Experimental Brain Research (2019) 237:1881–1888
https://doi.org/10.1007/s00221-019-05558-3

RESEARCH ARTICLE

High-beta/low-gamma frequency activity reflects top-down predictive coding during a spatial working memory test

Rebecca V. Zhang[1] · Robert E. Featherstone[2] · Olya Melynchenko[2] · Raymond Gifford[2] · Rachel Weger[1] · Yuling Liang[1] · Steven J. Siegel[2]

Received: 17 October 2018 / Accepted: 8 May 2019 / Published online: 15 May 2019

Abstract

Numerous mental health disorders are characterized by cognitive impairments that result in poor vocational and social outcomes. Among the cognitive domains commonly affected, working memory deficits have been noted in patients with attention-deficit/hyperactivity disorder (Martinussen et al. in J Am Acad Child Adolesc Psychiatry 44:377–384, 2005), post-traumatic stress disorder (Honzel et al. in Cogn Affect Behav Neurosci 14:792–804, 2014), and consistently with schizophrenia patients (Callicott et al. in Cereb Cortex 10:1078–1092, 2000; Lewis et al. in Front Hum Neurosci 10:85, 2005; Amann et al. in Brain Res Bull 83:147–161, 2010; Limongi et al. in Schizophr Res 197:386–391, 2018). Oscillations in neural activity from electroencephalogram (EEG) recordings are decomposed by frequency, and band-specific decreases in gamma power (> 30 Hz) have been correlated with working memory ability. This study examined within-subject changes in power of frequency-specific bands during sample versus choice trials during a spatial working memory paradigm (T-maze). EEG was recorded using a relatively novel wireless EEG telemetry system fully implanted within the mouse, enabling uninhibited movement during behavioral tasks. No significant differences were found between sample and correct choice phases in the alpha, theta or gamma frequency ranges. Evoked power was significantly higher during the choice phase than the sample phase in the high-beta/low-gamma frequency range. This frequency range has been implicated in the propagation of cortical predictions to lower levels of stimuli encoding in a top-down hierarchical manner. Results suggest there is an increase in brain activity during correct trials when the mouse enters the opposite arm during the choice phase compared to the sample phase, likely due to prediction error resulting from a discrepancy between present and prior experience. Future studies should identify specific cortical networks involved and investigate neural activity at the neuronal level.

Keywords Schizophrenia · Spatial working memory · EEG · T-maze · Predictive coding

Introduction

Cognition involves various domains in the processing of specific information including but not limited to perception, motivation, and memory. Cognitive problems that appear to arise more frequently include executive function and working memory. The PFC plays a role in cognition, decision-making, and other executive functions, and plays a critical role in working memory (Fuster and Alexander 1971; Miller and Cohen 2001; Barbey et al. 2013). Working memory deficits have been seen in patients with different mental health disorders. Many studies have shown spatial working memory deficits in particular, in schizophrenia (SZC) patients (Keefe et al. 1995; Perlstein et al. 2001; Lewis et al. 2005). While spatial working memory is dependent upon the prefrontal cortex (PFC), the underlying neural processes involved have yet to be elucidated (Duncan and Owen 2000; Wager and Smith 2003). The large number of connections to other brain areas contributes to the complexity of the prefrontal cortex, making it difficult to understand the specific mechanisms underlying cognitive control (Miller and Cohen 2001).

A useful quantitative method to measure brain activity in real time during cognitive performance tasks is by electroencephalogram (EEG) recordings. Oscillations

✉ Robert E. Featherstone
featherr@usc.edu

[1] Department of Psychiatry, University of Pennsylvania, Philadelphia, PA 19104, USA

[2] Department of Psychiatry and Behavioral Sciences, University of Southern California, 2250 Alcazar St., Los Angeles, CA 90033, USA

in neural activity are thought to reflect the summed synchronous activity of neurons that underlie neurocognitive processes, including spatial working memory (Basar et al. 2001; Dietrich and Kanso 2010). These oscillations are decomposed by frequency into frequency-specific bands, including delta (0–4 Hz), theta (4–8 Hz), alpha (8–12 Hz), beta (12–30 Hz), and gamma (> 30 Hz). Band-specific decreases in gamma power have been shown to correlate with working memory load in the prefrontal cortex and hippocampus of humans (Howard et al. 2003; Herrmann et al. 2010). Synchrony in the gamma frequency across the brain has been suggested to mediate numerous cognitive processes, including attention and working memory (Tallon-Baudry et al. 1998; Herrmann et al. 2010). Spatial memory deficits have been seen to correlate with reduced power in gamma frequencies, as it has been demonstrated consistently in patients with SCZ. Patients with SCZ consistently demonstrate reduced power in gamma frequencies, correlating well with their spatial working memory deficits (Ward 2003; Jensen et al. 2007). Decreased gamma band activity is evident in many animal models of SCZ, serving as a useful biomarker for pharmaceutical development (Billingslea et al. 2014; Featherstone et al. 2015; Tatard-Leitman et al. 2015).

To date, few studies have examined high-frequency EEG power during spatial working memory performance in rodents using translationally relevant methods. If changes in EEG power are seen during a T-maze task in rodents, it could serve as a potential biomarker for the deficit of spatial working memory in and could highlight neural and cognitive processes that underlie memory. The present study investigated within-subject changes in power of frequency-specific bands during sample versus choice trials in the discrete T-maze paradigm. In the discrete T-maze paradigm, only the choice trials require the recall of the previous sample trials, allowing spatial working memory to be localized on choice trials while sample trials serve as a control. It is hypothesized that high-frequency bands will exhibit higher power during choice trials versus that of sample trials, while low-frequency bands will not exhibit a difference in power between choice versus sample trials. The present study also implements an advanced wireless EEG recorder that is fully implanted within the mouse to enable free movement during behavioral task, eliminating the potential of restricted movement to serve as a confounding variable.

Materials and methods

Subjects

16 C57BL/6J mice (8–12 weeks) were obtained from the Jackson Laboratory (Bar Harbor, Maine). Mice were group-housed before electrode implantation then singly housed after implantation in ventilated cages in temperature-controlled rooms with a 12:12-h light/dark cycle (light onset at 07:00). Mice were provided food and water ad libitum, and cages were changed weekly. All procedures were performed in accordance with the NIH guide for the care and use of laboratory animals and approved by the Institutional Animal Care and Use Committee at the University of Pennsylvania (IUCUC). Studies were conducted during the light phase between 8:00 a.m. and 5:00 p.m.

T-maze task

A discrete T-maze apparatus with light bedding in dim lighting was used to assess spatial working memory. Mice are inherently motivated to explore novel environments to locate food, water, shelter, and other resources. Therefore, their natural tendency is to alternate their choice of goal arm when initially placed in the start arm, which requires them to remember the previous arm of choice (Deacon and Rawlins 2006).

An overhead video that recorded the mice was used to manually score performance. Mice were first placed in the test room in their home cages for approximately 30 min before starting the test for effective habituation. Each full trial included the sample phase followed by the choice phase. During the first trial, if an animal failed to run within 90 s, it was removed from the T-maze, placed back in its home cage, and tested again later. The criterion point for entering an arm was the point at which the animal crossed the halfway point in the arm. A correct choice was made if the mouse entered the opposite arm, during the choice phase, to that of the arm entered during the sample phase. EEG was analyzed from the time the animal's nose crossed a tape line halfway down the main arm, indicating the intent to travel down the arm, to the time the animal's nose crossed a tape line one-third down the choice arm, indicating a choice has been made.

Directly prior to the first trial of each animal, its home cage was placed next to the T-maze apparatus to serve as a resting place between trials. The transmitter was turned on/off using a magnet provided by Data Sciences International (DSI). After turning on the transmitter, the mouse was placed at the start of the T-maze and given unobstructed access to either arm. The mouse was allowed to choose an arm, completing the sample phase. The mouse was then placed at the start of the T-maze then allowed to choose an arm, completing the choice phase. The mouse made a "correct" choice if it chose the opposite arm during the choice phase as the one chosen during sample phase. After each choice phase, the mouse was placed back into its home cage for 30 s before starting the next trial. The mouse continued on the task until it failed to run within 90 s of being placed at the start of the T-maze. After turning off the transmitter, the maze was cleaned using 10% ethanol and clean bedding

was added. We evaluated the power of sample versus choice phases within mice that scored above 50% correct across trials. Power decomposition was accomplished using the Fast Fourier Transformation (FFT) function native to Spike2 (Hanning window, 0.81 Hz resolution) (Cambridge Electronic Design, Cambridge, UK).

For each trial, we calculated the FFT during the EEG analysis time period, which occurred when the animal reached the halfway point of the start arm until it reached the one-third point of the choice arm. We then averaged these FFT values across trials in the theta frequency range (4–7 Hz), alpha (8–12 Hz), beta (12–30 Hz), and gamma frequency range (30–80 Hz) for both sample and choice phases. We were particularly interested in the high-beta and low-gamma range (around 20–35 Hz) as previous studies have shown increases of power in this range during working memory and unexpected rewards processing tasks (Cohen et al. 2007; HajiHosseini et al. 2012; HajiHosseini and Holroyd 2015).

Electrode implantation

Animals were anesthetized with 1% isoflurane and underwent implantation of wireless transmitter (PhysioTel® ETA-F10, Data Sciences International). A single channel with two wires (lead and ground) was connected to transmitter body. Supplemental warmth during and after surgery was provided via heat lamps. Body hair was removed from the scalp down to the upper back using a hair clipper. The shaved areas were scrubbed with alcohol disinfecting wipes and betadine®. The mouse was secured on a sterile stereotax. A 2-cm midline incision was made from the scalp to the upper back using sterile surgical scissors. A pocket was formed under the skin of the upper back using blunt forceps. The transmitter was placed subcutaneously, with the flatter side of the transmitter touching the back and the other side touching the skin. After carefully tucking the wires into the pocket, the two wires were oriented towards the head.

The incision was extended until the entire skull area was exposed. Holes in the cranium were made using a stereotaxic drill at 2.8 mm anterior and 1 mm left (lead wire in PFC) of bregma and 3 mm posterior/2 mm right (ground wire) of bregma, being careful not to damage the dura mater. The silicone insulation was removed from the ends of both wires and were slightly bent at the tips and inserted through the respective holes and placed directly on the dura mater. The electrodes were fixed in place using a small amount of ethyl cyanoacrylate (Loctite; Henkel, Westlake, OH, USA) and dental cement (Ortho Ket; Lang Dental, Wheeling, IL, USA). After the cement was dried, the entire incision was closed using non-absorbable sutures (Ethicon, Somerset, NJ, USA). All mice were singly housed and recovered for 10 days prior to behavioral testing.

Statistics

Power was statistically analyzed by one-way ANOVA tests using Statistica software (version 6, StatSoft, Tulsa, OK, USA). All statistical measures taken at 95% confidence intervals.

Results

T-maze

All mice with successful electrode implants, a total of 12 mice, were run on the T-maze. Four mice had levels of performance below chance (50%) and, as such, were used to compare differences in EEG power amongst mice performing and not performing on the task. One mouse did not successfully complete a single T-maze trial, and as such, was excluded from further data analysis. In a series of trials, at a 30-s inter-trial interval; all mice, both performing and non-performing, showed no preference for the opposite arm during the sample phase to that explored during the choice phase of the previous trial; with a rate of 45%, below chance (50%). No significant difference in mean latency to choose a correct or incorrect arm was found in performing mice. No correlation in a linear regression was found between time of exploration during sample phase and latency to choose a correct or incorrect arm during choice phase. Performing mice showed improved accuracy with increasing time spent exploring during sample trial ($F(1,7) = 7.936$, $p = 0.0259$, Fig. 1). Time on arm during choice phases was not recorded. Mean performance of mice able to perform on the task was 83.96% correct, with a total of 6.75 correct and 1.75 incorrect trials. An average of eight trials was completed for each mouse.

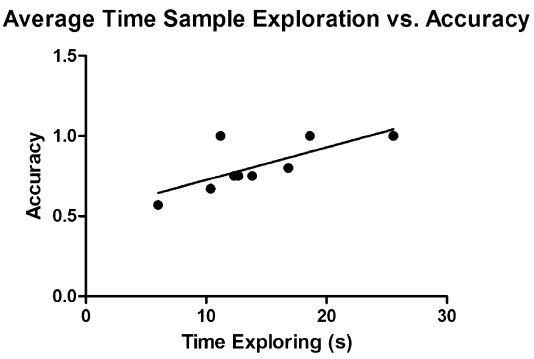

Fig. 1 Time on arm during sample phase on accuracy during choice phase ($y = 0.02034x + 0.5220$, $r^2 = 0.5313$)

EEG

An increase in average EEG power in high-beta/low-gamma frequency range was visible between the sample phase and choice phase of correct trials (Fig. 2). No correlation was found between time on arm during sample phase and EEG power increases or decreases in theta, alpha, beta, or gamma frequency ranges. No significant differences were found between sample and choice phases in the theta frequency range ($p > 0.05$, Fig. 3a).

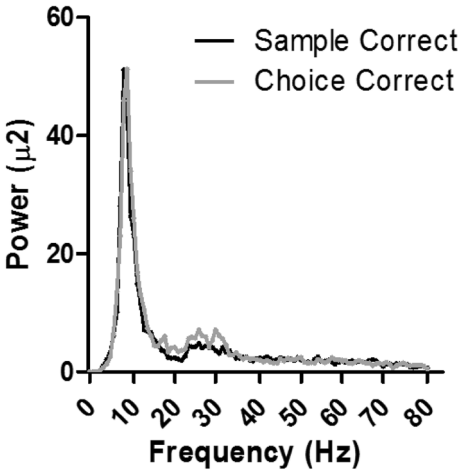

Fig. 2 EEG power on sample and choice in correct trials

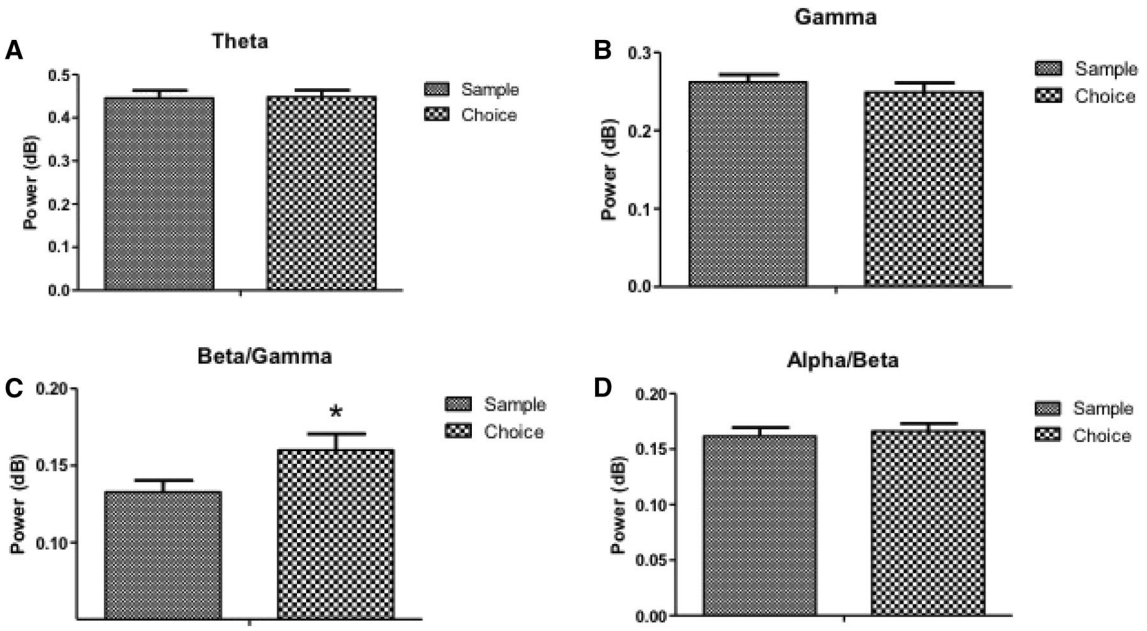

Fig. 3 Power on sample and choice trials. **a** No significant differences in theta power between sample and choice phases. **b** No significant differences in gamma power between sample and choice phases. **c** Significant increase in power during choice phase compared to sample phase in high-beta/low-gamma range ($p = 0.00116$). **d** No significant differences in alpha and low beta power between sample and choice phases

No significant differences were found between sample and choice phases in the alpha frequency range ($p > 0.05$, Fig. 3d). In the high-beta/low-gamma frequency range of performing mice, evoked power was significantly higher during the choice phase than the sample phase ($F(1, 7) = 15.872$, $p = 0.00530$, Cohen's $d = 0.96517$, Fig. 3c), indicating higher brain activity in the choice phase related to increased ability to recall previous choice during sample phase. Similarly, evoked power was significantly higher when making a "correct" decision during choice phases related to the sample phase ($F(8,8) = 1.673$, $p = 0.0444$, Cohen's $d = 0.661836$, Fig. 4c). No significant differences were found between sample and "correct" choice phases in the gamma frequency range ($p > 0.05$, Fig. 4d). No significant differences were found between sample and "correct" choice phases in the theta frequency range ($p > 0.05$, Fig. 4a). No significant differences were found between sample and "correct" choice phases in the alpha frequency range ($p > 0.05$, Fig. 4b). Non-performing mice showed no significant difference in EEG power between sample and choice phases nor between sample, and correct and incorrect decisions during choice phase in theta, alpha, beta, or gamma frequency ranges.

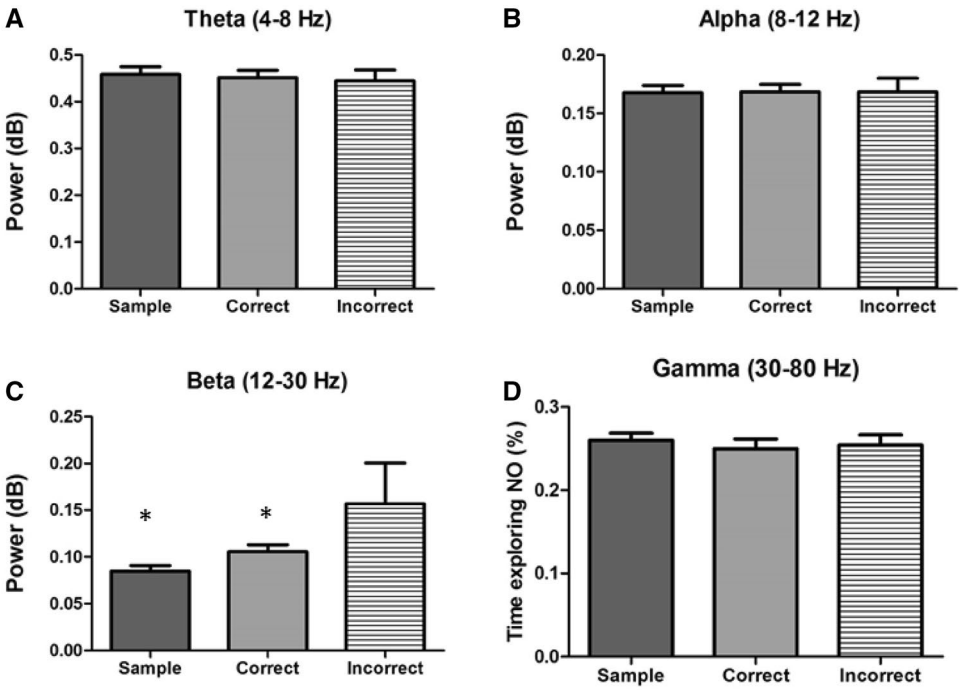

Fig. 4 Power on sample, correct and incorrect decisions of choice phase. **a** No significant differences in theta power between sample phase, and correct or incorrect decisions of choice phase. **b** No significant differences in alpha power between sample phase, and correct or incorrect decisions of choice phase. **c** Significant difference in beta power between sample phase and correct decision of choice phase ($p = 0.0444$). **d** No significant differences in gamma power between sample phase, and correct or incorrect decision of choice phase

Discussion

The current study investigated changes in EEG power during the choice and sample phases of a discrete trial T-maze task. Mice showed a selective increase in mid-frequency (beta) EEG power during correct alternation in a discrete T-maze task, with EEG power significantly higher during the choice phase relative to the sample phase. No changes in gamma oscillations were seen when assessed across the entirety of the 30–80 Hz frequency range commonly used to define this frequency band. This finding was unexpected, since gamma oscillations have been shown to vary as a function of cognitive performance across a wide range of tasks and species, and were predicted to be associated with T-maze performance. While the boundary of gamma EEG is well defined in humans, this is not necessarily the case in rodents, and there is not always a close correspondence between the ranges in humans and rodents. Thus, it is possible that the 22 and 34 Hz range identified here reflected gamma oscillations. This seems unlikely, however, since previous studies in our lab have shown robust and selective changes in the 30–80 Hz range following manipulations known to disrupt activity in interneuron populations that produce gamma oscillations (Featherstone et al. 2012; Billingslea et al. 2014; Tatard-Leitman et al. 2015). Such disruptions are observed across the entire 30–80 Hz range and not just in the lower ranges identified here. As such, it seems likely that the 22–34 Hz range identified here corresponds most closely to the beta EEG band. It is not clear why gamma was not more significantly altered during T-maze performance. It may be that the discrete T-maze procedure is not taxing enough to engage gamma related cognitive processes. Increases in gamma power correlate with increased memory load (Axmacher et al. 2007). It is possible that the mnemonic demands of the T-maze task may be too low to significantly tax memory load and thus alter gamma activity.

Although beta oscillations have frequently been associated with movement planning and execution (Feige et al. 2000; Muthukumaraswamy and Johnson 2004), it is unlikely that the EEG changes seen here reflected the activity of such processes, given that the motor requirements during both sample and choice phases are largely the same. Increases in beta power have been shown to occur in response to task-related feedback, including surprise following unexpected rewards and during task-switching paradigms (HajiHosseini et al. 2012; Poljac and Yeung 2014; HajiHosseini and Holroyd 2015). In task-switching paradigms, participants must switch between tasks across trials, either in an organized or random pattern. Performance on task-switching trials reflects a dynamic interaction between past experiences and current intentions (Kiesel et al. 2010). If subjects suddenly need to change the task, there is a level of uncertainty and surprise that accompany the unprepared behavior (Limongi et al. 2015). This uncertainty and surprise may lead to changes in expected outcomes, affecting brain activity from task-related feedback.

Traditionally, hierarchical sensory processing has been investigated as a bottom-up pathway, in which perception begins at the level of sensory stimuli (Mesulam 2008). A growing body of evidence now suggests that top-down

processing plays a larger role, primarily resulting from synchronized oscillatory activity from the cortex (Engel et al. 2001). The predictive coding scheme depends on top-down processing in which the brain generates inferences regarding the sources of sensory signals and brain activity reflects a process of correlating internally generated predictions to external stimuli (Arnal and Giraud 2012; Rauss and Pourtois 2013).

There are two routes of information propagation at work in predictive coding. Higher cortical layers send predictions to lower levels. Lower cortical levels reciprocate errors in predictions to higher levels to minimize prediction error and promote the current prediction. It is thought that there is preference for more precise prediction errors, which are thought to be represented by larger synaptic gain from ascending neurons (Friston 2008). Thus, mice would be expected to have increased activation in neurons projecting from higher cortical levels to lower cortical levels (beta frequency range), and decreased activation in neurons projecting from lower to higher (gamma frequency range) when going down a choice arm that is opposite to that of the sample arm. Mice not performing well on the spatial memory task showed no significant increase in EEG power, which would be expected with less synaptic gain resulting from less precise and less robust ascending predictive errors from lower cortical layers. The prediction error magnitude, or precision, is thought to reflect the balance between prior beliefs and present sensory information. In principle, an imbalance of the weight placed on prior beliefs and current sensory information may result in perceptions (hallucinations) and conceptual inference (delusions) (Moritz et al. 2015; Limongi et al. 2018). These perceptual errors are the hallmarks of psychotic symptoms of schizophrenia. It may be expected that gamma power increases with incorrect choice trials resulting from prediction error, and an increased gamma power with correct choice trials resulting from confirmed predictions, when compared to gamma power during the sample phase. Although there is a decrease in average gamma power in correct choice trials, the decrease is not significant. No discernible difference in gamma power was found between incorrect choice trails and the sample phase. This is not an expected result per the predictive coding conceptualization of working memory. It may be the case that mice are already at a threshold of surprise. Reaching a near maximum in synaptic gain from ascending neurons may wash out any effect that might be seen from an additional prediction error associated with arm location.

Measures were taken during testing to decrease the expected perception of volatility of the environment by standardizing testing conditions. It is thought that the higher the judgment of the volatility of the environment, the lower the inhibition of return per the disconnection hypothesis (Parr and Friston 2017a, b). Mice that assume state changes of the stimulus, or higher stimulus volatility, may have decreased inhibition of return. Thus, mice not performing well on the task may have perceived the environment to be more volatile than others. It might be expected that over time, these mice will begin to show increased inhibition of return as the location of the stimulus originally explored decreases in salience; as the perceived volatility may decrease with reoccurring exposure. Mice that perceive the environment to be less volatile will have the tendency to assume no further information to be gained from sampling of the location again, as they predict that the state of the environment has not changed. Having a prediction of the state, and knowing the location, is thought to decrease the salience of the location of the environment; increasing inhibition of return (Parr and Friston 2017a, b). Controlling the lighting of the maze helps to reduce bias associated with differences in the precision of sensory information obtained from exploring either arm. The dim lighting of the maze helps to decrease agoraphobic tendencies of rodents, but also decreases the sensory precision of either arm, making an observation of either arm to be less likely to cause large resolution of the uncertainty of its current state; thus, increasing the likeliness to return, as the stimulus may be perceived as more volatile. This decreased sensory precision in dim lighting may cause reduced synaptic gain from prediction errors, as a large amount of uncertainty of the explored arm remains. Random error associated with differences in the time of being replaced into the maze for the choice phase following the sample phase may lead to differences in accuracy. It is thought that the salience of recent observations will increase, compared to prior beliefs, with time (Parr and Friston 2017a, b). With time, there may be a higher perceived probability of the state of the environment transitioning to a new value.

The general high-beta/low-gamma frequency range (22–34 Hz) has been implicated in top-down predictive coding processing. Recent studies examine beta oscillations in predictive coding processing during a variety of sensory and behavioral tasks suggest that an increase in beta power results from the propagation of cortical predictions to lower levels of stimuli encoding in a top-down hierarchical manner (Bastos et al. 2012; Bressler and Richter 2015; Lewis et al. 2016; van Pelt et al. 2016). The ranges for beta oscillations used in these studies were all around 15–30 Hz, which largely correspond to our high-beta frequency range of 2–34 Hz. Thus, the data presented in this study support the existing literature and expand the field of top-down predictive coding processing that remains a largely elusive pathway. Applying computationally based theories to neuroscience research is imperative as it drives research of enigmatic brain and neurodevelopmental disorders, such as schizophrenia, to a more quantitative scope. Future studies in top-down predicting coding should identify specific cortical networks

involved and test neural activity at the level of these neurons rather than whole brain activity.

Funding Funding was provided by National Institutes of Health (Grant no. 1-P50-MH-096891-01).

References

Amann LC, Gandal MJ, Halene TB, Ehrlichman RS, White SL, McCarren HS, Siegel SJ (2010) Mouse behavioral endophenotypes for schizophrenia. Brain Res Bull 83:147–161

Arnal LH, Giraud AL (2012) Cortical oscillations and sensory predictions. Trends Cogn Sci 16:390–398

Axmacher N, Mormann F, Fernandez G, Cohen MX, Elger CE, Fell J (2007) Sustained neural activity patterns during working memory in the human medial temporal lobe. J Neurosci 27:7807–7816

Barbey AK, Colom R, Grafman J (2013) Dorsolateral prefrontal contributions to human intelligence. Neuropsychologia 51:1361–1369

Basar E, Basar-Eroglu C, Karakas S, Schurmann M (2001) Gamma, alpha, delta, and theta oscillations govern cognitive processes. Int J Psychophysiol 39:241–248

Bastos AM, Usrey WM, Adams RA, Mangun GR, Fries P, Friston KJ (2012) Canonical microcircuits for predictive coding. Neuron 76:695–711

Billingslea EN, Tatard-Leitman VM, Anguiano J, Jutzeler CR, Suh J, Saunders JA, Morita S, Featherstone RE, Ortinski PI, Gandal MJ, Lin R, Liang Y, Gur RE, Carlson GC, Hahn CG, Siegel SJ (2014) Parvalbumin cell ablation of NMDA-R1 causes increased resting network excitability with associated social and self-care deficits. Neuropsychopharmacology 39:1603–1613

Bressler SL, Richter CG (2015) Interareal oscillatory synchronization in top-down neocortical processing. Curr Opin Neurobiol 31:62–66

Callicott JH, Bertolino A, Mattay VS, Langheim FJ, Duyn J, Coppola R, Goldberg TE, Weinberger DR (2000) Physiological dysfunction of the dorsolateral prefrontal cortex in schizophrenia revisited. Cereb Cortex 10:1078–1092

Cohen MX, Elger CE, Ranganath C (2007) Reward expectation modulates feedback-related negativity and EEG spectra. Neuroimage 35:968–978

Deacon RM, Rawlins JN (2006) T-maze alternation in the rodent. Nat Protoc 1(1):7–12

Dietrich A, Kanso R (2010) A review of EEG, ERP, and neuroimaging studies of creativity and insight. Psychol Bull 136:822–848

Duncan J, Owen AM (2000) Common regions of the human frontal lobe recruited by diverse cognitive demands. Trends Neurosci 23:475–483

Engel AK, Fries P, Singer W (2001) Dynamic predictions: oscillations and synchrony in top-down processing. Nat Rev Neurosci 2:704–716

Featherstone RE, Liang Y, Saunders JA, Tatard-Leitman VM, Ehrlichman RS, Siegel SJ (2012) Subchronic ketamine treatment leads to permanent changes in EEG, cognition and the astrocytic glutamate transporter EAAT2 in mice. Neurobiol Dis 47:338–346

Featherstone RE, McMullen MF, Ward KR, Bang J, Xiao J, Siegel SJ (2015) EEG biomarkers of target engagement, therapeutic effect, and disease process. Ann N Y Acad Sci 1344:12–26

Feige B, Aertsen A, Kristeva-Feige R (2000) Dynamic synchronization between multiple cortical motor areas and muscle activity in phasic voluntary movements. J Neurophysiol 84:2622–2629

Friston K (2008) Hierarchical models in the brain. PLoS Comput Biol 4:e1000211

Fuster JM, Alexander GE (1971) Neuron activity related to short-term memory. Science 173:652–654

HajiHosseini A, Holroyd CB (2015) Reward feedback stimuli elicit high-beta EEG oscillations in human dorsolateral prefrontal cortex. Sci Rep 5:13021

HajiHosseini A, Rodriguez-Fornells A, Marco-Pallares J (2012) The role of beta-gamma oscillations in unexpected rewards processing. Neuroimage 60:1678–1685

Herrmann CS, Frund I, Lenz D (2010) Human gamma-band activity: a review on cognitive and behavioral correlates and network models. Neurosci Biobehav Rev 34:981–992

Honzel N, Justus T, Swick D (2014) Posttraumatic stress disorder is associated with limited executive resources in a working memory task. Cogn Affect Behav Neurosci 14:792–804

Howard MW, Rizzuto DS, Caplan JB, Madsen JR, Lisman J, Aschenbrenner-Scheibe R, Schulze-Bonhage A, Kahana MJ (2003) Gamma oscillations correlate with working memory load in humans. Cereb Cortex 13:1369–1374

Jensen O, Kaiser J, Lachaux JP (2007) Human gamma-frequency oscillations associated with attention and memory. Trends Neurosci 30:317–324

Keefe RS, Roitman SE, Harvey PD, Blum CS, DuPre RL, Prieto DM, Davidson M, Davis KL (1995) A pen-and-paper human analogue of a monkey prefrontal cortex activation task: spatial working memory in patients with schizophrenia. Schizophr Res 17:25–33

Kiesel A, Steinhauser M, Wendt M, Falkenstein M, Jost K, Philipp AM, Koch I (2010) Control and interference in task switching—a review. Psychol Bull 136:849–874

Lewis DA, Hashimoto T, Volk DW (2005) Cortical inhibitory neurons and schizophrenia. Nat Rev Neurosci 6:312–324

Lewis AG, Schoffelen JM, Schriefers H, Bastiaansen M (2016) A predictive coding perspective on beta oscillations during sentence-level language comprehension. Front Hum Neurosci 10:85

Limongi R, Silva AM, Gongora-Costa B (2015) Temporal prediction errors modulate task-switching performance. Front Psychol 6:1185

Limongi R, Bohaterewicz B, Nowicka M, Plewka A, Friston KJ (2018) Knowing when to stop: aberrant precision and evidence accumulation in schizophrenia. Schizophr Res. https://doi.org/10.1016/j.schres.2017.12.018

Martinussen R, Hayden J, Hogg-Johnson S, Tannock R (2005) A meta-analysis of working memory impairments in children with attention-deficit/hyperactivity disorder. J Am Acad Child Adolesc Psychiatry 44:377–384

Mesulam M (2008) Representation, inference, and transcendent encoding in neurocognitive networks of the human brain. Ann Neurol 64:367–378

Miller EK, Cohen JD (2001) An integrative theory of prefrontal cortex function. Annu Rev Neurosci 24:167–202

Moritz S, Goritz AS, Gallinat J, Schafschetzy M, Van Quaquebeke N, Peters MJ, Andreou C (2015) Subjective competence breeds overconfidence in errors in psychosis. A hubris account of paranoia. J Behav Ther Exp Psychiatry 48:118–124

Muthukumaraswamy SD, Johnson BW (2004) Primary motor cortex activation during action observation revealed by wavelet analysis of the EEG. Clin Neurophysiol 115:1760–1766

Parr T, Friston KJ (2017a) Uncertainty, epistemics and active inference. J R Soc Interface 14(136):20170376

Parr T, Friston KJ (2017b) Working memory, attention, and salience in active inference. Sci Rep 7:14678

Perlstein WM, Carter CS, Noll DC, Cohen JD (2001) Relation of prefrontal cortex dysfunction to working memory and symptoms in schizophrenia. Am J Psychiatry 158:1105–1113

Poljac E, Yeung N (2014) Dissociable neural correlates of intention and action preparation in voluntary task switching. Cereb Cortex 24:465–478

Rauss K, Pourtois G (2013) What is bottom-up and what is top-down in predictive coding? Front Psychol 4:276

Tallon-Baudry C, Bertrand O, Peronnet F, Pernier J (1998) Induced gamma-band activity during the delay of a visual short-term memory task in humans. J Neurosci 18:4244–4254

Tatard-Leitman VM, Jutzeler CR, Suh J, Saunders JA, Billingslea EN, Morita S, White R, Featherstone RE, Ray R, Ortinski PI, Banerjee A, Gandal MJ, Lin R, Alexandrescu A, Liang Y, Gur RE, Borgmann-Winter KE, Carlson GC, Hahn CG, Siegel SJ (2015) Pyramidal cell selective ablation of *N*-methyl-D-aspartate receptor 1 causes increase in cellular and network excitability. Biol Psychiatry 77:556–568

van Pelt S, Heil L, Kwisthout J, Ondobaka S, van Rooij I, Bekkering H (2016) Beta- and gamma-band activity reflect predictive coding in the processing of causal events. Soc Cogn Affect Neurosci 11:973–980

Wager TD, Smith EE (2003) Neuroimaging studies of working memory: a meta-analysis. Cogn Affect Behav Neurosci 3:255–274

Ward LM (2003) Synchronous neural oscillations and cognitive processes. Trends Cogn Sci 7:553–559