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Trial-by-trial neural variability is a stable individual trait of adult humans

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Abstract

A wide variety of sensory studies have shown that cortical neural activity varies dramatically across trials. This trial-by-trial neural variability is relatively large in the pre-stimulus period and considerably smaller (quenched) following stimulus presentation. Neural variability affects behaviour. For example, perceptual performance is better on trials and in individuals where variability quenching is larger. Furthermore, allocating attention to a stimulus improves behavioral performance by reducing neural variability. How consistent are neural variability measures of individual subjects? Here, we show that neural variability magnitudes are remarkably consistent across four different tasks with different attentional and cognitive demands as well as across experimental sessions separated by one year. These results suggest that, in adults, neural variability magnitudes are solidified individual traits, which change little with behavioral state or time, and predispose individual subjects to exhibit specific behavioral capabilities.

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Introduction

Neural activity in the mammalian brain is notoriously variable/noisy over time[1,2]. This variability is apparent across trials before the presentation of a stimulus (i.e., ongoing variability) and also after the presentation of a stimulus (i.e., stimulus-evoked variability)[3–5]. Recent research has shown that ongoing neural variability is considerably larger than stimulus-evoked variability, thereby demonstrating that sensory stimulation reduces ("quenches") ongoing neural variability [5]. Such variability quenching was consistently reported across studies examining a variety of cortical areas and arousal states, while using different types of stimuli, and when measuring neural activity with electrophysiology in animals [5–10] or neuroimaging in humans[11–13].

Several lines of evidence show that neural variability has a strong impact on behavioral performance. First, variability quenching is associated with better perceptual performance, whether examined across trials [13] or across individual subjects [14]. Second, actively allocating attention to a visual stimulus improves behavioral performance primarily by reducing the trial-by-trial response variability of single neurons [7] and the shared/correlated variability across the local neural population [15,16]. Third, increasing dopamine and norepinephrine levels increases the magnitude of neural variability in both humans [17] and animals [18,19] and generates behavior that is more exploratory (variable)[19].

While neural variability is under the flexible control of attention and neuromodulation to a certain extent, many of the mechanisms that generate and govern neural variability are likely to be a product of individual genetics and early development. For example, mechanisms that govern the reproducibility of neural activity by maintaining stable excitation-inhibition balances [20] and reliable synaptic transmission[21], are the product of individual genetics (which determine, for example, the structure and function of Sodium channels) and environmental exposure during early critical periods[22,23]. Since individual subjects have different genetics and experience different environmental exposures, one may expect intrinsic neural variability levels to differ across individuals and potentially predispose them to different behavioral capabilities.

To what extent is the level of trial-by-trial neural variability an individual human trait? To address this question we measured neural variability with EEG in 24 subjects as they performed four different visual tasks with different attentional and cognitive demands ranging from a simple reaction time task (i.e., respond when you see a stimulus) to a demanding 2-back working memory task (i.e. responds when the stimulus is identical to the

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one presented two trials ago). The same subjects performed these tasks in two experimental sessions separated by a year. This experimental design enabled us to examine the consistency of neural variability measures across tasks and over time within the same individuals and determine how differences in neural variability across subjects were related to differences in their behavioral performance.

Results

Twenty four subjects completed two experimental sessions separated by one year. Each session included four visual tasks: 1) presentation of a checkerboard annulus in the periphery while subjects performed a color-detection task at fixation, 2) a choice reaction time (CRT) task where subjects were instructed to respond with one button to a circle stimulus and with another button to a tringle stimulus , 3) a go-no-go task where subjects were instructed to respond only to the circles (go trials) and not to the triangles (no-go trials), and 4) a 2-back working memory task where subjects were presented with four Chinese letters and instructed to respond whenever the current letter matched the letter that was presented two trials before.

Neural variability quenching

We examined trial-by-trial neural variability as a function of time before and after stimulus presentation in each of the four experiments (Figure 1). Trial-by-trial variability was reduced (i.e., quenched) following stimulus presentation in all experiments and in both recording sessions performed a year apart. Variability quenching was sustained from 150 to 400ms after stimulus presentation and most evident in occipital electrodes (O1, O2, PO7 and PO8). We quantified variability quenching as the relative change (in units of percent change) between pre-stimulus (-200 to 0ms) and post-stimulus (150 to 400ms) periods, while focusing our analyses on the four electrodes noted above.

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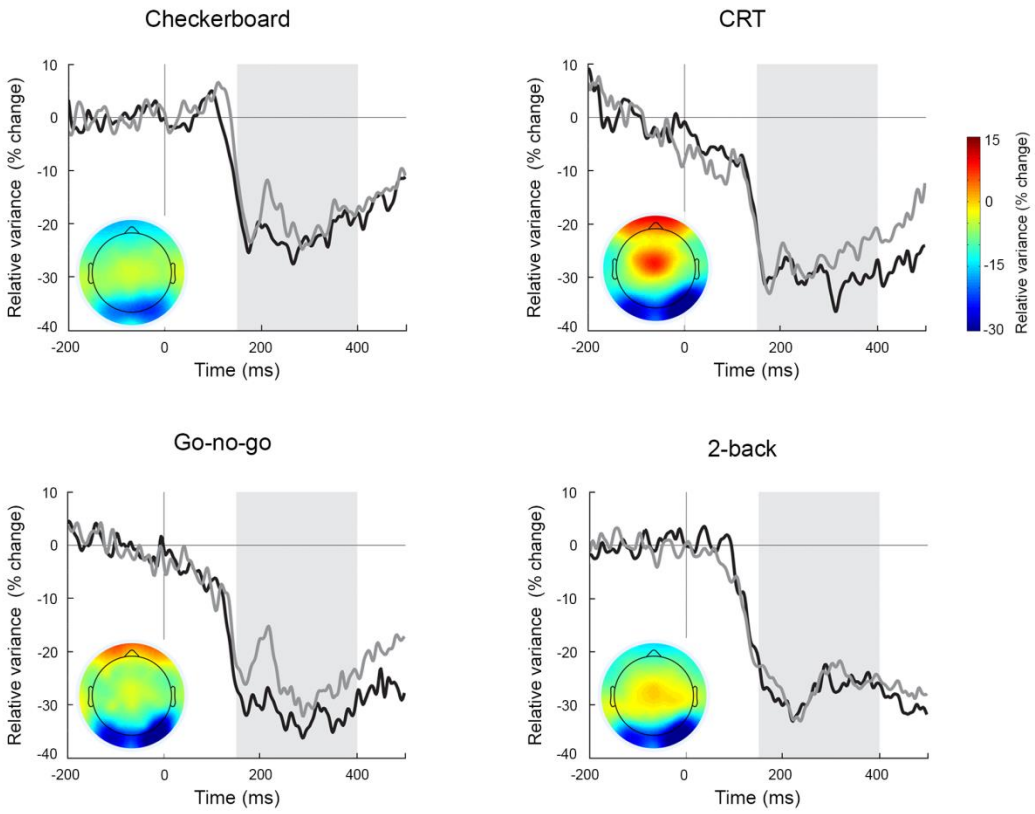

Figure 1: Temporal and spatial dynamics of trial-by-trial neural variability. Each time-course represents the changes in relative trial-by-trial variability (percent-change units relative to the pre-stimulus period) during the first (black) or second (grey) experimental session. Each panel displays the results of a different experiment. Gray background: 150-400ms post-stimulus period with sustained variability quenching that was selected for further analyses. Insets: topographic maps of variability quenching magnitudes during the 150-400ms window.

Neural variability is a stable individual trait

We quantified three measures of trial-by-trial variability for each subject. Absolute trial-by-trial variability was quantified in the pre-stimulus (-200 to 0 ms) and post-stimulus (150-400 ms) periods for each subject, in each of the four experiments, and each of the experimental sessions (see Methods). Variability quenching was quantified as the difference between variability magnitudes in the pre and post stimulus periods. All three measures of variability were strongly and significantly correlated across the two EEG recording sessions in each of the four experiments ($r(24) > 0.58$, $p < 0.003$, Figure 2). This demonstrates that the neural variability magnitudes of individual subjects barely changed over a one year period.

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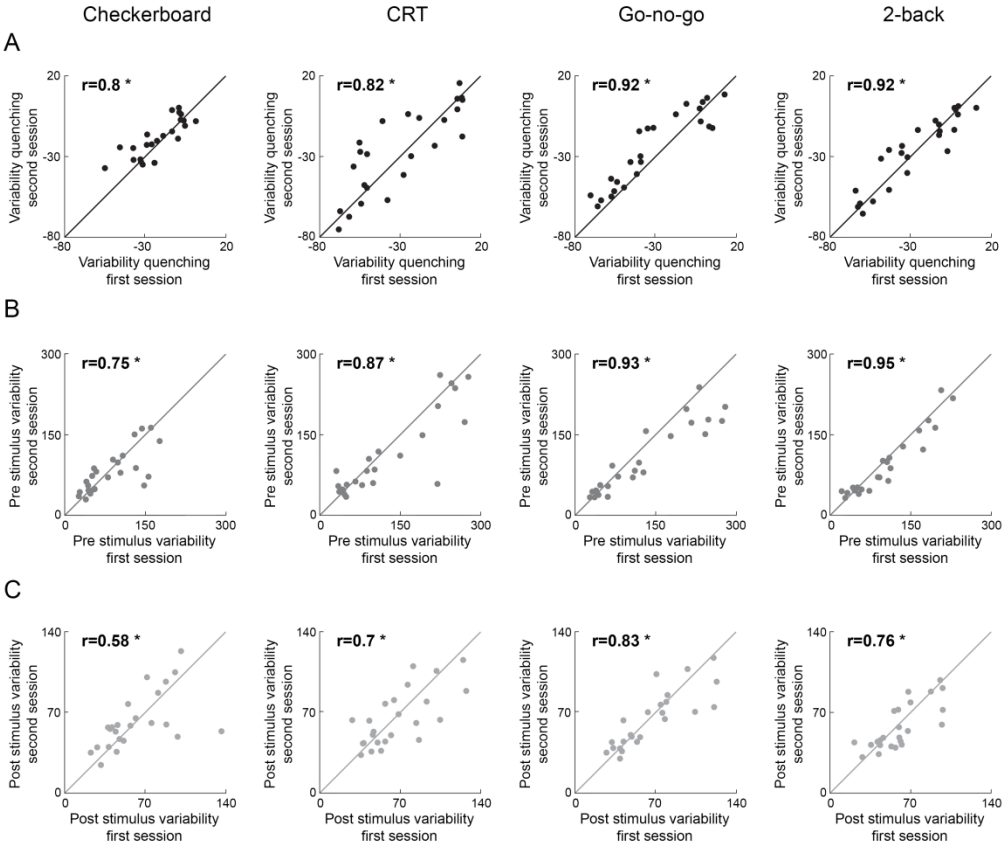

Figure 2: Individual neural variability magnitudes were consistent across experimental sessions separated by one year. Scatter plots present the magnitudes of variability quenching (A), pre-stimulus variability (B), and post-stimulus variability (C) in individual subjects during the first and second experimental sessions for each of the four experiments. The unity line is drawn for reference in each panel. Each point represents a single subject. Asterisks: significant correlation as assessed by a randomization test ($p<0.001$). Pearson's correlation coefficients are noted in each panel.

Individual variability magnitudes were also strongly correlated across experiments. Given the strong correlations across sessions (Figure 2), we averaged each of the three variability measures across the two sessions. We then compared individual variability magnitudes across the six experiment pairs. This analysis revealed strong, positive, and significant correlations across all pairs of experiments when examining variability quenching ($r(24)>0.73$, $p<0.001$, Figure 3), pre-stimulus variability ($r(24)>0.86$, $p<0.001$), or post-stimulus variability ($r(24)>0.9$, $p<0.001$) magnitudes.

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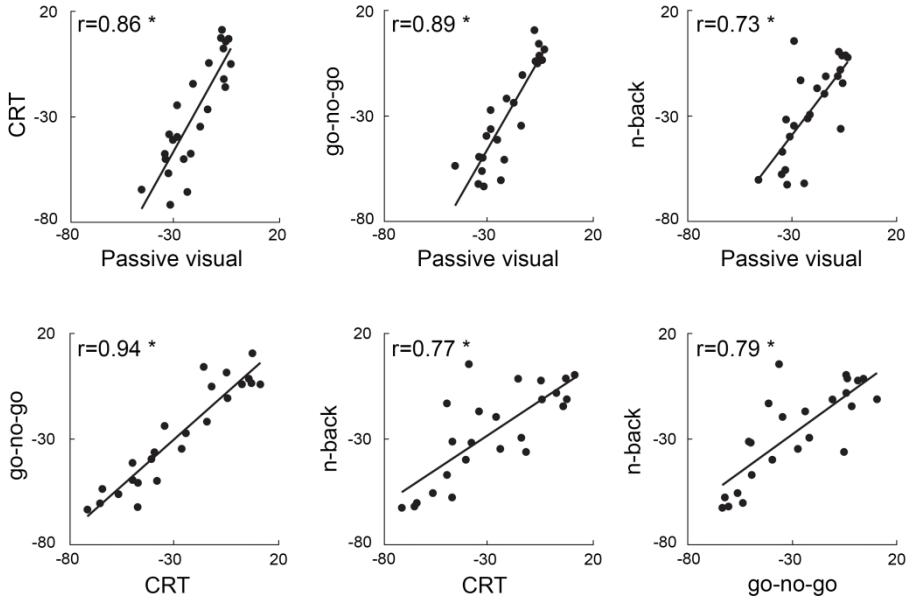

Figure 3: Individual variability quenching magnitudes were consistent across experiments. Scatter plots demonstrate the relationship between variability quenching magnitudes in each pair of experiments. Each dot represents a single subject. The linear fit is drawn for reference in each panel. Asterisks: significant correlation as assessed by a randomization test ($p<0.001$). Pearson's correlation coefficients are noted in each panel.

Differences in neural variability across tasks

The four tasks examined in this study imposed different cognitive and attentional demands. In the checkerboard experiment we quantified trial-by-trial neural variability to an unattended stimulus (i.e., attention was diverted to a task at fixation). In the three other experiments we quantified trial-by-trial neural variability to an attended stimulus, yet the cognitive load in the two-back task was considerably larger than in the CRT and go-no-go task as can also be seen in the behavioral performance (see below). Note that in the CRT and go-no-go tasks the subjects responded with a button press on all of the examined trials whereas in the other two tasks they did not.

Since previous research suggests that neural variability should decrease with attentional load, we compared both variability quenching and absolute variability in the pre and post stimulus periods across the four tasks (Figure 4). Variability quenching and pre stimulus variability were somewhat smaller in the checkerboard experiment in comparison to the cognitive tasks, but a one way ANOVA showed that there were no significant differences

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across tasks in any of the variability measures (Quenching: $F_{(3,92)} = 0.69, p = 0.56$; pre stimulus: $F_{(3,92)} = 1.47, p = 0.23$; post stimulus: $F_{(3,92)} = 0.46, p = 0.7$; Figure 4). These analyses reveal that neural variability measures differed across subjects to a much larger degree than they differed across tasks.

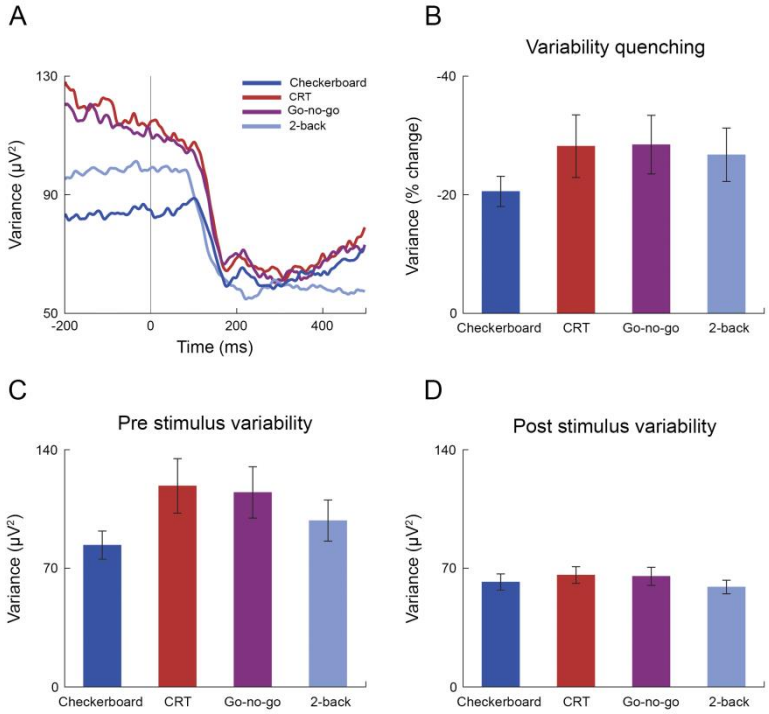

Figure 4: Neural variability differences across experiments. (A) Neural variability time courses (mean across subjects and sessions) demonstrating the change in trial-by-trial neural variability in each of the four experiments. (B) Neural variability quenching. (C) Neural variability in the pre-stimulus interval (-200 to 0ms). (D) Neural variability in the post-stimulus interval (150 to 400ms). Error bars: Standard error of the mean across subjects.

Neural variability and behavioral performance

We estimated three performance measures in each of the four experiments: accuracy, mean reaction time (RT) and RT variability (Figure 5). One way ANOVA analyses demonstrated that there were clear differences in the accuracy ($F_{(3,92)} = 56.7, p < 0.001$), mean reaction time ($F_{(3,92)} = 99.1, p < 0.001$), and reaction time variability ($F_{(3,92)} = 131.9\ , p < 0.001$) across the four tasks. Post-hoc Tukey's tests revealed that there were significant differences across all pairs of tasks, except for the CRT and Go-no-go tasks (p<0.01 for all behavioral

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measures). These results demonstrate that the CRT and Go-no-go tasks were relatively easy, while the color-detection task in the Checkerboard experiment and the 2-back task were relatively harder. Note that in the Checkerboard experiment the task diverted the subjects' attention away from the checkerboard stimulus, thereby allowing us to quantify trial-by-trial neural variability to an unattended stimulus. In contrast, the 2-back task required that subjects attend the stimulus, thereby allowing us to quantify trial-by-trial neural variability to a strongly attended stimulus.

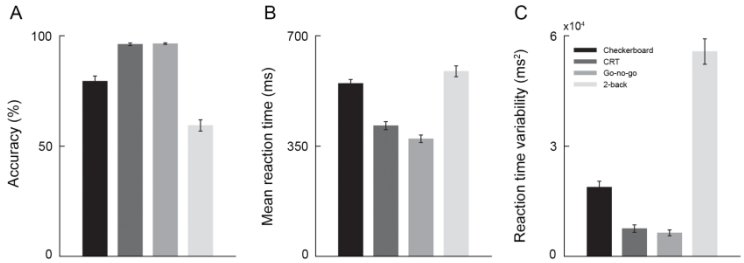

Figure 5: Behavioral performance measures. Mean across subjects and sessions for accuracy (A), reaction time (B) and reaction time variability (C) in each of the four tasks. Error bars: standard error of the mean across subjects. Significant differences across tasks are described in the text.

We found significant relationships between all three neural variability measures and accuracy on the 2-back working memory experiment, yet all other relationships were not significant (Figure 6). In the 2-back experiment, accuracy was positively correlated with the pre-stimulus variability magnitudes ($r(24)=0.45$, $p<0.05$; uncorrected) and post-stimulus variability magnitudes ($r(24)=0.44$, $p<0.05$; uncorrected). Accuracy was also negatively correlated with variability quenching magnitudes ($r(24)=-0.4$ $p<0.05$; uncorrected). Note that variability quenching magnitudes are negative such that larger (more negative) quenching was associated with higher accuracy on the 2-back task. While we did not correct these analyses for multiple comparisons, it is reassuring that all three significant findings were with the same behavioral measure in the same experiment (i.e., accuracy on the 2-back).

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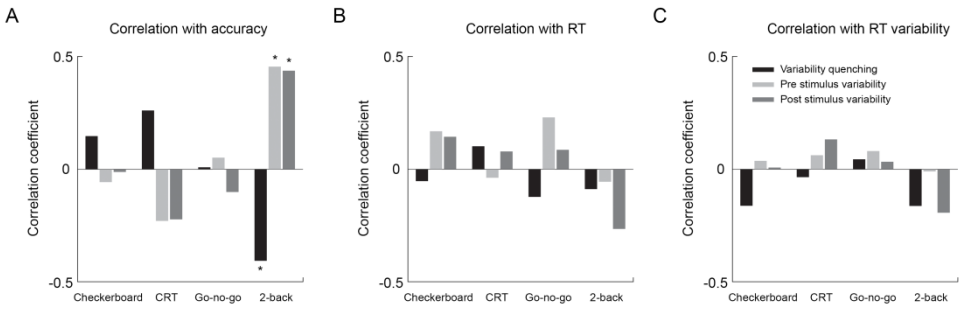

Figure 6: Relationships between neural variability and behavior. Pearson's correlation coefficients were calculated between each of the three behavioral measures: accuracy (left panel), mean RT (middle panel), RT variability (right panel) and each of the three variability measures: variability quenching (black bars), pre stimulus variability (light gray bars) and post stimulus variability (dark gray bars) in the first (A) and second (B) experimental sessions. Asterisks indicate significant correlations as assessed by a randomization analysis ($p<0.05$, uncorrected).

Alternative sources of trial-by-trial variability

We examined whether non-neural sources of variability, such as gaze variability or the quality of EEG recordings could explain our results regarding consistency across tasks or sessions. We utilized eye tracking data from the checkerboard experiment to determine whether neural variability measures were associated with the variability of gaze position across trials. Gaze position variability, however, was not significantly correlated with variability quenching magnitudes in either the first ($r(21)=-0.14$, $p=0.26$) or second ($r(21)=-0.28$, $p=0.1$) recording session. In addition, gaze variability was not significantly correlated across recording sessions ($r(24)=0.33$, $p=0.07$, Figure 7B). This reassured us that the magnitude of neural variability across trials was not associated with the ability of the subject to maintain fixation.

Electrode offset is a measure that quantifies the quality of the EEG recordings when using active electrode systems. Here we computed the electrode offset variability to determine whether trial-by-trial changes in electrode offset (indicative of an unstable EEG recording) were associated with the neural variability measures. Electrode offset variability, was not significantly correlated with the magnitude of variability quenching in any of the experiments performed in either the first or second session ($-0.26<r(24)<0.21$, $p>0.11$). Furthermore, electrode offset variability in each of the four experiments was not significantly correlated across the two sessions ($-0.05<r(24)<0.18$, $p>0.2$, Figure 7A). This reassured us that the strong and significant correlations of neural variability magnitudes

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across tasks and sessions were not due to between-subject differences in the quality of EEG recording.

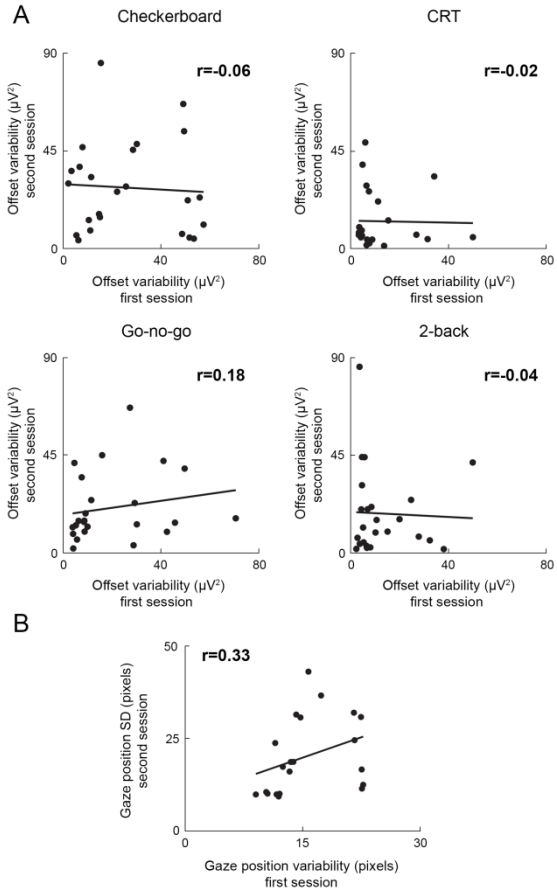

Figure 7: Electrode offset variability or gaze variability were not significantly correlated across sessions. (A) Scatter plots of electrode offset variability measure in the first and second EEG recording sessions, for each of the four experiments. (B) Correlation between gaze variability in the first and second session, as measured in the checkerboard task. Each dot represents a single subject, correlation coefficients are noted in each panel.

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Discussion

Our results demonstrate that neural variability magnitudes differ across adult subjects in a consistent and reproducible manner over long periods of time and regardless of the task that the subjects are performing. This was true for measurements of neural variability in either pre-stimulus or post-stimulus periods and also when computing relative variability quenching (Figures 2&3). These consistent individual differences in the magnitude of neural variability were much larger than differences across the tasks (Figure 4) despite the use of tasks with considerably different attentional and cognitive demands (Figure 5). Furthermore, when examining the task with the largest cognitive demands in our study, a two-back working memory task, we found that individuals with larger pre-stimulus variability, post-stimulus variability, and larger variability quenching exhibited more accurate detection of letter repeats. Taken together, these results reveal that neural variability magnitudes are mostly static individual traits that can be modified only slightly by mechanisms of attention or neuromodulation, yet can explain differences in behavioral capabilities across subjects when the task is demanding.

Neural variability: state or trait?

To what degree is neural variability under flexible behavioral control? Previous studies have reported that actively allocating attention to a visual stimulus reduces the trial-by-trial response variability of single neurons [7] and the shared/correlated variability across the local neural population [15,16]. Indeed, it has been proposed that attention improves behavioral performance primarily by reducing correlated trial-by-trial variability/noise [16]. Additional studies have reported that raising the levels of dopamine and/or norepinephrine increases the magnitude of neural variability in both humans [17] and animals [18,19]. It has been suggested that these neuromodulatory mechanisms are associated with activation of exploration versus exploitation states. In the exploration state, the animal behaves in a more variable manner that enables learning through trial-and-error, whereas in the exploitation state the animal behaves in a more reproducible manner in order to exploit previously learned information.

While attention and neuromodulation are invaluable mechanisms for flexibly changing the magnitude of trial-by-trial neural and behavioral variability, individual differences in neural variability magnitudes are also governed by a many other neurophysiological mechanisms. At the single cell level, these include the noisy response characteristics of peripheral sensors [24], the stochastic nature of synaptic transmission [21], and the dynamic changes caused by

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neural adaptation [25] and synaptic plasticity [26]. At the neural network level, additional variability is generated by adjustments of the excitation/inhibition balance [20] and continuous interaction and competition across large neural populations [27]. These mechanisms are likely to be the product of multiple genetic and environmental factors that create and modify developing neural circuits and eventually solidify their structure and function during specific critical periods in development[23].

Our results reveal that there are large differences in neural variability magnitudes across adult subjects and clearly show that individual neural variability magnitudes are remarkably consistent across tasks and over time. This suggests that they represent individual traits rather than flexible states. We speculate that examining these measures in young children would be particularly interesting for understanding how neural variability may change during development and then stabilize in adolescence or adulthood. Analogous behavioral research in humans[28] and birds[29] has already shown that behavioral variability diminishes during development and stabilizes in adulthood.

The behavioral significance of neural variability

There is ongoing debate regarding the potential behavioral significance of different measures of neural variability. On the one hand, several studies have demonstrated that smaller trial-by-trial neural variability is associated with better perceptual and cognitive performance. For example, fMRI studies have reported that trial-by-trial variability is smaller on trials where a threshold-level stimulus is detected [30] and on trials where a stimulus is later remembered [31] . Similarly, MEG and EEG studies have reported that neural variability quenching is larger on trials where a threshold-level stimulus is detected [13] and in individuals with lower (better) contrast discrimination thresholds [14] . Furthermore, excessive neural variability has been reported in different disorders including autism [32,33], ADHD [34], and schizophrenia [35], while electrophysiology studies have reported that neural responses are more variable in elderly animals [36,37] and humans [38] who exhibit cognitive decline. These results are in line with signal detection theory principles, which suggest that intrinsic variability/noise reduces the detection and discrimination abilities of a perceptual system[39]. Other studies, however, have reported that younger individuals exhibit larger fMRI time-course variability than elderly individuals [40] and that this coincides with faster and more consistent responses when performing cognitive tasks such as perceptual matching, attentional cueing, and delayed match to sample [41]. It has been proposed that such increased ongoing variability may be beneficial for cognitive performance, because it allows for higher neural complexity and enables a neural network to flexibly switch between

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different states [42]. A possible compromise between these potentially contradictory studies is that large ongoing neural variability together with large quenching may yield the best perceptual and cognitive performance [13,14]. An important conclusion from both lines of research is that it is essential to carefully de-compose neural variability into distinct components such as ongoing variability and stimulus-evoked variability when examining relationships with behavioral measures[43].

Our results also represent a potential compromise between the two views described above. We found significant positive correlations between the accuracy of performance on the two-back task and pre-stimulus or post-stimulus neural variability magnitudes as well as a significant negative correlation with variability quenching magnitudes (Figure 6). This suggests that a combination of larger ongoing neural variability along with stronger variability quenching are associated with better behavioral performance. These effects were only found with respect to the two-back task, which was the hardest task in our study (Figure 5). We speculate that this evidence suggests that individual differences in neural variability magnitudes exhibit a behavioral impact mostly in tasks that involve considerable attentional and cognitive loads.

Measurement noise

Measures of trial-by-trial neural variability may be biased by subject-specific measurement noise of non-neural origin. We examined two potential sources of non-neural variability in our study: eye-gaze variability (indicative of the stability of fixation across trials) and trial-by-trial variability in electrode offset (indicative of the stability of the EEG recording). We did not find any significant correlation between electrode-offset variability or gaze-position variability and neuronal measures of variability. Furthermore, electrode offset variability or gaze position variability were not significantly correlated across recording sessions (Figure 7). These results demonstrate that the individual magnitudes of trial-by-trial variability were not associated with potential sources non-neural measurement noise.

Conclusions and future directions

This study adds to accumulating evidence demonstrating that neural variability measures of individual subjects are remarkably useful for understanding their individual behavioral capabilities. While neural variability is to some degree under flexible control of attention and neuromodulation, our results demonstrate that, in adults, neural variability magnitudes are mostly consistent across distinct tasks and recording sessions. We, therefore, suggest that neural variability magnitudes represent stable between-subject differences in fundamental neural characteristics that were forged by genetics and environmental exposures during

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early development. Revealing how neural variability magnitudes change during early development and predispose individuals to exhibit different behavioral capabilities and/or specific developmental disorders is likely to be of great interest for further research [43].

Methods

Subjects. Twenty four subjects (eight males, mean age during the first session= 23.7 years, SD= 1.4) took part in this study. All subjects had normal or corrected-to-normal vision. The study was approved by the Ben-Gurion University Internal Review Board. Subjects provided written informed consent during both experimental sessions and were either paid for their participation or received research credit.

Experimental design. All subjects completed four experiments in each of two experimental sessions. The gap in time between the first and the second session was 12.3 months on average (SD = 1.1). The study was performed in a dark and sound proof room. The stimuli were presented using MATLAB (Mathworks, Inc., USA) and Psychtoolbox [44].

Checkerboard experiment: The visual stimulus consisted of a circular, doughnut shaped, checkerboard with an inner radius of 0.6° visual angle and an outer radius of 3.7° visual angle. The experiment consisted of 600 trials; 400 trials containing a stimulus and 200 trials where the stimulus was omitted. Stimuli were presented for 50ms and were followed by a randomized inter-trial interval lasting 750-1200ms. The experiment included an orthogonal color-detection task at fixation, which was intended to divert attention away from the checkerboard stimuli. Subjects were instructed to press a key whenever the black fixation cross changed its color to gray. The experiment contained 80 random color changes, which lasted 30ms and subjects had one second to respond. Correct and incorrect responses were indicated by changing the fixation cross to green or red, respectively.

Choice Reaction time (CRT) experiment: In each trial, either a black triangle or a circle was presented at the center of the screen for 300ms and subjects were instructed to press the right or left arrow keys, respectively, as quickly as possible using their right index finger. Each trial was followed by an inter-trial interval of 1200ms. A total of 400 trials were presented, 200 trials of each of the two stimuli.

Go-no-go experiment: Stimuli and structure were identical to those described in the CRT experiment, except that participants were instructed to press the spacebar as quickly as possible with their right index finger whenever they saw a circle (“go” trial) and not when

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the triangle was presented ("no go" trial). A total of 600 trials were presented and 80% of the trials contained the "go" stimulus.

2-back experiment: Stimuli were composed of 4 Chinese letters, presented at the center of the screen and participants were asked to press the "J" key whenever the current letter matched the one that was presented 2 trials before. Each letter was presented for 500ms and followed by an inter-trial interval of 500ms. A total of 600 trials were presented with 20% of them containing a 2-back repeat.

EEG and eye tracking recordings. EEG data were recorded using a 64-channel BioSemi system (Biosemi Inc., Netherlands), connected to a standard EEG cap according to the international 10-20 system. Data were referenced to the vertex electrodes. Electrooculography (EOG) was recorded using two electrodes at the outer canthi of the left and right eyes and one electrode placed below the right eye. In the checkerboard experiment, the position of the right eye was recorded using an eye-tracker (EyeLink 1000, SR-research) at a sampling rate of 1000Hz.

EEG preprocessing. Data was analyzed using Matlab (Mathworks, Inc.) and the EEGLAB toolbox [45]. Continuous EEG data was down sampled to 512Hz, filtered using a 1-40 Hz band pass filter, and re-referenced to the bilateral mastoid electrodes. EEG epochs were extracted using a time window of 700ms (200ms pre-stimulus to 500ms post-stimulus) and baseline correction was not performed so as not to alter trial-by-trial variability in the pre-stimulus interval. In the checkerboard experiment only trials where stimulus was presented were extracted, in the CRT experiment trials with both stimuli (circle or triangle) were extracted, in the go-no-go experiment only the "go" trials were extracted and in the 2-back experiment trials with the four different stimuli (Chinese letters) were extracted. Epochs where the absolute amplitude exceeded 70µV or where the power exceeded 25db in the 20-40Hz frequency range were identified as containing eye blinks or muscle artifacts, respectively, and were removed from further analysis. In the checkerboard experiment identification of eye blinks was confirmed by eye tracking - trials containing horizontal or vertical eye movements that exceeded 1.5 SD of the mean were identified as trials where fixation was not maintained (i.e. trials containing saccades) and excluded from EEG analyses. Mean number of trials across subjects and sessions after trials rejection in the four experiment was 252 trials in the checkerboard experiment (SD=46), 150 trials in the CRT experiment (SD=37), 162 trials in the go-no-go experiment (SD=52), and 256 trials in the 2-back experiment (SD=42). Mean number of trials did not differ between the first and second experimental sessions.

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EEG data analysis. Trial by trial variability was computed for each time-point in the extracted epochs (-200 to 500ms) for each of the 64 electrodes, in each subject separately. Trials from the first and second sessions were analyzed separately. Absolute level of trial-by-trial variability in the pre-stimulus interval was computed as the mean variance within a time window of -200ms and 0ms pre-stimulus. Absolute level of trial-by-trial variability in the post-stimulus interval was computed as the mean variance within a time window of 150-400ms post-stimulus.

Relative trial-by-trial variability was computed by converting the variability time courses to percent change units relative to the mean trial-by-trial variability in the pre-stimulus period (-200 to 0ms). We then estimated variability quenching for each subject in each task and session by computing the difference in variability between the pre-stimulus period (-200 to 0ms) and post stimulus period (150 to 400ms). We focused our analyses on the four occipital electrodes (O1, O2, PO7 and PO8) with the strongest visual responses.

Behavioral data analysis. Mean accuracy, mean reaction time (RT) and reaction time variability (across trials) was computed for each subject and each session, in CRT, go-no-go and two-back tasks as well as the color-detection task in the checkerboard experiment. The first 10 trials in each block, trials with RT below 200ms and trials with incorrect responses were excluded from the analysis.

Statistical tests. We assessed relationships across measures using Pearson's correlations. The statistical significance of the correlation coefficients was assessed with a randomization test where we shuffled the labels of the subjects before computing the correlation coefficient. This procedure was performed 10,000 times while shuffling the labels across subjects randomly each time to generate a null distribution for each pair of EEG/behavioral measures. For the true correlation coefficient to be considered significant it had to be higher than the 95th percentile or lower than the 5th percentile of this null distribution (i.e., equivalent to a p-value of 0.05 in a one tailed t-test). Comparisons across experiments/tasks were performed using a one-way ANOVA with task as the only factor, followed by post hoc Tukey's tests when the initial result indicated significant differences.

Electrode offset variability. The Biosemi EEG system utilizes active electrodes, which do not yield a measure of impedance. Instead, fluctuations in electrode offset (i.e. slow changes in the voltage potential over time) are considered the best indication for the quality of EEG recording [46]. We, therefore, computed the electrode offset variability across trials for each subject during each of the experiments in each experimental session. We computed the

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offset value for each trial, the variability across trials in each of the four electrodes, and finally the mean across electrodes in each experiment. We then correlated offset variability with the EEG variability measures to check if differences in the quality of EEG recordings across individuals could explain our results.

Gaze variability. Gaze position was measured during the checkerboard experiment only. We computed the distance from the fixation cross at each time point from stimulus onset to 500ms post stimulus, then computed the standard deviation across trials for each time point, and finally averaged across all time points (0-500ms) to generate a single measure of gaze variability per subject. We correlated gaze variability across the first and second sessions to determine whether individual subjects exhibited reproducible gaze variability across sessions. Three subjects were excluded from this analysis due to difficulties in the calibration process of the eye tracker in one of sessions.

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