



Estimating direction in brain-behavior interactions: Proactive and reactive brain states in driving

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ABSTRACT

Conventional neuroimaging analyses have ascribed function to particular brain regions, exploiting the power of the subtraction technique in fMRI and event-related potential analyses in EEG. Moving beyond this convention, many researchers have begun exploring network-based neurodynamics and coordination between brain regions as a function of behavioral parameters or environmental statistics; however, most approaches average evoked activity across the experimental session to study task-dependent networks. Here, we examined on-going oscillatory activity as measured with EEG and use a methodology to estimate directionality in brain-behavior interactions. After source reconstruction, activity within specific frequency bands (delta: 2–3 Hz; theta: 4–7 Hz; alpha: 8–12 Hz; beta: 13–25 Hz) in *a priori* regions of interest was linked to continuous behavioral measurements, and we used a predictive filtering scheme to estimate the asymmetry between brain-to-behavior and behavior-to-brain prediction using a variant of Granger causality. We applied this approach to a simulated driving task and examined directed relationships between brain activity and continuous driving performance (steering behavior or vehicle heading error). Our results indicated that two neuro-behavioral states may be explored with this methodology: a *Proactive* brain state that actively plans the response to the sensory information and is characterized by delta-beta activity, and a *Reactive* brain state that processes incoming information and reacts to environmental statistics primarily within the alpha band.

Introduction

The brain is composed of roughly 160 billion neural and non-neural support cells that coalesce into neuronal assemblies of coordinated activity (Azevedo et al., 2009), and neuroscientists have used neuroimaging techniques including EEG (Luck, 2014; Michel et al., 2004) and fMRI (Huettel et al., 2004) to reveal the local specialization of neuronal populations within brain regions. Recently, however, there has been increased interest in examining how the brain coordinates activity across these spatially disperse regions (Alivisatos et al., 2012), and novel functional connectivity methods have enabled research on the symphony of neural processing rather than a compartmentalized snapshot of the brain's dynamic response (e.g., Li et al., 2009; Sakkalis, 2011). Overall, connectivity-based neuroimaging methodologies show promise for augmenting our understanding of how dynamic changes in brain networks support millisecond fluctuations in behavior

(Alivisatos et al., 2012; Friston, 1994; Sporns et al., 2004).

Synchronized frequency oscillations are posited as a mechanism to form transient networks that can integrate information across local, specialized brain regions (He et al., 2015; Klimesch et al., 2007), and the resulting global brain dynamics constitute a brain state that underlies either rest activity or task dependent behavior (LaConte et al., 2007; Sidlauskaitė et al., 2014; Buzsáki and Draguhn, 2004; DeSalvo et al., 2014). Researchers have shown how resting state brain activity modifies incoming information (Wörgötter et al., 1998) or disrupts behavioral performance (Silvanto et al., 2008), and task state activity can be used to modulate performance in neurofeedback paradigms (LaConte et al., 2007; Koush et al., 2013). In this research, we were particularly interested in quantifying ongoing brain network dynamics that show context (i.e., pre-stimulus activity) dependencies in brain and behavior relationships, and we used EEG to study whole-brain oscillatory activity and capitalize on its temporal precision

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(Buzsáki and Draguhn, 2004; Engel et al., 2001; Steriade, 2001).

Here, we investigate temporal dynamics of brain activity and continuous behavioral performance in a simulated driving task. Driving is a complex visuo-motor task that requires interaction among cognitive systems to successfully navigate from one location to another, keep a safe distance from other vehicles, and maintain a consistent lane location while in motion. Despite the complexity of the task, experienced drivers successfully perform this task, with ease, often in a near-automatic fashion. Studies have investigated the underlying neural mechanisms in both real (Sandberg et al., 2011) and simulated (Calhoun et al., 2002; Spiers and Maguire, 2007) driving environments, explored networks that produce task failures (Simon et al., 2011), and used neural measures to predict vehicle parameters (Lin et al., 2005). Thus, a simulated driving task affords the opportunity to study relationships between continuous behavioral measurements and brain dynamics in a naturalistic, everyday task.

Our neuro-behavioral analysis method calculated time-varying asymmetries between fluctuations in oscillatory activity and continuous driving performance, employing a granger casual framework to look at the predictive relationship between brain and behavior. Classical granger causal estimates of connectivity assume a stationary and linear representation of multichannel or multisource EEG activity, an assumption that is often inaccurate when modeling EEG data. Here, we estimated cortical source activity on a whole-brain mesh, parcellated mesh vertices using the Desikan-Killiany atlas (Desikan et al., 2006), and selected 12 *a priori* regions of interest from previous driving research (Calhoun et al., 2002; Spiers and Maguire, 2007). We then used a time-varying model, a dual extended Kalman filter (DEKF), to link brain activity to behavior for four common frequency bands (delta: 2–3 Hz; theta: 4–7 Hz; alpha: 8–12 Hz; beta: 13–25 Hz).

We studied brain-behavior relationships using two measures of driving performance, steering wheel angle and vehicle heading error. Previous research has suggested that heading error of the vehicle is used to determine the steering response and tightly coupled with brain dynamics (Hildreth et al., 2000; Li and Cheng, 2011). In this framework, the heading error is a kinematic variable used to scale a steering response, and the steering response relates back to the heading error by a dynamic transfer function that accounts for vehicle speed and current heading, among other parameters. Importantly, these performance measurements continuously varied during the drive as the participant adjusted the vehicle's position to remain in the center of the lane, and this provides an avenue to examine the continuous relationship between neural dynamics related to vehicle heading error and steering behavior during the “closed loop” control of the vehicle. From this analysis, we defined two distinct neuro-behavioral brain states: a *Proactive* state where the brain activity predominantly causes behavior and a *Reactive* state where the brain activity is predominantly caused by behavior. We apply an analysis of variance to investigate the effects of ROI, frequency band, and experimental factors on the proportion of time spent in each state, as well as the transition probability within and between states. Our results suggest that the Proactive state actively plans the response to the sensory information and the Reactive state processes incoming information and reacts to statistics of the environment.

Method

Participants

Twenty-eight neurologically healthy volunteers (17 Male, Age 18–40, $M = 28.6$) participated in this experiment. This study was conducted in accordance with IRB requirements (32 CFR 219 and DoDI 3216.02).

Behavioral Measurements

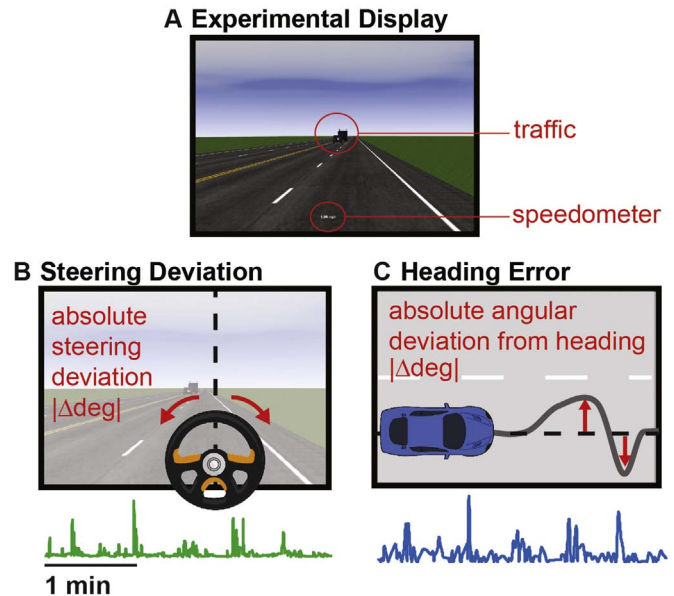


Fig. 1. Experimental display and behavioral measurements. A) In this experiment, subjects were asked to maintain course in the far-right lane whilst on-going traffic and perturbations were introduced. A speedometer reading in the center bottom of the display indicated current speed. B) Continuous steering deviation, the absolute angular difference from the stationary angle (deg). Lower time course is the steering deviation from approximately 3 min of the experiment for one participant. C) Heading error, the absolute angular deviation the vehicle was positioned from the center of the right lane (deg). Lower time course is the heading error from approximately 3 min of the experiment from one participant.

Experimental task

Upon arrival to the lab, participants were introduced to the driving environment and instructed how to perform the task. Subjects were asked to maintain the vehicle in the center of the rightmost lane of a four-lane highway (two lanes in each direction) and to maintain consistent vehicle speed at 45 mph as precisely as possible (See Fig. 1 for a diagram of the display). Lateral perturbations resembling wind gusts were periodically imposed on the vehicle causing changes in its heading, and the participants were instructed to counter them by steering the vehicle back into the center of the rightmost lane as quickly and accurately as possible. Training on the task consisted of participants driving for 10–15 min until subjects reported comfort with the simulated environment and control of the steering and speed were demonstrated. They were then outfitted and prepped for the EEG acquisition.

Following completion of the training and experimental setup, the participants proceeded to drive in a 45-min experimental condition where traffic density was manipulated (sparse, heavy). Vehicle perturbations (‘wind gusts’) were also presented in blocks of either high (every 8–10 s) or low (every 24–30 s) rates. These manipulations were introduced to make the driving experience more naturalistic and to investigate whether either factor imposed a modulation on the measured neuro-behavioral states.

Neuro-behavioral analysis

An overview of the analysis steps are graphically described in Figs. 2 and 3 and succinctly introduced here. First, standard preprocessing of EEG was completed on the raw signal, and continuous behavioral measures were temporally resampled and synchronized with the EEG signal. Next, cortical current source density (CSD) was estimated using cortically constrained low resolution electrical tomo-

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