commands. An fMRI study. Neuroscience 190, 135-144.

Field, D. and Wann, J. (2005). Perceiving time to collision activates the sensorimotor cortex. Current Biology 15, 453-458.

Filip, P., Gallea, C., Lehéricy, S., Bertasi, E., Popa, T., Mareček, R., ... & Bareš, M. (2017). Disruption in cerebellar and basal ganglia networks during a visuospatial task in cervical dystonia. Movement Disorders, 32(5), 757-768.

Gougelet, R. J. (2019). Neural oscillation dynamics of emerging interest in neuroergonomics. In Ayaz, H., Dehais, F. (Eds) Neuroergonomics: The Brain at Work and in Everyday Life. (pp. 87 - 92) 10.1016/B978-0-12-811926-6.00014-2.

Gowen, E., & Miall, R. C. (2007). Differentiation between external and internal cuing: an fMRI study comparing tracing with drawing. Neuroimage, 36(2), 396-410.

Haber, S. N. (2003). The primate basal ganglia: parallel and integrative networks. Journal of chemical neuroanatomy, 26(4), 317-330.

Haber, S. N., & Knutson, B. (2010). The reward circuit: linking primate anatomy and human imaging. Neuropsychopharmacology, 35(1), 4.

Ivry, R. B., & Keele, S. W. (1989). Timing functions of the cerebellum. European Journal of Neuroscience, 1(2), 136-152.

Ivry, R. B., & Schlerf, J. E. (2008). Dedicated and intrinsic models of time perception. Trends in cognitive sciences, 12(7), 273-280.

Kane, M. J., & Engle, R. W. (2002). The role of prefrontal cortex in working-memory capacity, executive attention, and general fluid intelligence: An individual-differences perspective. Psychonomic bulletin & review, 9(4), 637-671.

Kiebel, S., & Holmes, A. P. (2003). The general linear model. Human brain function, 2, 725-760.

Krauzlis, R. J. (2004). Recasting the smooth pursuit eye movement system. Journal of neurophysiology, 91(2), 591-603.

Lanciego, J. L., Luquin, N., & Obeso, J. A. (2012). Functional neuroanatomy of the basal ganglia. Cold Spring Harbor perspectives in medicine, 2(12), a009621.

Lawrenson, C. L., Watson, T. C., & Apps, R. (2016). Transmission of predictable sensory signals to the cerebellum via climbing fiber pathways is gated during exploratory behavior. Journal of Neuroscience, 36(30), 7841-7851.

Lencer, R. and Trillenberg, P. (2008). Neurophysiology and neuroanatomy of smooth pursuit in humans. Brain and Cognition 68, 219-228.

Lungu, O., Bares, M., Liu, T., Gomez, C., Cechova, I., Ashe, J. (2016). Trial-to-trial adaptation: Parsing out the roles of cerebellum and basal ganglia in predictive motor timing. European Journal of Neuroscience 28 (7), 920-934.

Middleton, F. A., & Strick, P. L. (2000). Basal ganglia and cerebellar loops: motor and cognitive circuits. Brain research reviews, 31(2-3), 236-250.

Miller, E. K., & Cohen, J. D. (2001). An integrative theory of prefrontal cortex function. Annual review of neuroscience, 24(1), 167-202.

Mink, J. W. (1996). The basal ganglia: focused selection and inhibition of competing motor programs. Progress in neurobiology, 50(4), 381-425.

Menon, V., & Uddin, L. Q. (2010). Saliency, switching, attention and control: a network model of insula function. Brain Structure and Function, 214(5-6), 655-667.

Negel, M., Sprenger, A., Zapf, S., Erdmann, C., Kompf, D., Heide, W., Binkofski, F., and Lencer, R. (2006). Parametric modulation of cortical activation during smooth pursuit with and without target blanking. An fMRI study. NeuroImage 29, 1319-1325.

Ohlendorf, S., Kimmig, H., Glauche, V., and Halier, S. (2007). Gaze pursuit, ‘attention pursuit’ and their effects on cortical activations. European Journal of Neuroscience 26, 2096-2108.

Parasuraman, R. (2003). Neuroergonomics: Research and practice. Theoretical issues in ergonomics science, 4(1-2), 5-20.

Preibisch, C., Castrillon, J., Buhrer, M., Riedl, V. (2015). Evaluation of multiband EPI acquisitions for resting state fMRI.

Schmahmann, J. D. (1996). From movement to thought: anatomic substrates of the cerebellar contribution to cognitive processing. Human brain mapping, 4(3), 174-198.

Schmahmann, J. D. (2004). Disorders of the cerebellum: ataxia, dysmetria of thought, and the cerebellar cognitive affective syndrome. The Journal of neuropsychiatry and clinical neurosciences, 16(3), 367-378.

Schmahmann, J. D. (2010). The role of the cerebellum in cognition and emotion: personal reflections since 1982 on the dysmetria of thought hypothesis, and its historical evolution from theory to therapy. Neuropsychology review, 20(3), 236-260.

Senot, P., Baillet, S., Renault, and Berthoz, A. (2008). Cortical dynamics of anticipatory mechanisms in interception: A neuromagnetic study. European Journal of Neuroscience 20 (10), 1827-1838.

Setsompop, K., Gagoski, B., Polimeni, J., Witzel, T., Wedeen, V., Wald, L. (2012). Blipped-controlled aliasing in parallel imaging for simultaneous multislice echo planar imaging with reduced g-factor penalty. Magn Reson Med. 67(5), 1210-24. doi: 10.1002/mrm.23097.

Todd, N., Moeller, S., Auerbach, E., Yacoub, E., Flandin, F., Weiskopf, N. (2016). Evaluation of 2D multiband EPI imaging for high-resolution, whole-brain, task-based fMRI studies at 3T: Sensitivity and slice leakage artifacts. NeuroImage 124, 32-42.

Uchiyama, Y., Ebe, K., Kozato, A., Okada, T., & Sadato, N. (2003). The neural substrates of driving at a safe distance: a functional MRI study. Neuroscience letters, 352(3), 199-202.

Wilson, M. (2002). Six views of embodied cognition. Psychonomic bulletin & review, 9(4), 625-636.

Yarkoni, T., Poldrack, R. A., Nichols, T. E., Van Essen, D. C., & Wager, T. D. (2011). Large-scale automated synthesis of human functional neuroimaging data. Nature methods, 8(8), 665.

CHAPTER THREE
Theta and Alpha EEG Dynamics in a Dart-Throwing Working Memory Task

Abstract

We designed an EEG experiment to extend traditional, yet minimalist, visuospatial working memory EEG findings to the full-body and everyday task of throwing darts. Subjects either viewed and kept random target locations in working memory or the targets remained visible, both over a random and lengthy delay period. For these memory and non-memory conditions, and at two different stages prior to the release of the dart, the delay and pre-throw periods, we examined theta (3-8 Hz) and alpha (8-12 Hz) frequency EEG amplitude at frontal and posterior sites. During the delay period, contrary to traditional neuroscience findings, we did not find frontal theta and alpha amplitude to distinguish the memory and non-memory conditions. Instead, we observed a frontal alpha amplitude decrease and even greater posterior alpha decrease for both conditions. Only during the pre-throw period did theta amplitude increase at frontal sites, together with an increase in posterior sites of lesser degree, yet only posterior theta distinguished conditions. We also observed an increase in frontal alpha amplitude that did not distinguish memory and non-memory conditions, whereas a decrease in posterior alpha amplitude did marginally distinguish conditions. We interpret a frontoposterior alpha decrease mediates a non-memory, likely attentional, process that maintains delay stability until call-to-action, whereupon frontal theta- and alpha-increase-mediated non-memory processes with both posterior theta-increase- and likely alpha-decrease-mediated memory processes unfold. Altogether, we suggest working memory EEG findings in traditional neuroscience might become overshadowed by the non-memory dynamics that will be found in the study and execution of full-body, memory-guided actions themselves.

Introduction

Rather than from modular and localized brain regions, the central executive and storage component functions of working memory (Baddeley & Logie, 1999) may emerge from highly distributed attentional activation of internal sensorimotor and long-term memory representations, potentially coordinated via goal-directed frontostriatal neuromodulatory (D'Esposito & Postle, 2015), or frontoposterior cortico-cortical or thalamo-cortical (Eriksson, Vogel, Lansner, Bergström, & Nyberg, 2015), reentrant loops. State-based models of working memory, in particular, posit that working memory involves this highly distributed attentional recruitment of the same internal representations that would be employed in non-memory situations (D’Esposito & Postle, 2015).

Network communication via modulation and coupling of neural oscillations likely supports this highly coordinated and distributed process of working memory (Jensen, Kaiser, & Lachaux, 2007; Fell & Axmacher, 2011; Klimesch, 2012) and cognition more generally (Siegel, Donner, & Engel, 2012). More specifically, neural oscillatory modulation and coupling measurable via scalp electroencephalography (EEG) likely supports working memory in humans (Fuster & Bressler, 2012; Roux & Uhlhaas, 2014), particularly through oscillatory activity from the theta (3 to 8 Hz) and alpha (8 to 12 Hz) frequency bands (Klimesch, 1999).

Theta activity in anterior and central scalp regions, commonly referred to as frontal midline theta, has received widespread attention for its association with working memory (Gevins, Smith, McEvoy, & Yu, 1997; Onton, Delorme, & Makeig, 2005; Jensen & Tesche, 2002; Hsieh & Ranganath, 2014). It has also been associated with mental activity that involves sustained internal effort without external input or response (Sauseng, Griesmayr, Freunberger, & Klimesch, 2010; Cavanagh & Frank, 2014). Meanwhile, alpha activity has been implicated as a mediating mechanism for the central executive processes of working memory via frontoparietal coherence (Sauseng, Klimesch, Schabus, & Doppelmayr, 2005). Alpha activity's apparent role in inhibiting internal or external distractors during working memory (Klimesch, Sauseng, & Hanslmayr, 2007; Bonnefound & Jensen, 2012) may be driven by this frontoparietal coherence and be seen as further expression of these central executive processes.

An open question is the extent to which these oscillation-mediated memory processes overlap with non-memory processes and unfold in relation to complex guided actions, despite such an emphasis on action in the working memory literature (Fuster & Bressler, 2012), the lack of reconciliation between cognitive behavioral and neurophysiological data in the working memory literature (D'Esposito, 2007), and its decided importance in memory and all aspects of cognition (Glenberg, 1997; Wilson, 2002). One might expect that the dynamics of network oscillations in the form of EEG theta and alpha frequency amplitude responses are just as involved or more so in working memory tasks that involve full-body, complex actions rather than those in stationary, minimalist experimental designs.

We here examine neural oscillatory dynamics in the context of working memory and the everyday full-body action of throwing darts. Our a priori hypothesis-driven analysis sought to replicate results indicating the involvement of frontal-midline theta and frontoparietal alpha activity in working memory. A posteriori, we also sought to examine theta and alpha relationships with both task performance, expressed as the distance from target bull's-eye to the landed dart, and with the time taken to throw the dart after hearing the cue to throw, which is similar to reaction time in typical neuroscience experiments. These operationalizations place emphasis on the importance of actions, their dynamics, and their outcomes. We also applied both single-trial or trial-level and within-subject, subject-aggregate, or subject-level, statistical analyses to highlight and account for potential individual differences in the performance of such a relatively complex action.

Methods

Subjects

Ten subjects volunteered for this study. The subject population consisted of young, healthy, right-handed adult undergraduate students drawn from the University of California, San Diego (UCSD) campus. Subjects were recruited after having participated in a previous EEG study and opted to be contacted again. The subjects were screened for history of neurological or psychiatric disease and had no or corrected visual impairment. Subjects received $15 per hour for their participation. The experimental protocol was reviewed and approved by the UCSD ethical review board.

Stimuli and Apparatus

The task for this experiment involved throwing darts, e.g. those found in a pub or poolhall, at visible or remembered targets projected onto a large screen. See Figure 3.1 for details on the task and visit (https://github.com/rgougelet/darts) for a video recording of a trial. Subjects threw darts at a target stimulus projected randomly onto one of 17 fixed positions in the visual field of the subjects. The 17 fixed target positions were comprised of two concentric rings of eight targets along the cardinal directions, in addition to the center position. The target stimulus resembles a dart board, with a bull’s-eye surrounded by concentric circles corresponding to decreasing distance and point values. Stimulus presentation was conducted using SNAP (Simulation and Neuroscience Application Platform, https://github.com/sccn/SNAP), an in-house experiment presentation software that controls presentation of task stimuli and transmits a data stream of task events for synchronization.

Task stimuli were projected using a ceiling mounted projector onto a 1.83 x 1.22 m (6 x 4 ft) screen of white cotton. The screen was mounted on a same-sized three-panel 0.125” MDF board, with a 0.125” layer of cork glued to the front. This design allowed for the darts to pass through the screen and remain fixed for scoring. The center of the screen was 1.20 m from the ground. The distance from the center of the screen to the subjects was kept constant at approximately 2.43 m, thus the screen spanned 113 degrees of the subjects’ horizontal visual angle and 90 degrees of the subjects’ vertical visual angle.

Procedure

At the beginning of every trial, the experimenter would retrieve the dart from the board and hand it to the subject. Continuous real-time motion capture tracked whether the subjects were motionless in a throwing stance for three seconds in preparation to see a target, while a 250 Hz tone was played. The target was then displayed for 250 milliseconds before the target randomly disappeared for 70% of the trials, differentiating the heretofore named “Target Absent”, or “memory”, and “Target Present”, or “non-memory”, experimental conditions. See Figure 3.1 for more detail on these conditions. After target display onset, the subjects then remained motionless for a period heretofore identified as the “delay” period, which spanned a randomly variable three to nine integer second delay during which a 250 Hz tone was played. The time spanned by the delay period is heretofore identified as “delay time”. If the subjects moved during this period, as detected by real-time motion capture, the trial restarted; this ensured movement artifacts during the delay period were minimal. After the delay, a 350 Hz, half-second tone prompted the subjects to throw the dart they held at their own pace to the displayed or remembered position of the target. The time period from the onset of the throw cue to the release of the dart is heretofore identified as the “pre-throw” period, and the time it spanned is heretofore identified as “throw time”. The release of the dart was detected via a wired hand circuit that opened when the dart left the grip of the subject.

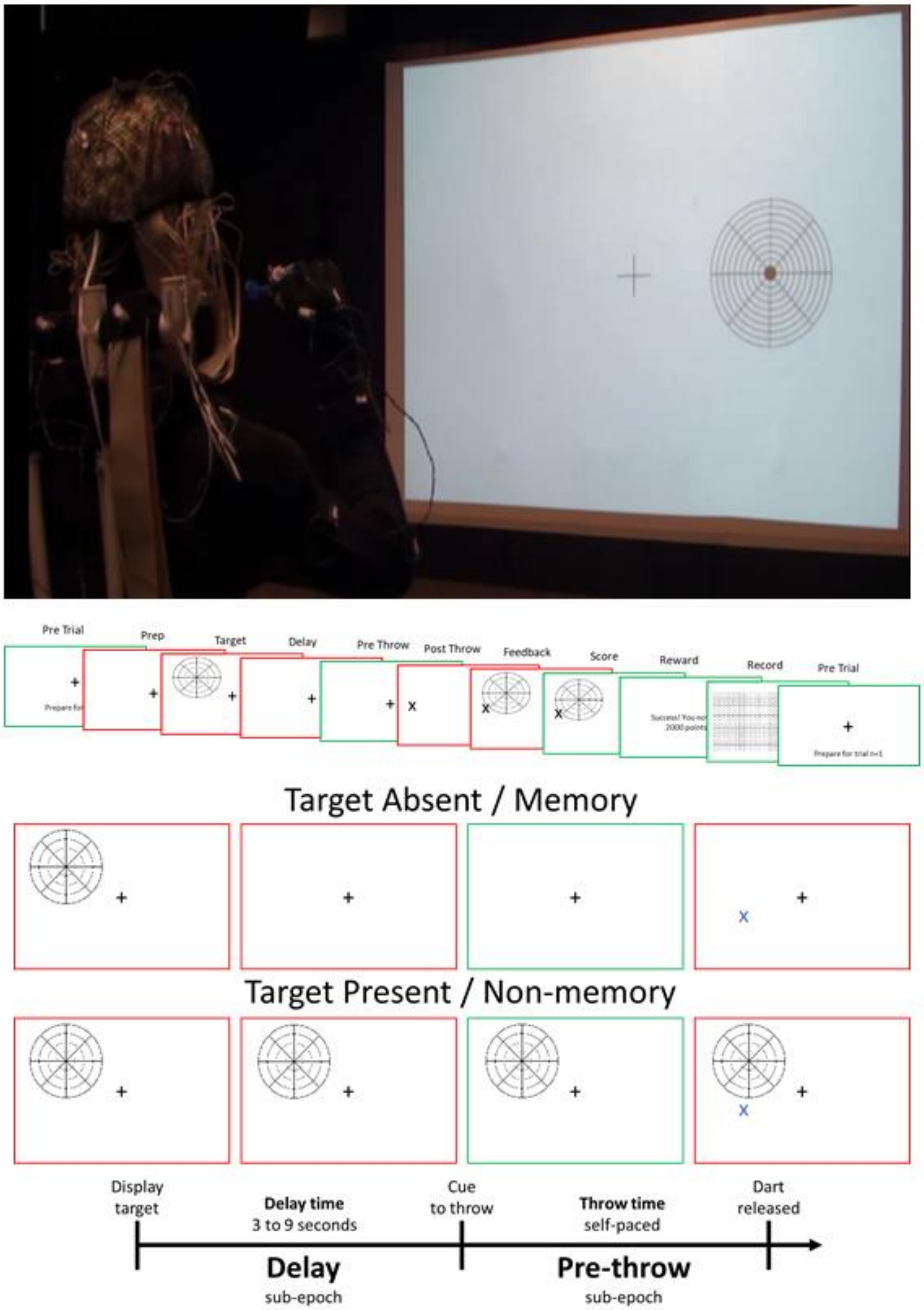


Figure 3.1. Experimental task. (Top) Picture of a subject preparing to throw a dart at a projected target during the Target Present condition (Middle) Schematic of the experimental conditions. Visit https://github.com/rgougelet/darts for a video recording of a trial. (Bottom) Labels and depictions of sub-epochs as the focus of analysis and variables of interest “delay time” and “throw time”.

Subjects threw the dart while remaining fixated on the center crosshair. When present for 30% of the trials, for the Target Present condition, the target would disappear at the release of the dart. After the throw, a two second rest period occurred in which the subjects were told to lower their throwing arm and relax. During the rest period, like during the preparatory period, subjects could move freely, and the trial did not progress until they remained still for two seconds, as detected by real-time motion capture. During the rest periods, subjects were also asked to fixate on where they threw the dart until the target was presented again for one second.

After each rest period, a scoring target was presented so an experimenter could manually enter in the point score for the trial. After this, the subjects received motivating points based on their performance, while they compared their score to an unattainable high score at the top of the screen. Points were added incrementally at the end of the trial to the subjects' current scores, with each increment indicated by a dinging sound. One ding corresponded to each concentric circle of the target stimulus, with the bull's-eye counting for twice its position, i.e. the outermost ring was worth 100 points and one ding, and the bull's-eye was worth 2000 points and twenty dings. If the subject missed the target, they scored no points for a trial and heard a buzzer sound.

At the end of each trial, a grid was displayed on the screen and the location of the dart was manually recorded for each trial by an experimenter using an 8.5 x 11 in paper version of the grid. The trial number and a dot were written down to represent where the dart fell for each trial (detailed in the Behavioral Preprocessing section). Subjects were encouraged to take as many breaks as possible, and the typical session lasted a total of four hours, with 1.75 hours for setup and 2.25 hours of data collection and breaks. Subjects were given a practice period during the beginning of the session, and recording did not start until subjects were reliably hitting the board. No subjects were anomalous in their performance after the practice period.

EEG Recording

Continuous EEG data were collected using 128 active electrodes with a 512 Hz sample rate, using the Biosemi Active 2 amplifier. Horizontal and vertical electrooculography (EOG) and electromyography (EMG) from the right throwing arm were also collected at 512 Hz sample rate using a bipolar lead setup. The locations of every electrode were recorded using the Zebris electrode location digitization apparatus and software. EEG wires were suspended using a backpack with PVC braces built in, providing neck relief and reduced tension and greater slack for EEG electrodes. A hairnet was also used to suppress possible high-frequency oscillations of the thinner individual electrode wires during movement and to prevent electrode displacement.

Behavioral Preprocessing

Measuring task performance precisely after each trial during each experimental session was found to be impractical and was deferred to a post-hoc “analog” approach. After each trial during the experimental session, a reference grid was displayed on the projection screen and the trial number and landed location of the dart was marked as a dot on an 8.5 x 11 in paper version of the grid. After each subject session, this 8.5 x 11 in paper recording of the results for every trial was converted to numerical "digital" distances by an experimenter, or “analog-to-digital converter”, using a hand ruler. Each trial’s dart’s distance, which operationalizes error in behavioral performance, was measured from the center of each trial’s target location--one of 17 possible locations--using a ruler in unit centimeters in estimable increments of 0.025 cm. The horizontal span of the projection screen of 6 feet is mapped by a piece of paper to 11 inches, which is a map approximately from 182.88 cm to 27.94 cm. Thus, a distance measure of 1 cm on paper is approximately equivalent to 1 / 27.94th of 182.88 cm, or roughly 6.55 centimeters (2.58

in) of distance from the dart to the center of the target. For the analysis, paper distances were transformed to board or “real life” distances in centimeters.

There are justifications for various transformations of the distance variable: no transformation, because a halving of distance could be considered only twice as difficult; squaring, because a linear increase in distance is a squared increase in spanned target area and therefore a halving of distance is considered four-times as difficult; and square rooting, to make the positive skew of the distance variable more normally distributed to better satisfy assumptions of parametric statistical tests. We decided to avoid transformations altogether and use non-parametric bootstrap confidence intervals or permutation statistical tests. Three previously mentioned behavioral variables were digitally recorded during the recording session and included in the analysis; delay time, throw time, and experimental condition.

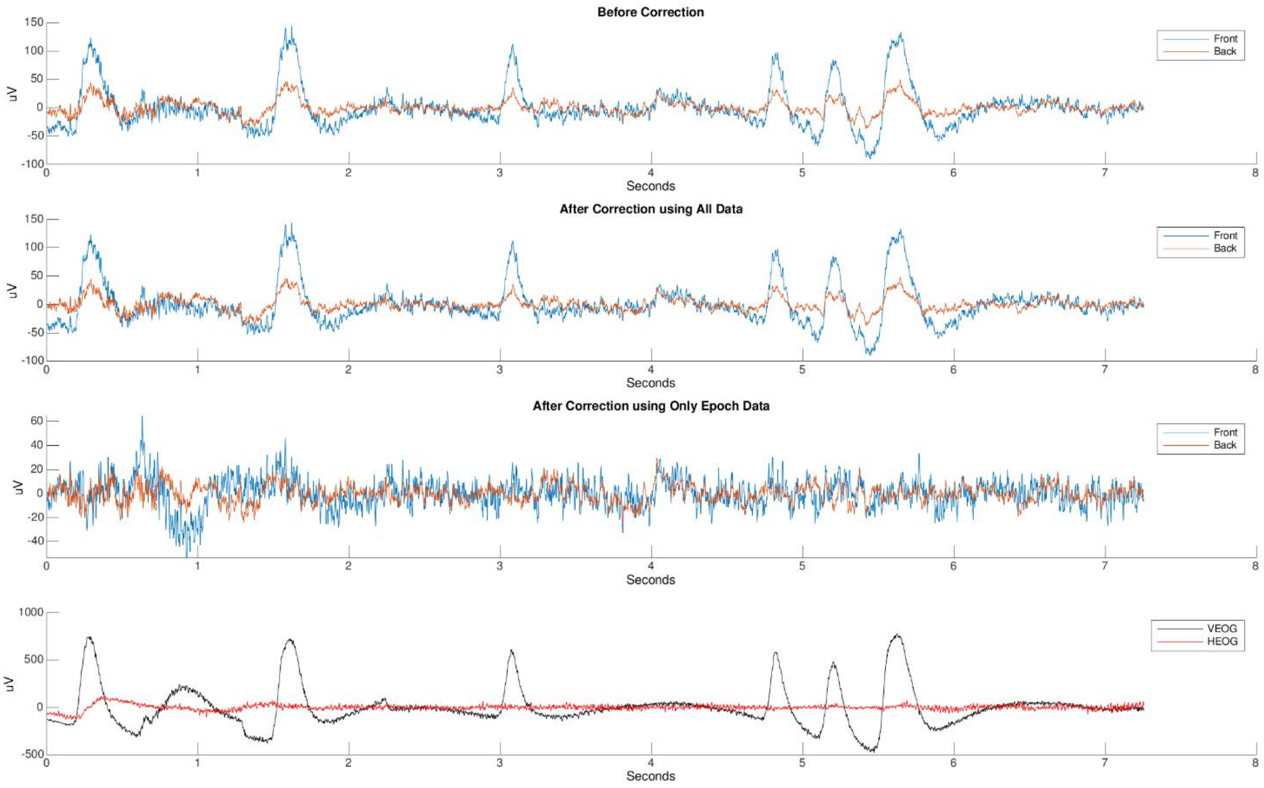
EEG Preprocessing

EEG data were processed using EEGLAB (Delorme & Makeig, 2004) and custom-made MATLAB scripts (https://github.com/rgougelet/darts). Data were collected via BioSemi active electrodes referenced to FCz and re-referenced to linked-mastoids. The channel data were then averaged into two channel clusters. While subject channel locations were digitally recorded for each subject and determined individually, according to the 10-20 international system the first cluster or “anterior” cluster was approximately centered at Fz and its nearest six neighboring channels, and the second cluster or “posterior” cluster was centered at Pz and its nearest six neighboring channels.

A highpass Butterworth infinite-impulse response (IIR) filter was then used with the passband edge at 1 Hz, and -6 dB magnitude cutoff at 0.90 Hz, meanwhile the average absolute magnitude deviation due to passband ripple was less than 10^{-6} dB. Such a steep roll-off and minimal passband ripple was achieved using a high filter order (n = 43). Typically, higher order Butterworth and IIR filters are unstable due to the propagation of quantization, e.g. numerical precision and round-off, errors. Meanwhile, Butterworth IIR filters are the best filters to minimize passband ripple. This problem can be well-addressed, at least for EEG purposes, using the second-order section (SOS) representation of IIR filters, which is an algorithmic refactoring and reordering of the filter's higher order transfer function representation into a series of cascading biquadratic IIR filters. These more fundamental biquadratic filters are subject to substantially less quantization error, while still offering the improved performance of higher-order filters.

Using MATLAB's signal processing toolbox, we found the simplest and most accurate approach for this process is capturing the output of the butter() function in its steady-state [A, B, C, D] form and converting it into an SOS representation using the ss2sos() function with only a single output. Then the sosfilt() function can be used in the forward and backward directions using the flip() function to nullify the filter's phase-response. When using IIR filters, we also recommend using the finest numerical machine precision as possible, e.g. 64-bit double() precision in MATLAB. Butterworth notch filters in SOS form at 60 Hz and harmonics were also used to remove the mains hum, with passband edges at $f_{center} \pm 0.25$ Hz and -6 dB magnitude cutoffs at $f_{center} \pm 0.23$ Hz.

After artifact removal, the filter-Hilbert method (Cohen, 2014) was used to obtain instantaneous amplitude within the theta (3 to 8 Hz), alpha (8 to 12 Hz) frequency bands at the two channel clusters. Butterworth bandpass filters in SOS form were used to isolate theta- and alpha-filtered voltage data with passband edges at 3-8 Hz and 8-12 Hz respectively, with ±0.2 Hz -6 dB minimum magnitude cutoffs. The absolute value of the output of the hilbert() MATLAB function was used to obtain instantaneous amplitude among the two filtered time-series for each of the two frequency bands.


Before Correction

After Correction using All Data

After Correction using Only Epoch Data

Figure 3.2. Eye artifact removal via regression. This is an example epoch from a single subject. The first trace shows the original, raw data. The second trace shows how a regression model that is trained across the concatenation of all of the raw trial data does little to remove these artifacts. The third trace, on the other hand, shows how only using the data from each subject to train individual regression models for each trial works exceptionally well. The fourth trace shows the underlying artifacts measured via vertical and horizontal bipolar electrooculogram. These channels were used as the regressor variables in the model, the front and back channel cluster raw data were treated as separate regressands. The derived least-squares regression coefficients were applied to the EOG data and then subtracted from the raw data to give the data in the first and second trace.

The continuous instantaneous amplitude time-series were then split into epochs of variable length, each of which contained two sub-epochs we identified: a delay sub-epoch, an experimentally varied time ranging from 3 to 9 seconds spanning the time from target display onset to throw cue onset; and a pre-throw sub-epoch, spanning the throw time of the subject, which is similar in concept to "reaction time" but instead reflects the subject-paced time between the onset of the cue for the subject to throw the dart and when they released the dart.

After epoching, eye blinks and saccades were removed from the data via linear regression. Each of the two channel cluster time-series were treated as separate regressands in two regression models, whereas bipolar referenced vertical and horizontal electrooculogram (EOG) channel data were treated as regressors in both models. This method was exceptional at removing eye artifacts and some EMG artifacts without distorting the underlying data. See Figure 3.2 for an example. We also found that, considering the length of the epochs, there were enough data to generate regression coefficients for each epoch, and, when compared to using regression with the concatenated trial data, this approach performed much better. This is also shown in Figure 3.2. Note also that the regression was done on band-filtered data to avoid edge artifacts from filtering individual epochs. The ordering of filtering prior to regression vs regression prior to filtering does not affect the results, since both are linear transformations.

After artifact removal, each sub-epoch's instantaneous amplitude time-series was time-averaged to thus obtain the average amplitude for the theta and alpha frequency bands for the two sub-epochs. A within-frequency-band average baseline amplitude from the 250 milliseconds prior to each sub-epoch was subtracted from each sub-epoch's subsequent average amplitude.

We also found it important to account for the influence of time on trial averages of band amplitudes. A sustained average amplitude of 10 uV over 9 seconds is more considerable than an average amplitude of 10 uV over 3 seconds. We account for this via simple multiplication of trial average amplitude by the trial-varying time span over which it was derived, by either delay time or throw time. An effect might appear or disappear with this rescaling.

Results

Behavioral Results

A total of 1399 trials were collected, but 12 trials were removed due to data collection failures. The remaining 1387 trials were analyzed. For 952 of the trials, subjects threw to remembered targets, whereas for 435 trials the targets remained visible during the delay and pre-throw periods.

Relevant behavioral variables for each trial were: whether the trial was in the memory or "Target Absent" vs. non-memory or "Target Present" condition; task performance measured as the distance from each trial's dart to the trial's target's bull's-eye; length in seconds of the delay period, from target onset to throw cue onset, i.e. delay time; and length of the pre-throw period, the seconds taken to throw the dart for each trial, from throw cue onset to dart release.

The distribution of distances that each dart fell from its intended target's bull's-eye was unimodal right-skewed with mean 11.1 cm (4.37 in), while the median was 10.15 cm (4 in). The standard deviation of these trial distances was 6.57 cm (2.59 in). Figures 3.3 and 3.4 shows the distribution of distance at the trial- and subject-levels, respectively. Visual inspection shows how individual differences in task performance were minor.

Delay time was uniformly distributed between 3 and 9 seconds according to experimental design. Throw time was subject-paced, unimodal right-skewed with an average of 1.61 seconds, median of 1.55 seconds, and standard deviation of 0.60 seconds. Figures 3.5 and 3.6 shows the distribution of throw time at the trial- and subject-levels, respectively. Visual inspection shows how the individual differences in throw time were quite large in central tendency and variability.

Trial-level results

Relationships among behavioral variables were tested using non-parametric bootstrap or permutation statistics, except where noted. Distance from bull’s-eye was significantly different between the two memory conditions; throwing from memory was more difficult than not (11.436 > 10.364 cm, p = .004). Subjects took longer to throw in the non-memory, Target Present, condition with near significance (1.597 < 1.663 s, p = .052).

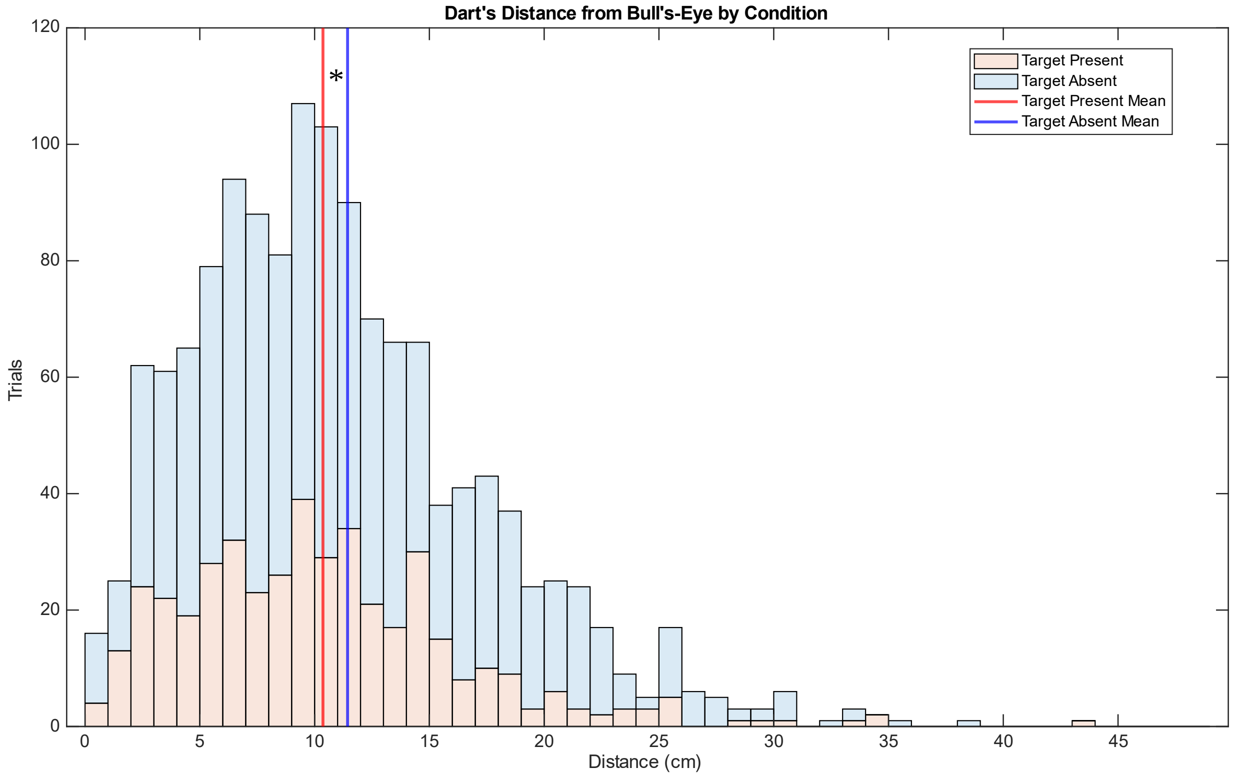


Figure 3.3. Single-trial distance from target’s bull's-eye by condition. Performance during the memory, Target Absent, condition is statistically significantly worse than the non-memory, Target Present, condition (greater distance is worse performance).

The length of the delay period prior to the throw cue was not significantly correlated with performance in neither memory and non-memory conditions separately, nor was there a significant difference between the separate condition correlations using a parametric studentized difference in correlations z-test. On the other hand, throw time was significantly correlated with distance from bull's-eye in the Target Absent condition (r = 0.091, p = .004), whereas throw time was not significantly correlated with distance from bull's-eye in the Target Present condition.

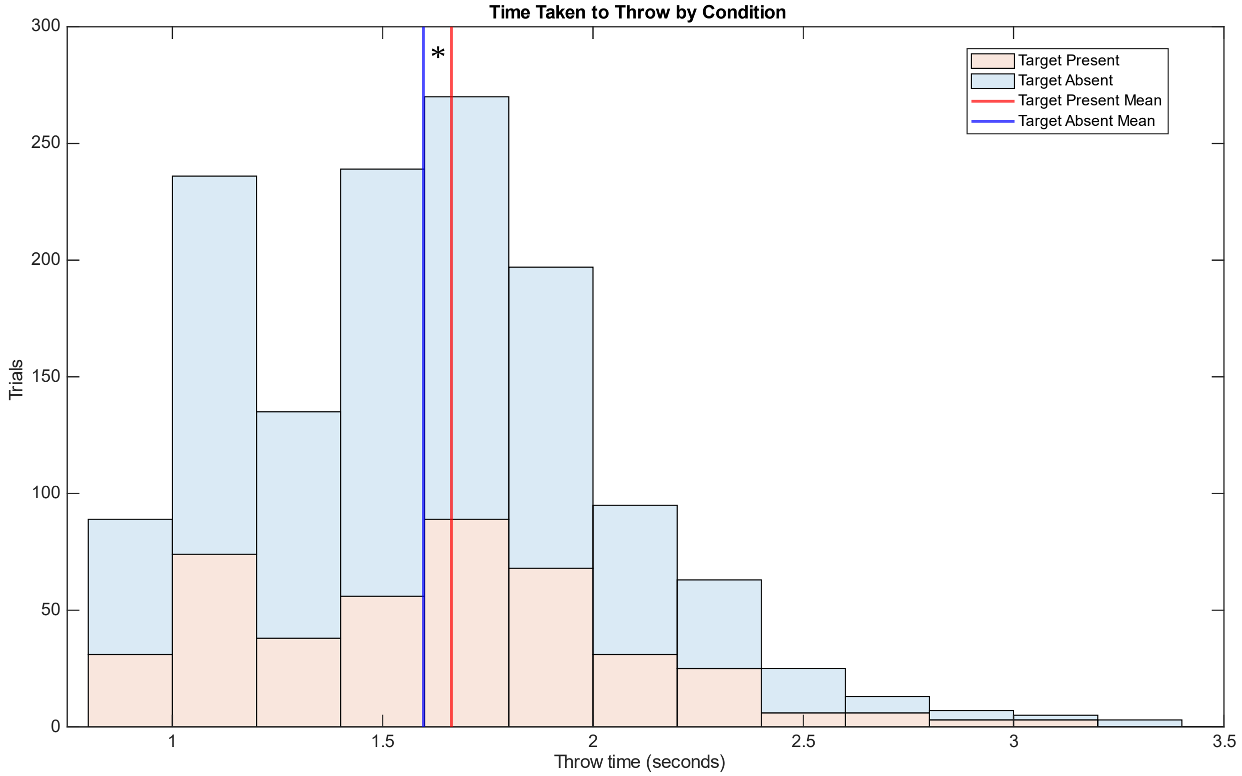


Figure 3.4 – Single-trial time taken to throw by condition. Throw time during the memory, Target Absent, condition is statistically significantly shorter than the non-memory, Target Present, condition. This perhaps indicates a likely non-conscious strategy to throw sooner to minimize memory decay.

Subject-level results

Distance from bull's-eye and throw time were averaged for each of the 10 subjects. Averages of these averages were compared across memory and non-memory and delay time 3 to 9 second integer conditions. Non-parametric permutation statistics were used. There was a clear within-subject difference between distance from bull's-eye in the memory vs non-memory conditions, such that throwing from memory was more difficult than not (11.445 > 10.358 cm, p = 0)[1].

---

[1] Note that p-values of 0 mean that none of the permutation statistics were as extreme as the original test statistic

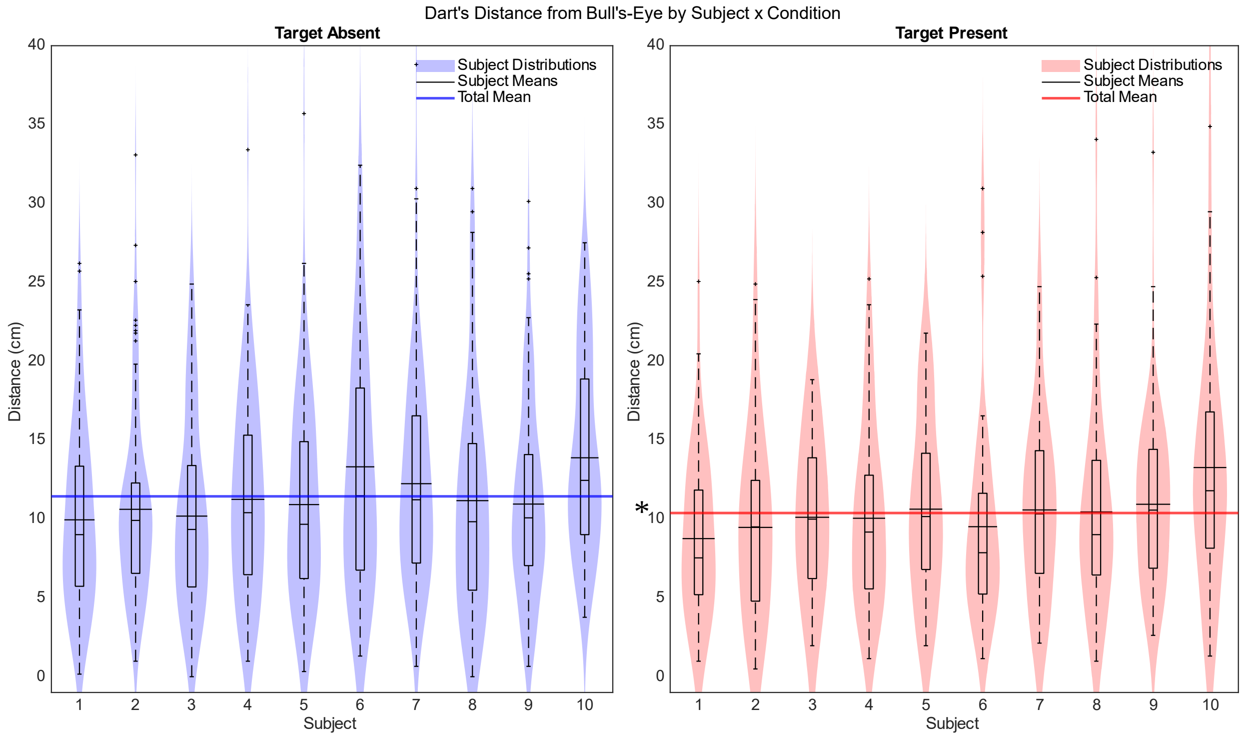


Figure 3.5. Distance from target's bull's-eye by subject and condition. Note no sizable difference in performance between subjects within conditions. Performance during the memory, Target Absent, condition is statistically significantly worse than the non-memory, Target Present, condition (greater distance is worse performance).

Subjects took significantly longer to throw in the non-memory, Target Present, condition (1.588 < 1.657 s, p = .008). Subject means of distance from bull's eye and throw time for each 7 of the randomly variable 3 to 9 second integer delay times and for each of the memory and non-memory conditions were tested against delay times via correlation. No significant correlations were found, although there was a trending within-subject difference between the two conditions' throw times (delta r = 0.022 – (-0.065) = 0.193, p = .112), such that, during the memory condition, throw time correlated positively with distance from bull's-eye (decreased performance) while throw time correlated negatively with distance from bull's-eye (increased performance) in the non-memory condition.

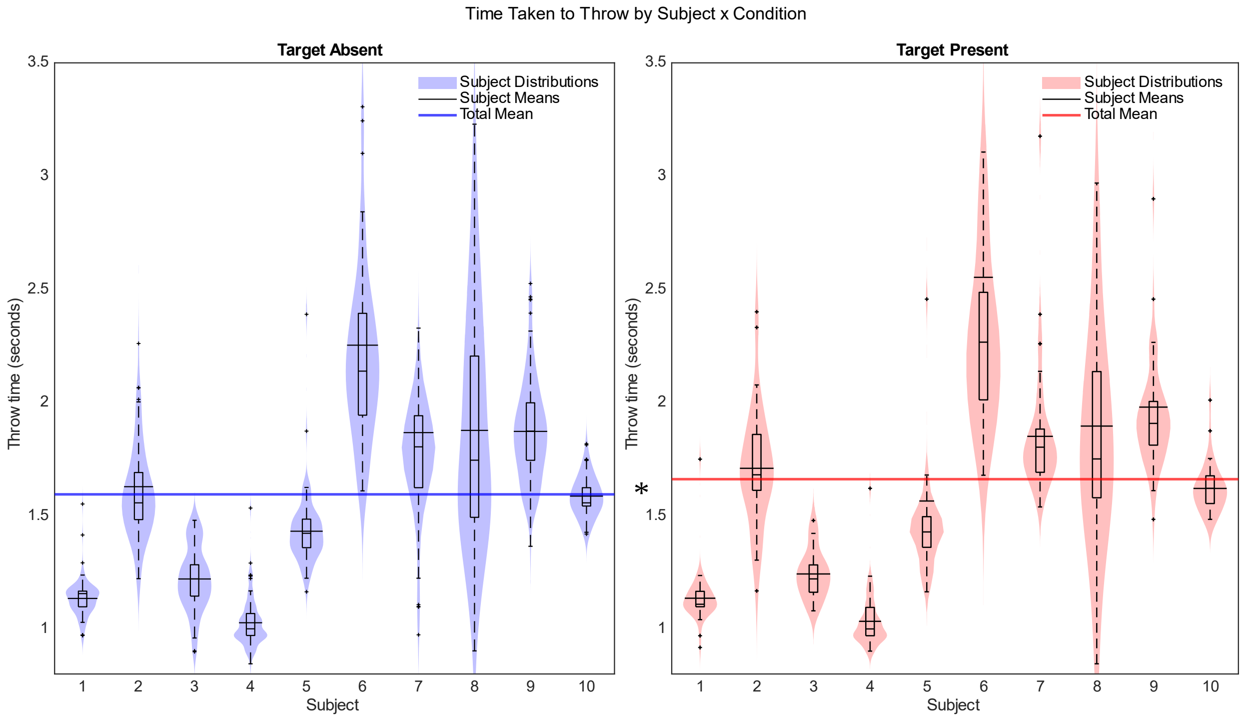


Figure 3.6. Time taken to throw by subject and condition. The time taken to throw was the time spanned between throw cue onset and release of the dart from the hand. Note the large variability in means and variances of throw time between subjects. Throw time during the memory, Target Absent, condition is statistically significantly shorter than the non-memory, Target Present, condition.

EEG Results

Trial-level results. Non-parametric bootstrap confidence intervals were used to test significant differences in single-trial theta and alpha amplitudes relative to their baseline periods. We also tested differences in single-trial EEG theta and alpha amplitudes between the two memory conditions. See Table 3.1 and Table 3.2 for a summary of the results for the anterior and posterior channel clusters, respectively. We also tested for correlations between single-trial EEG theta and alpha amplitudes during the delay and pre-throw periods against the dart’s distance from bull’s-eye and the time taken to throw the dart after hearing the cue to throw. Only the posterior channel cluster exhibited any significant relationships, so see Table 3.3 for a summary of these results. Most results were derived with 10,000 permutation or bootstrap samples, however in cases when precision seemed important the number of samples was increased to 1,000,000.

Anterior Channel Cluster.

Target Absent. In the anterior channel cluster, during the delay period of the Target Absent condition, theta amplitude was not found to significantly differ from the baseline period prior to target onset. Alpha amplitude, however, was found to significantly decrease from baseline during the delay period with 95% CI [-0.275, -0.004 uV] but this effect did not survive rescaling by delay time. During the pre-throw period of the Target Absent condition, theta amplitude was significantly increased from baseline with 95% CI [0.794, 1.234 uV], and this effect survived rescaling by throw time. Similarly, pre-throw alpha amplitude during the Target Absent condition was significantly increased from baseline with 95% CI of [0.282, 0.557 uV] and this effect survived rescaling by throw time.

Target Present. In the anterior channel cluster, during the delay period of the Target Present condition, theta amplitude was not found to significantly differ from baseline, nor was alpha amplitude. During the pre-throw period, however, theta amplitude was significantly increased from baseline with 95% CI [0.828, 1.423 uV], and this effect survived rescaling by throw time. Similarly, alpha amplitude significantly increased from baseline with 95% CI [0.182, 0.602 uV] and this effect survived rescaling by throw time.

Target Absent vs. Target Present. No significant differences in theta and alpha amplitudes between the memory and non-memory condition were found, neither during the delay nor pre-throw periods. Rescaling by delay or throw time did not affect significance, either.

Posterior Channel Cluster.*Target Absent.* In the posterior channel cluster, during the delay period of the Target Absent condition, theta amplitude was found to be near significantly decreased from baseline with a 95% CI [-0.280, .0001 uV]. Meanwhile, this near significant effect became significant after rescaling with delay time. Alpha amplitude during the delay period was found to be statistically decreased from baseline with a 95% CI [-1.059, -0.508 uV] and survived rescaling with delay time. During the pre-throw period of the Target Absent condition, theta amplitude was significantly increased from baseline with 95% CI [0.516, 0.805 uV], and this effect survived rescaling by throw time. Pre-throw alpha amplitude during the Target Present condition was not significantly different from baseline even after rescaling.

Table 3.1. Differences in anterior single-trial theta and alpha amplitudes within and between the memory vs. non-memory conditions. Bold-faced statistics are statistically significant. Statistics with an asterisk indicate their significance after scaling by the variable length of time over which they were derived. All entries except p-values are in units of microvolts.

Anterior EEG Amplitude (uV)	Target Absent		Target Present		Target Absent > Present	
	$\bar{x}_{TA}$	95% CI	$\bar{x}_{TP}$	95% CI	$\bar{x}_{TA}$ - $\bar{x}_{TP}$	p-value
Delay Theta	-0.005	[-0.200, 0.181]	0.019	[-0.263, 0.292]	-0.024	0.894
Delay Alpha	-0.137	**[-0.275, -0.004]**	-0.144	[-0.336, 0.043]	0.007	0.953
Pre-throw Theta	1.016	**[0.794, 1.234]***	1.125	**[0.828, 1.423]***	-0.109	0.571
Pre-throw Alpha	0.418	**[0.282, 0.557]***	0.390	**[0.182, 0.602]***	0.028	0.828

Target Present. In the posterior channel cluster, during the delay period of the Target Present condition, theta amplitude did not exhibit a significant difference from baseline. Alpha amplitude, however, did exhibit a significant decrease from baseline with 95% CI [-1.356, -0.547 uV] and this effect survived rescaling. During the pre-throw period of the Target Present condition, theta amplitude did exhibit a significant increase from baseline, with 95% CI [0.508, 0.805 uV]. Moreover, during the pre-throw period, alpha exhibited a significant decrease in amplitude relative to baseline 95% CI [-0.627, 0.000 uV].

Target Absent vs. Target Present. In the posterior channel cluster, no significant differences in theta and alpha amplitudes between the memory and non-memory condition were found during the delay period. During the pre-throw period, however, there was significantly greater theta amplitude for the Target Absent condition (0.658 > 0.313 uV, p = .013) and this effect survived rescaling. Alpha amplitude during the pre-throw period was greater during the Target Absent condition with trending significance (0.029 > -0.304 uV, p = 0.070) and this effect did not survive rescaling by throw time.

Table 3.2. Differences in posterior single-trial theta and alpha amplitudes within and between the memory vs. non-memory conditions. Bold-faced statistics are statistically significant. Statistics with an asterisk indicate their significance after scaling by the variable length of time over which they were derived.

Posterior EEG Amplitude (uV)	Target Absent		Target Present		Target Absent > Present	
	$\bar{x}_{TA}$	95% CI	$\bar{x}_{TP}$	95% CI	$\bar{x}_{TA}$ - $\bar{x}_{TP}$	p-value
Delay Theta	-0.139	[-0.280, 0.001]*	-0.059	[-0.264, 0.143]	0.080	0.530
Delay Alpha	-0.774	**[-1.059, -0.508]***	-0.942	**[-1.357, -0.547]***	0.168	0.499
Pre-throw Theta	0.658	**[0.516, 0.805]***	0.313	**[0.073, 0.549]**	**0.345**	**0.013***
Pre-throw Alpha	0.029	[-0.167, 0.216]	-0.304	**[-0.627, 0.000]***	0.333	0.070

Correlations among EEG amplitudes, distance from bull's-eye, and throw time. In both channel clusters, we tested relationships between single-trial EEG amplitudes and the distance of the dart from the target's bull's-eye, i.e. task performance. Additionally, in both channel clusters, we tested relationships between single-trial EEG amplitudes and the time subjects took to throw the dart. We also tested if these effects survived rescaling by delay or throw time.

In the anterior channel cluster, for both Target Absent and Target Present conditions, no significant relationships were found between theta and alpha amplitudes and distance from bull’s-eye, neither during the delay nor pre-throw periods. Moreover, for both Target Absent and Target Present conditions, no significant relationships were found between theta and alpha amplitudes and throw time during the delay period. The one exception in the anterior channel cluster was that theta amplitude of the pre-throw period during the Target Present condition was found to negatively correlate with throw time (r = -0.111, p = .023). Given this solitary result, no table is provided for correlations tested regarding the anterior channel cluster.

Results regarding correlations in the posterior channel cluster are presented in Table 3.3. During the Target Absent condition average single-trial theta amplitude during the delay period significantly correlated negatively with dart’s distance from bull’s-eye (r = -0.0746, p = .022), i.e. when theta amplitude increased then the dart’s distance from bull’s-eye decreased, and thus task performance increased. This effect marginally survived scaling by delay time (r = -0.0614, p = .061). No relationships were found between theta and alpha amplitudes and distance from bull’s-eye for the Target Present condition.

During the delay period of the Target Absent condition, single-trial theta amplitude did not exhibit a relationship with throw time, whereas alpha amplitude did exhibit a negative relationship with throw time (r = -0.177, p = 0). During the pre-throw period of the Target Absent condition, theta amplitude was significantly negatively correlated with throw time (r = -0.083, p = .01). Similarly, alpha amplitude was significantly negatively correlated with throw time during the pre-throw period (r = -0.208, p = 0). Results during the Target Present condition reflected those of the Target Absent condition, such that alpha amplitude during the delay period exhibited a negative correlation with throw time (r = -0.217, p = 0), as did pre-throw alpha amplitude (r = -0.106, p = .028) and pre-throw theta amplitude (r = -0.189, p = 0). Alpha amplitude during the delay period of both Target Absent and Target Present conditions survived rescaling by delay time, whereas rescaling pre-throw amplitudes by throw time to test their relationships with throw time is nonsensical.

Table 3.3. Posterior single-trial correlations. Correlations between trial theta and alpha amplitudes and both the dart's distance from bull's-eye and how long the subjects took to throw after hearing the cue to throw. Statistics with an asterisk indicate significance after scaling by the length of time over which they were derived.

Posterior EEG Amplitude Correlations	Target Absent Distance		Target Present Distance		Target Absent Throw time		Target Present Throw time	
	r	p-value	r	p-value	r	p-value	r	p-value
Delay Theta	**-0.075**	**0.020***	-0.041	0.389	-0.023	0.480	0.016	0.738
Delay Alpha	-0.006	0.825	-0.013	0.778	**-0.177**	**0***	**-0.217**	**0***
Pre-throw Theta	0.018	0.589	-0.023	0.628	**-0.083**	**0.010**	**-0.106**	**0.028**
Pre-throw Alpha	0.049	0.119	0.061	0.197	**-0.208**	**0**	**-0.189**	**0**

Subject-level results. Similar to what was done in our behavioral analysis, we averaged theta and alpha amplitudes, dart's distance from bull's-eye, and throw time, for each of the 10 subjects. Averages of these averages were compared across memory and non-memory and delay 3 to 9 integer second conditions. Non-parametric bootstrap confidence intervals were used to test significant differences in subject-averaged theta and alpha amplitudes relative to their baseline periods. See Table 3.4 and Table 3.5 for a summary of the results for the anterior and posterior channel clusters, respectively. We also tested for correlations between subject-averaged EEG theta and alpha amplitudes during the delay and pre-throw periods against the subject-averaged dart's distance from the target's bull's eye and the subject-averaged time taken to throw the dart after hearing the throw cue. See Table 3.4 and Table 3.5 for a summary of the results for the anterior and posterior channel clusters, respectively. Most results were derived with 10,000 bootstrap samples, however in cases when precision seemed important the number of samples was increased to 1,000,000. Similar to our single-trial analysis, we tested additional rescalings of theta and alpha amplitudes by throw time to account for time span.

Anterior Channel Cluster.

Target Absent. In the anterior channel cluster during the Target Absent condition, no significant differences from baseline for subject-averaged theta and alpha amplitudes were found during the delay period, and rescaling by delay time had no effect. On the other hand, both theta and alpha amplitudes were significantly greater during the pre-throw period, with theta 95% CI [0.610, 1.406 uV] and alpha 95% CI [0.161, 0.707 uV], and both effects survived rescaling by throw time.

Table 3.4. Differences in subject-averaged theta and alpha amplitudes within and between the two memory conditions. Bold-faced statistics are statistically significant. Statistics with an asterisk indicate their significance after scaling by the variable length of time over which they were derived. All entries are in units of microvolts.

Anterior EEG Amplitude (uV)	Target Absent		Target Present		Target Absent > Present	
	$\bar{x}_{TA}$	95% CI	$\bar{x}_{TP}$	95% CI	$\bar{x}_{TA}$ - $\bar{x}_{TP}$	p-value
Delay Theta	-0.040	[-0.276, 0.187]	0.034	[-0.206, 0.266]	-0.075	0.622
Delay Alpha	-0.161	[-0.449, 0.023]	-0.125	[-0.413, 0.103]	-0.036	0.608
Pre-throw Theta	0.978	**[0.610, 1.406]***	1.09	**[0.75, 1.392]***	-0.112	0.475
Pre-throw Alpha	0.427	**[0.161, 0.707]***	0.413	**[0.204, 0.627]***	0.014	0.886

Target Present. In the anterior channel cluster during the Target Present condition, and similarly to the Target Absent condition, no significant differences from baseline for subject-averaged theta and alpha amplitudes were found during the delay period. On the other hand, both theta and alpha amplitudes were significantly greater during the pre-throw period, with theta 95% CI [0.75, 1.392 uV] and alpha 95% CI [0.204, 0.627 uV], and both effects survived rescaling by throw time.

Target Absent vs. Target Present. In the anterior channel, no significant differences were found between Target Absent and Target Present theta and alpha amplitudes during neither the delay nor pre-throw periods.

Posterior Channel Cluster.

Target Absent. In the posterior channel cluster during the Target Absent condition, theta amplitude exhibited a near significant decrease from baseline with 95% CI [-0.283, 0.007], though this was not made significant be rescaling by delay time. Alpha amplitude during the delay period of the Target Absent condition did exhibit a significant decrease from baseline with 95% [-2.126, -0.068], and this effect survived rescaling by delay time. Theta amplitude exhibited a significant increase from baseline with 95% CI [0.438, 0.897], and this effect survived rescaling by throw time. Alpha amplitude during the pre-throw period of the Target Absent condition did not exhibit a significant difference from baseline.

Target Present. In the posterior channel cluster during the Target Present condition, neither theta nor alpha amplitude exhibited a significant difference from baseline, even after rescaling by delay time. During the pre-throw period of the Target Present condition, theta amplitude exhibited a significant increase from baseline, 95% CI [0.049, 0.588], with and without rescaling by throw time, whereas alpha amplitude did not.

Target Absent vs. Target Present. No significant differences in theta and alpha amplitudes between Target Absent and Target Present conditions were found during the delay period. A significant difference in theta amplitude between Target Absent and Target Present conditions was found (0.638 > 0.310 uV, p = .027) during the pre-throw period, and this effect survived rescaling by throw time. No significant difference in alpha amplitude was found between conditions during the pre-throw period.

Table 3.5. Differences in subject-averaged theta and alpha amplitudes within and between the two memory conditions. Bold-faced statistics are statistically significant. Statistics with an asterisk indicate their significance after scaling by the variable length of time over which they were derived. All entries are in units of microvolts.

Posterior EEG Amplitude (uV)	Target Absent		Target Present		Target Absent > Present	
	$\bar{x}_{TA}$	95% CI	$\bar{x}_{TP}$	95% CI	$\bar{x}_{TA}$ - $\bar{x}_{TP}$	p-value
Delay Theta	-0.136	[-0.283, 0.007]	-0.009	[-0.224, 0.222]	-0.127	0.294
Delay Alpha	-0.849	**[-2.126, -0.068]***	-1.003	[-2.826, 0.023]	0.154	0.644
Pre-throw Theta	0.638	**[0.438, 0.897]***	0.310	**[0.049, 0.588]***	0.328	**0.027***
Pre-throw Alpha	0.014	[-0.615, 0.492]	-0.249	[-1.086, 0.330]	0.263	0.142

Correlations among EEG amplitudes, distance from bull's-eye, and throw time. In both channel clusters, we tested relationships between subject-average EEG amplitudes and the distance of the dart from the target's bull's-eye, i.e. task performance. We also tested relationships between single-trial EEG amplitudes and throw time.

Regarding distance from bull's-eye, in both the anterior and posterior channel clusters, for both Target Absent and Target Present conditions, no significant relationships were found between theta and alpha amplitudes and distance from bull's-eye, neither during the delay nor pre-throw periods. A single trending result was found for the delay period of the Target Present condition in the anterior cluster, such that theta amplitude during the delay period was negatively correlated with distance from bull's-eye (r = -0.589, p = 0.089), i.e. greater theta amplitude increased task performance.

Regarding throw time, in the anterior channel cluster, for both Target Absent and Target Present conditions, no significant relationships were found between theta and alpha amplitudes and throw time during the delay period nor pre-throw period.

Table 3.6 – Posterior subject-averaged correlations. Correlations between within both theta and alpha amplitudes and both the dart's distance from bull's-eye and how long the subjects took to throw after hearing the cue to throw. Statistics with an asterisk indicate significance after scaling by the length of time over which they were derived.

Posterior EEG Correlations	Target Absent Distance		Target Present Distance		Target Absent Throw time		Target Present Throw time	
	r	p-value	r	p-value	r	p-value	r	p-value
Delay Theta	-0.317	0.363	-0.47	0.146	-0.443	0.196	-0.324	0.347
Delay Alpha	-0.478	0.302	0.279	0.311	-0.598	0.082	-0.635	0.196
Pre-throw Theta	-0.269	0.453	-0.168	0.648	-0.464	0.178	-0.681	**0.029**
Pre-throw Alpha	-0.534	0.195	0.099	0.801	-0.828	**0.002***	-0.763	**0.023***

Discussion

For our dart-throwing working memory task, we note some interesting behavioral findings. Subjects performed worse when throwing from memory, as expected. Interestingly, subjects also took longer to throw when the target was visible, i.e. not throwing from memory. Throwing from memory may have created a time pressure to throw quickly before the target decayed in memory. On the other hand, subjects could have simply been more lackadaisical with their throws since they had nothing to visual aim toward. Although, when subjects took longer to throw from memory during the Target Absent condition, they performed worse. This further suggests a memory decaying effect but could also reflect a degree of inattention with no target to maintain their attention over the lengthy delay period. In contrast, we also found that taking longer to throw had no significant effect on performance during the Target Present condition.

Frontal channel cluster. EEG results regarding the anterior channel cluster are summarized in Tables 3.1 and 3.4, for single-trial and subject-level results, respectively. Contrary to previous findings regarding frontal midline theta (Gevins, Smith, McEvoy, & Yu, 1997; Onton, Delorme, & Makeig, 2005; Jensen & Tesche, 2002; Hsieh & Ranganath, 2014) we found no significant frontal theta activity in the anterior channel cluster during the Target Absent, or memory, condition's delay period. This was true for both trial-level and subject-level comparisons, and regardless if we compared it to within-trial baseline or to the average theta amplitude found during the delay period of the Target Present, or non-memory, control condition. On the other hand, we found a significant trial-level reduction in alpha amplitude from baseline during the delay period of the Target Absent condition, although alpha amplitude during the Target Present condition heavily mirrored this reduction, though not significantly.

Trial-level, and nearly subject-level, frontal alpha activity inverted upon transition from the delay period to the pre-throw period of the trial for both Target Absent and Target Present conditions. In other words, frontal alpha activity increased during the pre-throw period after decreasing in the delay period. Trial-level and subject-level theta amplitude increased simultaneous to this alpha amplitude increase during the pre-throw period, but not from a state of attenuation during the delay period. These results suggest that frontal theta and alpha oscillatory activity is largely associated with performance of the action itself, rather than a reflection of any memory processes. This contrasts with claims of the involvement of frontal theta and alpha activity in working memory.

We therefore found no qualities of frontal theta and alpha activity that distinguish throwing from memory vs not. This is contrary to our behavioral findings that did distinguish the memory condition from the non-memory condition. When correlated with behavior, the only half-distinguishing trial-level frontal EEG features we found was that an increase in frontal theta amplitude during the pre-throw period coincided with a decrease in throw time during the Target Present condition, whereas this effect was not reproduced in subject-level tests. An increase in within-subject theta amplitude during the delay period did coincide with an increase in task performance during the Target Present condition but not in the trial-level tests.

These findings would reflect previous working memory findings if they had occurred during the Target Absent condition, but they did not. Instead, they appear to support the common notion that frontal theta involves concerted effort and attention in both memory and non-memory tasks (Sauseng, Griesmayr, Freunberger, & Klimesch, 2010; Cavanagh & Frank, 2014). More specifically, we suspect that sustained frontal theta activity during the delay period likely coincided with internal rehearsal or focus that improved throw confidence, thereby speeding up subject reaction time to the throw cue and consequently improved performance. These dynamics apparently disappeared when throwing from memory and may have only been employed by a subset of subjects since the effect on performance was washed out at the trial level.

The clear equivalent increases in frontal pre-throw theta and alpha activity for both Target Absent and Target Present conditions could further corroborate the above interpretation. The increases in frontal pre-throw theta and alpha amplitude might coincide with a period of heightened attention and engagement prior to the throw. These equivalent increases in frontal pre-throw theta and alpha activity further suggests alpha and theta dynamics of the majority of subjects were deferred to the pre-throw period rather than during the delay period. The clear decrease in single-trial frontal alpha activity during the delay period of the Target Absent condition and somewhat of the Target Present condition is an indication of an active encoding process, likely occurring early on in the delay period, that allowed this deference to the Target Absent condition. The fact that this alpha effect during the delay period of the Target Absent condition disappeared when rescaling by the within-trial delay time over which it was derived suggests it was a more transient than sustained effect. Qualitative inspection of the early delay period does suggest an early alpha decrease that appeared to decay further into the delay period.

Overall, the results from the frontal channel cluster imply that much of frontal theta and alpha activity dynamics were deferred to the pre-throw period for both memory and non-memory conditions. The exception is a decrease in frontal alpha during the delay period. This decrease is likely a transient non-memory encoding process that allows deference of activity to the pre-throw period. This is supported by the notion that a reduction in alpha activity is indicative of an increase in cortical activity via withdrawal of inhibition (Gevins et al., 1997; Klimesch, Sauseng, & Handslmayr, 2007).

Posterior channel cluster. More apparent theta and alpha EEG dynamics were found in the posterior channel cluster, located most directly over parietal cortex (Table 3.2 for single-trial and Table 3.5 for subject-level). Here there was significantly decreased trial-level theta activity during the delay period of the Target Absent condition, but only when theta amplitude was rescaled by the time over which it spanned for each trial. In other words, a sustained reduction in theta activity was more apparent than an overall reduction. This is further contrary to reports of increases in theta activity during working memory. Meanwhile, in unison with the frontal alpha activity during the delay period of both conditions, subject-level and nearly subject-level posterior alpha activity was significantly reduced in both memory and non-memory conditions. When comparing confidence intervals, this posterior alpha decrease was significantly greater than frontal alpha decrease during the delay period of both conditions. Since these effects appear to be more sustained effects due to significance after rescaling by delay time, we suspect these reflect sustained attentional processes rather than transient ones.

Compared to frontal channels, it would appear that posterior EEG activity is more responsible for an active memory and non-memory attentional process during the delay period and that this is primarily mediated by a decrease in alpha activity. This activity however does not distinguish the two memory conditions, therefore pertains more to the action itself rather than any memory processes. The half-distinguishing feature would be decreased trial-level and subject-level posterior theta activity during the delay period. This decrease in theta activity is reversed to an increase upon transition to the pre-throw period in preparation to throw, and this reversal is most distinguishable for the memory condition. These results are further contrary to the involvement of frontal theta in working memory.

Regarding the pre-throw period, posterior pre-throw theta activity clearly distinguishes the two memory conditions, such that there was greater theta activity during the Target Absent condition, whereas anterior pre-throw theta activity does not distinguish them. While there is a huge increase in pre-throw theta during the Target Present condition in the anterior channels, the posterior channel does not increase as much. This is reflected in the difference in pre-throw theta between the two memory conditions in the posterior channel. If we define coupling as a concurrent anterior-posterior, or frontoparietal, increase in amplitude, i.e. amplitude-amplitude coupling, we can distinguish the Target Absent condition by greater anterior-posterior theta coupling during the pre-throw period from the Target Present condition.

Moreover, while pre-throw frontal alpha activity increased during both conditions, pre-throw posterior alpha activity *decreased* during the Target Present condition and made no change during the Target Absent condition. This suggests significant amplitude-amplitude anti-coupling of pre-throw alpha during the Target Present condition, such that posterior pre-throw alpha decreases while anterior pre-throw alpha increases during the Target Present condition. Since the Target Absent condition did not exhibit this posterior pre-throw alpha decrease, this implies an absence of anti-coupling, or more likely, and in line with the literature (Sausen, Klimesch, Schabus, & Doppelmayr, 2005), the presence of frontoparietal alpha coupling. When considered with the findings from the frontal channel cluster, these results suggest that frontoparietal interactions that differentiate memory from non-memory are largely manifest in posterior theta and alpha changes during the pre-throw period rather than the delay period, whereas anterior theta and alpha activity remains stable between memory conditions.

Behavioral correlations with theta and alpha activity were primarily found in the posterior channel cluster, rather than the anterior cluster. Interestingly, posterior theta delay activity during the Target Absent condition was the only oscillatory activity to correlate at all with task performance, such that greater activity improved performance. This opposes our finding that posterior theta delay activity during the Target Absent condition was significantly reduced from baseline. This opposition implies that a smaller reduction in posterior theta activity during the delay period improved performance. This could be connected to the subsequent increase of theta activity during the pre-throw period, reflecting a priming or precursor of a theta increase in the Target Absent condition that lead to its ultimate differentiation from the Target Present condition. It also implies that posterior theta activity is lost to working memory, and the less that loss the better the performance.

One possibility is that posterior theta activity during the delay period reflects active attention to perceptual representations pertaining to the target, but, while attention is still maintained, the perceptual content itself diminishes in the memory condition. In other words, this might reflect the notion from state-based models that working memory involves attentional activation of representations involved in non-memory tasks (D’Esposito & Postle, 2015), and that this is posterior-theta mediated. Still, these results are tenuous because posterior theta activity did not significantly differentiate the memory and non-memory conditions.

Conclusion. This experiment serves as proof of concept for extending typical EEG findings for working memory to complex, everyday actions. Contrary to findings elsewhere, we found little association of frontal EEG theta and alpha activity with working memory. Instead, increases in anterior theta and alpha activity remained stable between memory and non-memory conditions and differences were instead largely manifested in concurrent posterior theta and alpha changes. This suggests that frontal EEG theta and alpha activity are more involved in the throwing action itself, rather than working memory.

Working memory instead appears mediated by both theta and alpha amplitude-amplitude coupling, whereas the dart throwing action itself appears mediated by frontoparietal alpha amplitude-amplitude anti-coupling. Moreover, these dynamics were most apparent upon call-to-action rather than during the working memory delay period, except for alpha suppression in posterior channels for both memory and non-memory conditions and theta suppression for the memory condition. This suggests that active posterior alpha-mediated and non-memory, likely attentional, and theta-mediated memory processes maintain stability until call-to-action whereupon further disparate memory and non-memory theta and alpha dynamics unfold.

Considering the poor reproduction of previous well-known working memory findings, these results call in to question how generalizable results are from minimalist experiments to real-world actions. Still this small study is only one of few attempts to answer this question of generalizability, and from our experience in this study we believe what is more likely is that additional and likely stronger oscillatory dynamics are introduced that overshadow results otherwise found in traditional, minimal experiments. Moreover, considering the heavier involvement and unfolding of oscillatory dynamics in the pre-throw vs. delay period, likely these stronger dynamics will pertain more to the preparation and performance of actions themselves, of which underlying memory and other cognitive processes are only a small part.

Addendum

The above writing is intended for submission for publication to a neuroscience journal, hence neuroergonomics is not explicitly mentioned. Below are considerations regarding this article/chapter, and EEG research more generally, that speak directly to neuroergonomics.

This chapter contributes to neuroergonomics as a field by studying one of only a few tasks that incorporate naturalistic full-body action in humans. It serves as proof of concept that such experiments are possible. Moreover, it demonstrates how neuroergonomics-oriented research can still inform the neuroscience from which it originates, but it still lacks a direct link to neuroergonomics by its very nature as a neuroscience publication. Still, this chapter has helped reveal some apparent incongruities between neuroscience research as it is traditionally done and how it might be done with orientation towards neuroergonomics. Namely, there are statistical and neuroergonomic implications of aggregating data in EEG and neuroscience research in general.

EEG and much of neuroscience research involves the aggregation of trials into subject-, condition-, or group-level summary statistics; summary statistics that are thereafter tested using t-tests, ANOVAs, correlation coefficients, or other, usually parametric, statistical tests. This summary statistic approach is fundamental to the production of evidence necessary for the progression of the scientific method. It is also considered necessary for adequate generalizability to populations of humans rather than, e.g., EEG trials.

Unfortunately, the aggregation of data in any form has serious implications on the underlying statistical assumptions of statistical models; implications that are widely marginalized as an unwritten social understanding, at best. These assumptions are that data are independently and identically distributed, or IID, which is reflected in the basic process of simple random sampling. Even non-parametric or distribution-free tests make this assumption. By aggregating data in various forms, primarily into summary statistics for individual subjects, neuroscientists are changing their underlying distributions and sometimes independence, in an effort to identify effects that are generalizable to all humans.

This aggregation or summary statistic issue has been directly addressed in fMRI analysis (Friston, Stephan, Lund, Morcom, & Kiebel, 2005), wherein the primary remedy is balanced experimental designs. Balanced experimental designs imply that the same quantities and qualities of experimental units, be them trials within-subject or within-conditions, or subjects within-groups, are ensured among these aggregates. This assumption is usually acceptable in fMRI because the experimental designs are relatively simple and stable, and the image/signal processing rarely involves discarding blocks or trials. On the other hand, EEG data are exceptionally noisy and dynamic, with some subjects having significantly fewer not-too-noisy trials than other subjects, with still widely variable EEG dynamics. This has the potential for creating unbalanced designs and data aggregations that violate IID assumptions. This concern will only worsen in complex and everyday neuroergonomic contexts.

Moreover, with an additional emphasis on complex and real-life activities, especially with the hugely idiosyncratic and individualized approaches humans might have toward their everyday tasks, neuroergonomics EEG research will be confronted with fundamental statistical and experimental concerns of balanced experimental designs and generalizability. This confrontation is reduced to the same tension between case studies and large sample, multi-site studies; practical significance vs. statistical significance.

Solutions? As stated, these concerns transcend non-parametric statistical approaches. Single-trial approaches, as suggested by some like Cohen and Cavanagh (2011), suffer from inadequate generalizability to populations of humans, but at least respect the true underlying distributions of brain activity in vivo. Moreover, these approaches are subject to much greater noise. The summary statistic, random-effects+fixed-effects approach, as in fMRI, could be useful as long as balanced experimental designs and judicious minimization of between-aggregate vs within-aggregate differences are emphasized. Mixed-effects, or hierarchical, regression models, which treat individual differences as random variables in their own right, likely work best, but these differences become difficult to interpret and the models have no closed-form solution. The best solution appears to involve an iterative process that continuously reconciles the ground-truth activity of neurophysiologies in context and transcendent scientific truth, as the next chapter discusses.

Acknowledgements

Chapter 3, in part, was submitted for publication of the material as it may appear in European Journal of Neuroscience, 2020, Gougelet, Robert J. & Miyakoshi, Makoto. Bradley Voytek was also acknowledged in the acknowledgement section of the publication as it may appear. The dissertation author is the primary investigator and author of this paper.

References

Alekseichuk, I., Turi, Z., de Lara, G. A., Antal, A., & Paulus, W. (2016). Spatial working memory in humans depends on theta and high gamma synchronization in the prefrontal cortex. Current Biology, 26(12), 1513-1521.

Baddeley, A. D., & Logie, R. H. (1999). Working memory: The multiple-component model.

Barsalou, L. W. (2008). Grounded cognition. Annu. Rev. Psychol., 59, 617-645.

Bonnefond, M., & Jensen, O. (2012). Alpha oscillations serve to protect working memory maintenance against anticipated distracters. Current biology, 22(20), 1969-1974.

Cavanagh, J. F., & Frank, M. J. (2014). Frontal theta as a mechanism for cognitive control. Trends in cognitive sciences, 18(8), 414-421.

Cohen, M. X. (2014). Analyzing neural time series data: theory and practice. MIT press.

Cohen, M. X., & Cavanagh, J. F. (2011). Single-trial regression elucidates the role of prefrontal theta oscillations in response conflict. Frontiers in psychology, 2, 30.

Delorme, A., & Makeig, S. (2004). EEGLAB: an open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. Journal of neuroscience methods, 134(1), 9-21.

D'Esposito, M., & Postle, B. R. (2015). The cognitive neuroscience of working memory. Annual review of psychology, 66, 115-142.

Eriksson, J., Vogel, E. K., Lansner, A., Bergström, F., & Nyberg, L. (2015). Neurocognitive architecture of working memory. Neuron, 88(1), 33-46.

Fell, J., & Axmacher, N. (2011). The role of phase synchronization in memory processes. Nature reviews neuroscience, 12(2), 105.

Fuster, J. M., & Bressler, S. L. (2012). Cognit activation: a mechanism enabling temporal integration in working memory. Trends in cognitive sciences, 16(4), 207-218.

Friston, K. J. (2009). Modalities, modes, and models in functional neuroimaging. Science, 326(5951), 399-403.

Friston, K. J., Stephan, K. E., Lund, T. E., Morcom, A., & Kiebel, S. (2005). Mixed-effects and fMRI studies. Neuroimage, 24(1), 244-252.

Gevins, A., Smith, M. E., McEvoy, L., & Yu, D. (1997). High-resolution EEG mapping of cortical activation related to working memory: effects of task difficulty, type of processing, and practice. Cerebral cortex (New York, NY: 1991), 7(4), 374-385.

Gougelet, R. J. (2019). Neural oscillation dynamics of emerging interest in neuroergonomics. In Ayaz, H., Dehais, F. (Eds) Neuroergonomics: The Brain at Work and in Everyday Life. (pp. 87 - 92) 10.1016/B978-0-12-811926-6.00014-2.

Glenberg, A. M. (1997). What memory is for. Behavioral and brain sciences, 20(1), 1-19.

Jensen, O., Kaiser, J., & Lachaux, J. P. (2007). Human gamma-frequency oscillations associated with attention and memory. Trends in neurosciences, 30(7), 317-324.

Jensen, O., & Tesche, C. D. (2002). Frontal theta activity in humans increases with memory load in a working memory task. European journal of Neuroscience, 15(8), 1395-1399.

Kayser, J., & Tenke, C. E. (2015). Issues and considerations for using the scalp surface Laplacian in EEG/ERP research: a tutorial review. International Journal of Psychophysiology, 97(3), 189-209.

Klimesch, W. (1999). EEG alpha and theta oscillations reflect cognitive and memory performance: a review and analysis. Brain research reviews, 29(2-3), 169-195.

Klimesch, W. (2012). Alpha-band oscillations, attention, and controlled access to stored information. Trends in cognitive sciences, 16(12), 606-617.

Klimesch, W., Schack, B., & Sauseng, P. (2005). The functional significance of theta and upper alpha oscillations. Experimental psychology, 52(2), 99-108.

Klimesch, W., Sauseng, P., & Hanslmayr, S. (2007). EEG alpha oscillations: the inhibition–timing hypothesis. Brain research reviews, 53(1), 63-88.

Onton, J., Delorme, A., & Makeig, S. (2005). Frontal midline EEG dynamics during working memory. Neuroimage, 27(2), 341-356.

Parasuraman, R., & Rizzo, M. (Eds.). (2008). Neuroergonomics: The brain at work (Vol. 3). Oxford University Press.

Roux, F., & Uhlhaas, P. J. (2014). Working memory and neural oscillations: alpha–gamma versus theta–gamma codes for distinct WM information?. Trends in cognitive sciences, 18(1), 16-25.

Sarnthein, J., Petsche, H., Rappelsberger, P., Shaw, G. L., & Von Stein, A. (1998). Synchronization between prefrontal and posterior association cortex during human working memory. Proceedings of the National Academy of Sciences, 95(12), 7092-7096.

Sauseng, P., Griesmayr, B., Freunberger, R., & Klimesch, W. (2010). Control mechanisms in working memory: a possible function of EEG theta oscillations. Neuroscience & Biobehavioral Reviews, 34(7), 1015-1022.

Sauseng, P., Klimesch, W., Schabus, M., & Doppelmayr, M. (2005). Fronto-parietal EEG coherence in theta and upper alpha reflect central executive functions of working memory. International journal of Psychophysiology, 57(2), 97-103.

Sauseng, P., Klimesch, W., Doppelmayr, M., Pecherstorfer, T., Freunberger, R., & Hanslmayr, S. (2005). EEG alpha synchronization and functional coupling during top-down processing in a working memory task. Human brain mapping, 26(2), 148-155.

Scheeringa, R., Petersson, K. M., Oostenveld, R., Norris, D. G., Hagoort, P., & Bastiaansen, M. C. (2009). Trial-by-trial coupling between EEG and BOLD identifies networks related to alpha and theta EEG power increases during working memory maintenance. Neuroimage, 44(3), 1224-1238.

Wilson, M. (2002). Six views of embodied cognition. *Psychonomic Bulletin & Review*, *9*(4), 625–36. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/12613670

CHAPTER FOUR
Future Directions in Neuroergonomics

Fallman (2003) highlights a difference between knowledge-generating "design-oriented research," and artifact-generating "research-oriented design." Viewed from a pragmatic perspective, design itself is an iterative process by which both the design problem and its solution are worked out simultaneously. Until the emergence of neuroergonomics, neuroscience has been a knowledge-generating field, with only slight to moderate orientation toward design, and has therefore largely trended toward an overly positivistic and unpragmatic exercise of identifying solutions to many problems that do not yet, or may not, exist. This is not to discount the necessity of basic research, which fundamentally reveals potential solutions to problems that we are incapable of foreseeing or recognizing. In this sense, neuroscience is performing exactly as intended. Instead, this is all to say that it is only timely that neuroergonomics has emerged as a necessary parallel to neuroscience; as a new field of artifact-generating, neuroscience-oriented design.

The next steps are to clarify this distinction from neuroscience and emphasize artifact generation rather than knowledge generation, since my personal anecdotal observation is that many neuroergonomists are still clinging to neuroscience and research principles rather than design principles. Further, we ought to take steps in reorienting neuroscience toward design and reinforcing an iterative simultaneous relationship with neuroergonomics as a new neuroscience-oriented design. Original writings on neuroergonomics saw this reorientation as a fundamental benefit of its introduction as a field.

To speculate a little more on future directions, a useful tool in design is the “What if?” brainstorming technique:

- What if actions and mistakes can be predicted before they are made and with enough time to optimize their ultimate outcome? Could event-related potentials directly address this?
- What if thoughts and memories could be redirected to educate, stimulate insight, and guide action?
- What if individual differences could be accounted for to optimize outcomes?
- What if culture and emotions could be directly accessed and redistributed to eliminate conflict?
- What if individual perception and action were neurally antiquated by virtual and networked realities?
- What if the evolution of nervous systems could be accelerated?

An immediate impression from these questions is how they are tainted with underlying moral and philosophical assumptions. What are the potential implications of realizing these imaginings? Perhaps then another step for neuroergonomics is to serve as the medium through which human morality and neuroscience come to terms, apropos to the human-centeredness of any field of design.

References

Fallman, D. (2003, April). Design-oriented human-computer interaction. In Proceedings of the SIGCHI conference on Human factors in computing systems (pp. 225-232).

APPENDIX
Lessons learned

Suggestions to the PhD student and scientist in general:

- Experience the peer-review process as soon as possible
- Research is an iterative process, start small and do not overcommit
- Pilot your experiments *and your analyses*
- Every scientist is a writer before all else. Science is only useful to the extent it is communicated.
- Read less, write more. The writing will lead naturally to the reading.
- Choose harmony over hard work
- Collaborate wisely, but do collaborate
- Take classes at your leisure, or as needed, enjoy them, and make friends
- Starting/during any project, ask yourself: "Am I doing this for the experience, or am I doing this to produce a finished product?" Both are fine, but the former is easier to walk away from, and the latter has a tangible reward.
- Keep a “lab notebook” in digital or perhaps preferably analog form
- Good ideas are a dime-a-dozen and rarely original, follow-through and results are more valuable
- Attend talks and conferences leisurely or otherwise sparingly
- Always collect EOG data with EEG data
- Synchronize all clocks and use both relative and absolute time stamps when collecting data and do not pause data streams
- Collect a short recording of common artifacts for each subject
- Do you really need to collect more data, or is there enough out there already?
- Replication is the best statistic (Steven Luck and Steven Hillyard said this)
- Spend more time collecting good data and less time trying to clean it
- Start with tables before figures
- Collect, reduce, reuse, and recycle code, preferably by creating a personal “toolbox”
- There is no perfect experiment – Marta Kutas
- Prefer statistically balanced experimental designs, equal group sizes, etc.
- Plan carefully so as not to switch email addresses, file hosting, and backup services, etc. The added convenience of the newest tool is heavily outweighed by the inconvenience of discontinuity.
- Take into serious account the retirement intentions of any collaborator, committee member, or even graduate coordinator within the next 5 to 10 years
- Annual funding opportunities or fellowships could end at any time
- Plan your research only as far as the funding will take you. Do not end up analyzing data for free.
- Make a point to familiarize yourself with faculty outside the department to have a wide selection when assembling a dissertation committee