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The contribution of pre-stimulus neural oscillatory activity to spontaneous response time variability

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ABSTRACT

Large variability between individual response times, even in identical conditions, is a ubiquitous property of animal behavior. However, the origins of this stochasticity and its relation to action decisions remain unclear. Here we focus on the state of the perception–action network in the pre-stimulus period and its influence on subsequent saccadic response time and choice in humans. We employ magnetoencephalography (MEG) and a correlational source reconstruction approach to identify the brain areas where pre-stimulus oscillatory activity predicted saccadic response time to visual targets. We find a relationship between future response time and pre-stimulus power, but not phase, in occipital (including V1), parietal, posterior cingulate and superior frontal cortices, consistently across alpha, beta and low gamma frequencies, each accounting for between 1 and 4% of the RT variance. Importantly, these correlations were not explained by deterministic sources of variance, such as experimental factors and trial history. Our results further suggest that occipital areas mainly reflect short-term (trial to trial) stochastic fluctuations, while the frontal contribution largely reflects longer-term effects such as fatigue or practice. Parietal areas reflect fluctuations at both time scales. We found no evidence of lateralization: these effects were indistinguishable in both hemispheres and for both saccade directions, and non-predictive of choice — a finding with fundamental consequences for models of action decision, where independent, not coupled, noise is normally assumed.

Introduction

The extent to which apparently random fluctuations in behavior are predictable is of fundamental theoretical and practical interest. The time taken to initiate even the most basic responses to highly salient stimulations typically varies four- to five-fold (Fig. 1A). It remains largely unknown why and when this variability occurs: how much is related to the experimental design (experimental factors, trial history, fatigue, practice etc.) and how much is stochastic; and to what extent it is predicted by pre-stimulus brain states. Although historically attributed to 'noise' (an unavoidable limitation of neural systems) and averaged away rather than investigated, variability is crucial to free an organism from predictable and stereotypic behavior. Indeed, models of sensorimotor decisions make an explicit link between variability in response time (RT) and variability in choice/decision (Brown and Heathcote, 2005; Carpenter, 2004; Rouder et al., 1998; Usher and McClelland, 2001).

After stimulus appearance, associations between neuronal activity and response time on each trial are clearly detectable both through monkey single unit and human whole-brain electrophysiology (Lee et al., 2010; Papadopoulou et al., 2010; Schall, 2001; Smyrnis et al., 2011). However, evidence for predicting response time variability from pre-stimulus neural markers is much less consistent, even though this time-period is increasingly thought to contain the seeds of the variance in electrophysiological responses to a stimulus (Arieli et al., 1996; Nikulin et al., 2007).

Our central interest lies in better understanding the sources of the large spontaneous variability observed in the speed of simple actions, such as an orienting response toward salient visual stimuli (Sumner, 2011). The present work focuses on characterizing and quantifying the contribution of pre-stimulus oscillatory activity to this variability. Existing literature directly related to this question only provides a fragmented, sometimes inconsistent, picture. In monkey, local field potentials suggest a complex pattern of positive and negative correlations of spontaneous alpha/beta fluctuations over dorsal areas with manual latency in a go–no go discrimination task (Zhang et al., 2008). Unfortunately, inconsistency across monkeys and the multi-component nature of the task make these data difficult to interpret. In humans, fluctuations in visuo-manual detection speed have been linked to

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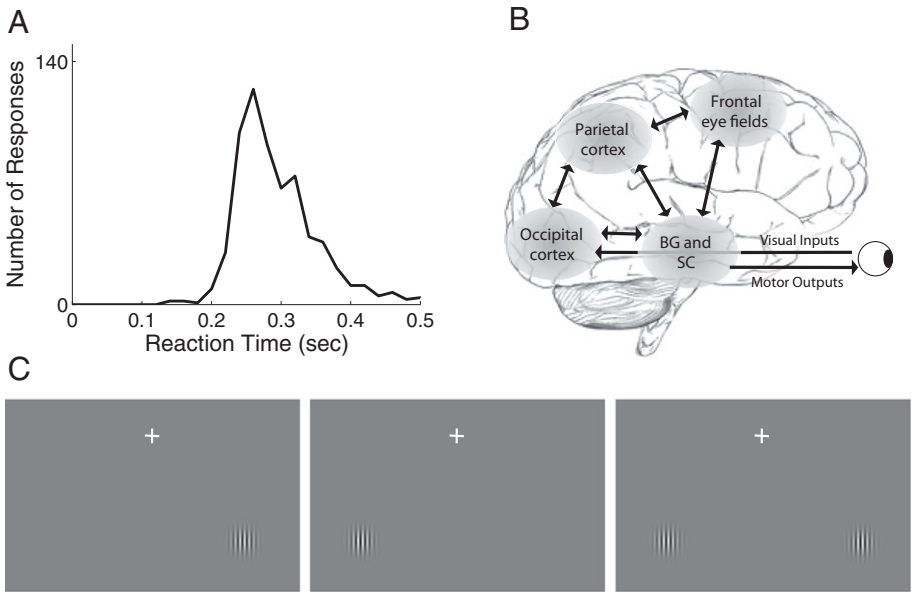

Fig. 1. A. Reaction time distribution from one observer. B. A sketch of the sensory-motor saccade network, from where most of the oculomotor response variability must somehow arise. C. The simple tasks employed here. High-contrast Gabor patches were used as saccade targets. After a fixation period of between 3 and 4 s, the patch appeared in periphery either on the left or the right (single target trials) or on both sides simultaneously (choice trials).

increased fronto-parietal gamma power (Gonzalez Andino et al., 2005), while auditory-manual oddball detection speed has been linked to decreased fronto-centro-parietal gamma power (Reinhart et al., 2011). Saccadic speed has been linked to a slowly rising pre-stimulus EEG potential (Everling et al., 1997), and with the phase of alpha/beta oscillations either in occipital (Hamm et al., 2010) or frontocentral areas (Drewes and VanRullen, 2011). However, the analyses in EEG sensor space in Drewes and VanRullen (2011) and Everling et al. (1997) do not allow concurrent independent assessment of the contribution of each cortical area in the saccade generation network (Fig. 1B) to RT variability, while the absence of temporal jitter in the inter-trial-interval in Hamm et al. (2010) does not allow a distinction to be made between components related to motor response and target processing. Moreover, the actual predictive power of these markers has not been quantified to assess their contributions to predicting behavioral variability. Last, in most existing studies, trial-to-trial variance is assumed to represent spontaneous variance only, and the contribution from non-spontaneous sources (experimental conditions, trial order etc.) was not considered.

A related field of research relies on empirical modulations (rather than spontaneous variations) of pre-stimulus alpha power via sensory stimulation, and has suggested both positive (Kirschfeld, 2008) and negative (Del Percio et al., 2007) correlations with subsequent RT. However, beyond this apparent inconsistency, there is currently no evidence to tell us whether such empirical modulations in oscillatory activity should even be expected to have similar effects to spontaneous variability. Another related field of research focuses on the relationship between spontaneous pre-stimulus oscillatory activity and the visibility of near-threshold stimuli (Busch et al., 2009; Mathewson et al., 2009; van Dijk et al., 2008). However, the sources of visibility variation of near-threshold stimuli are unlikely to be identical to the sources of action variability to salient stimuli, as there has been long-term debate on the extent to which perception and action rely on dissociated neural pathways (see Milner and Goodale, 2008, for a review on this debate). There are certainly examples where factors with clear influence on RT do not affect perception (e.g. we respond slower to color changes than to luminance changes, but we do not perceive color changes as occurring later than luminance changes — Bompas and Sumner, 2008).

For all these reasons, to what extent MEG activity before stimulus onset predicts the spontaneous variance in action speed to clearly visible stimuli is still largely an open question. Our study aimed to resolve this question, by investigating both amplitude and phase of oscillatory activity, while also addressing related fundamental questions: Is variance correlated across the brain and across response options? How does such variance relate to choice outcome?

We therefore use a very simple task that maps a highly visible stimulus (no added noise and no perceptual uncertainty), presented alone or in pairs (free-choice trials) with temporal jitter, onto a highly practiced motor response (saccadic eye movements are among the quickest and most common sensorimotor actions we make, and the visuo-oculomotor network is well established, Fig. 1B), without further manipulation (Fig. 1C). We then searched for the MEG predictors of both saccadic reaction time in the no-choice trials and decision outcome in choice trials, using the pre-target period at which time the participants did not know which type of trial was about to appear. We use a variation of the beamformer source reconstruction approach to identify those areas where pre-stimulus amplitude predicted subsequent reaction time and quantify their contributions.

To characterize the contribution of spontaneous vs non-spontaneous sources, we compare our results when using, as regressors, the raw reaction times on each trial, or the reaction times corrected for main effects due to inter-trial-interval, experimental conditions or blockwise trends such as fatigue and practice. To further characterize the temporal dynamics and frequency spectra of this relationship, we reconstruct the activity at each step of cortical processing: in anatomical primary visual cortex (V1), intra-parietal sulcus (IPS), frontal eye field (FEF) and supplementary eye field (SEF). We then use the activity in V1 to assess correlations and independent contributions to RT across the brain. We also searched for predictors of choice outcome in two-target trials, and for a relationship between phase and reaction times.

Materials and methods

Observers

Twelve volunteers (4 female), with normal (or corrected to normal) vision participated (and received payment). The study received ethical approval from an independent local ethics board.