

# Cortical Local Field Potential Power Is Associated with Behavioral Detection of Near-threshold Stimuli in the Rat Whisker System: Dissociation between Orbitofrontal and Somatosensory Cortices

Rachel E. Rickard, Andrew M. J. Young, and Todor V. Gerdjikov

## Abstract

■ There is growing evidence that ongoing brain oscillations may represent a key regulator of attentional processes and as such may contribute to behavioral performance in psychophysical tasks. OFC appears to be involved in the top-down modulation of sensory processing; however, the specific contribution of ongoing OFC oscillations to perception has not been characterized. Here we used the rat whiskers as a model system to further characterize the relationship between cortical state and tactile detection. Head-fixed rats were trained to report the presence of a vibrotactile stimulus (frequency = 60 Hz, duration = 2 sec, deflection amplitude = 0.01–0.5 mm) applied

to a single vibrissa. We calculated power spectra of local field potentials preceding the onset of near-threshold stimuli from microelectrodes chronically implanted in OFC and somatosensory cortex. We found a dissociation between slow oscillation power in the two regions in relation to detection probability: Higher OFC but not somatosensory delta power was associated with increased detection probability. Furthermore, coherence between OFC and barrel cortex was reduced preceding successful detection. Consistent with the role of OFC in attention, our results identify a cortical network whose activity is differentially modulated before successful tactile detection. ■

## INTRODUCTION

Considerable evidence supports the role of prefrontal cortex in higher-order sensory processing including stimulus categorization and the top-down control of sensory inputs (Ding, 2015; McKee, Riesenhuber, Miller, & Freedman, 2014; Fritz, David, Radtke-Schuller, Yin, & Shamma, 2010; Fritz, Elhilali, David, & Shamma, 2007; Everling, Tinsley, Gaffan, & Duncan, 2006). Rodent OFC specifically receives sensory input from several sensory modalities, including somatosensory cortex (Aronoff et al., 2010). Sensory responses are observed in OFC, and these are related to the identity as well as the valence of sensory stimuli (Ongur & Price, 2000; Reep, Corwin, & King, 1996). This region thus appears to be involved in sensory integration. In humans, active as opposed to passive exploration of tactile stimuli is associated with increased OFC activity; in primates, OFC lesions produce deficits in tactile discrimination (Frey, Zlatkina, & Petrides, 2009; Passingham & Eitlinger, 1972). Behaviorally, OFC has a critical role in associative learning and decision-making through its representation of the reward and punishment value of sensory cues. These observations suggest that sensory information in this structure is subject to top-down cognitive and/or attentional modulation

(Cooch et al., 2015; Neubert, Mars, Sallet, & Rushworth, 2015; Bouret & Richmond, 2010; Takahashi et al., 2009; Kringelbach, 2005).

OFC activity may reflect ongoing attentional state and is thus likely to affect perceptual decisions. There is strong evidence that the neural encoding of sensory information shows strong state dependence in both cortical and noncortical regions (Ding, 2015; Panzeri, Macke, Gross, & Kayser, 2015; Hawking & Gerdjikov, 2013; Castro-Alamancos, 2009). The behavioral correlates of these observations have not been investigated in non-human animals and neither has the specific contribution of OFC. For example, quiet wakefulness, which is associated with high amplitude slow oscillations, may serve to heighten sensitivity to sensory input and decrease detection thresholds (Castro-Alamancos, 2009). Behavioral evidence that prestimulus cortical oscillatory activity modulates detection of near-threshold stimuli comes primarily from human EEG studies in regions other than OFC (Pleger & Villringer, 2013; Schubert, Haufe, Blankenburg, Villringer, & Curio, 2009; Linkenkaer-Hansen, Nikulin, Palva, Ilmoniemi, & Palva, 2004). For example, prestimulus beta and mu band activity over prefrontal and sensorimotor cortex was related to detection performance in a backward masking task (Schubert et al., 2009). Other work implicated prestimulus activity in the ~10, 20, and 40 Hz bands over human somatosensory

cortex and higher frequency oscillations over parietal cortex in the detection of weak electrical stimuli to the finger (Zhang & Ding, 2010). The notable lack of work done in OFC may reflect the fact that orbitofrontal surfaces are not accessible to scalp recordings in humans.

In summary, there is evidence that ongoing behavioral state affects prefrontal and sensory cortical representations, yet even though OFC shows robust sensory responses and neurophysiological interactions with sensory cortices, the role of ongoing fluctuations in this structure in perceptual decisions has not been studied. To begin to address this issue, we trained head-fixed rats in a vibrotactile detection task and monitored prestimulus activity in OFC and somatosensory cortex to near-detection stimuli. Experiments focussed on rat primary somatosensory cortex receiving signals from individual whiskers (i.e., barrel cortex). We found a clear dissociation between OFC and somatosensory cortex: In over-trained animals, stronger delta oscillations in OFC but not in somatosensory cortex were associated with higher detection probability. Further supporting the dissociation between structures, we also found that higher detection probability was associated with lower prestimulus coherence between the two regions.

## METHODS

### Animals and Surgery

Male Sprague–Dawley rats ( $n = 4$ ), obtained from Charles River (Margate, Kent, UK) and weighing between 200 and 250 g on arrival, were housed in pairs on a 12-hr reversed light–dark cycle (lights on at 1900 hr) at an average temperature of 21°C and humidity of 40–70%. Water and food (LabDiet 5LF5, PMI Nutrition Intl., Brentwood, MO) were freely available. The experiments were carried out under institutional ethics approval and appropriate project and personal license authority granted by the U.K. Home Office under the Animals (Scientific Procedures) Act 1986.

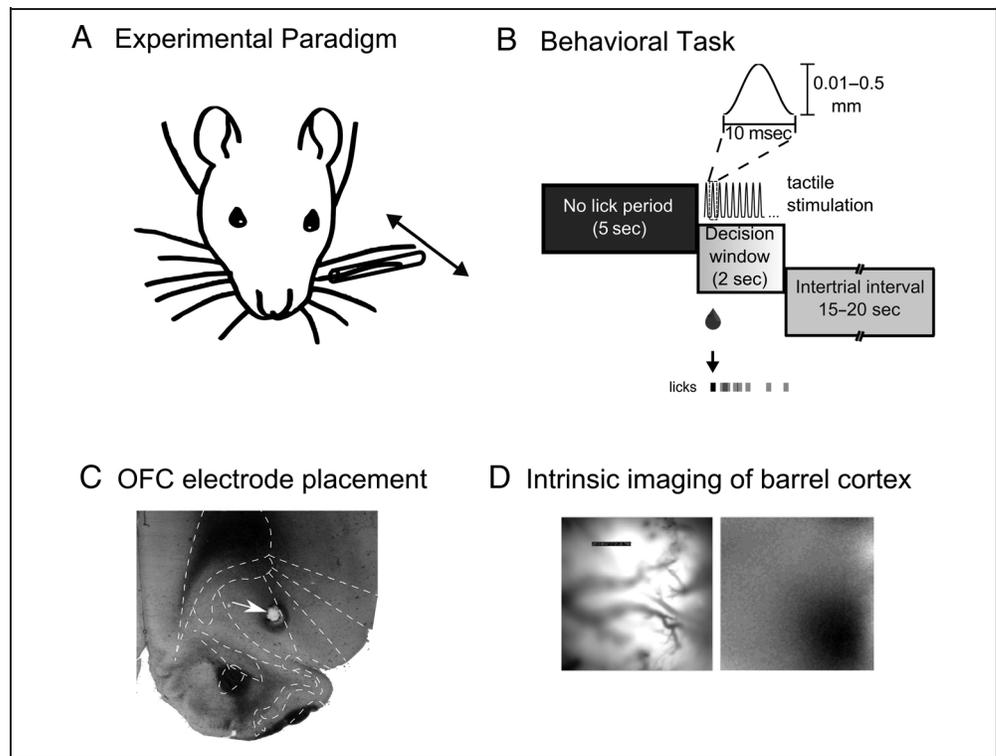
Rats were habituated to the experimenter and behavioral setup for at least 2 weeks before surgery. Surgery was performed to implant microelectrodes and a post for head fixation. Oral antibiotics (Baytril, Bayer, Leverkusen, Germany, 2.5% 2 ml in 200 ml of H<sub>2</sub>O) were given daily for 3 days before surgery in the drinking water. Rats were anesthetized with isoflurane (2–3%). Core temperature was monitored rectally and maintained at 37°C using a homeothermic pad (Harvard Apparatus, Boston, MA). For fluid replacement, 5% glucose was continuously administered via an infusion pump (3 ml/hr sc; Instech, K. D. Scientific, Holliston, MA). Glycopyrronium bromide (40 µl/kg im; Anpharm, Warsaw, Poland) was given to reduce respiratory tract secretions. Animals were fixed into a stereotaxic frame, and the head was adjusted so that lambda and bregma were on the same horizontal plane. To prevent corneal desiccation, Lacri-Lube Eye Ointment (Allergan, Wespport, Ireland) was applied to the eyes. Burr

holes (0.7 mm diameter) were made in the skull and were fitted with self-tapping stainless steel screws (Morris Co., Southbridge, MA, part number 0X 1/8 flat) to anchor the implant. Craniotomy was performed over barrel cortex, and a single whisker column was located by mapping the cortex with a single intracerebral electrode or intrinsic optical imaging of the exposed cortical surface (Figure 1D). Intrinsic optical imaging was performed using the Helioscan software (Langer et al., 2013). Images were captured through a custom macroscope constructed from two front-to-front coupled 50-mm f/0.95 lenses (DO-5095, Navitar, Rochester, NY) on a CCD camera (Basler avA1000-120km) controlled by a camera link acquisition board (PCI-1426, National Instruments, Austin, TX). Illumination was provided by three high-brightness deep-red LEDs (655 nm; product no. LXM3-PD01, Philips Lumileds, San Jose, CA) mounted directly on the objective. The software acquired 75 × 75 resolution images at 20 Hz over ten 5-sec sweeps of 60-Hz sinusoidal stimulation of a single whisker (1 mm displacement at 5 mm from the snout; see below for stimulation hardware). Images were averaged and subtracted from a 5-sec stimulation-free baseline. For mapping, the intrinsic optical signal was compared with an image of the blood vasculature acquired under green light. A screw placed above the cerebellum was used for grounding the animal during electrophysiological recordings. The skull surface was treated with a bonding agent (Self-Etching Bond, Henry Schein, Inc., Melville, NY), and microelectrodes were implanted and embedded together with the microscrews in an implant built up from layers of light curing dental composite (Flowable Composite, Henry Schein, Inc.). OFC implantation coordinates were AP +3.2, ML 2–4, DV –4 (Paxinos & Watson, 2007; Figure 1C). Antibiotic ointment (Fuciderm, Dechra Veterinary Products, Uldum, Denmark) was applied to the wound, and the skin was sutured around the implant. Analgesia (Carprieve, 5 mg/kg sc; Norbrook Laboratories Ltd., Corby, UK) was administered 2–3 hr before recovery and twice daily for 3 days postsurgery or longer as needed. Glucose solution (5%, 5 ml/day ip) was given for 2–3 days after surgery or as needed.

### Apparatus

All behavioral experiments were conducted inside a dark experimental box, and the animals were monitored using an infrared camera. Rats were head-fixed in a small acrylic tunnel (height = 11 cm, depth = 21 cm, width at back end = 7 cm, width at front end = 5 cm), with the head-post clipped to a metal bracket extruding from the front of the tunnel. The apparatus and general behavioral approach have been described previously (Gerdjikov, Bergner, Stuttgart, Waiblinger, & Schwarz, 2010; Schwarz et al., 2010). A spout was placed in front of the rat, and licks were registered by monitoring spout deflections via a piezo film sensor glued to the spout (Part No. FS-2513P, Farnell, Leeds, UK). Water delivery was controlled by a

**Figure 1.** Overview of experimental paradigm. (A) Schematic illustration of the whisker stimulation. (B) Illustration of the whisker stimulation task. Tactile stimulation was delivered at 60 Hz during the decision window, and pulse amplitude varied between 0.01 and 0.5 mm. Each lick during the no-lick period shifted stimulus onset by 5 sec. (C) Bright-field photomicrograph ( $\times 5$ ) of a coronal section indicating OFC recording electrode location (white arrow) marked by an electrolytic lesion. (D) Intrinsic optical imaging of barrel cortex. Blood vasculature landmarks (left) were used to locate the sensory cortical column (right; darker region) activated by stimulation of the target whisker (C1). Cortical curvature at the level of somatosensory cortex produced the blur observed away from the center of the image.



magnetic valve (Takasago Electric, Inc., Nagoya, Japan; WTA-2R-N3F). A data acquisition board (National Instruments PCI-6229) and a custom-written software were used for experimental control and behavioral data acquisition (Labview, National Instruments).

### Tactile Stimuli

The whisker stimulator was constructed from a glass capillary (1 mm o.d.) glued to a piezo bender (Physik Instrumente, Karlsruhe, Germany). The tip of the capillary was further thinned through heating until a whisker hair could rest snugly inside the tip opening. Voltage commands were programmed in Matlab (The MathWorks, Natick, MA) and delivered using a custom-written LabVIEW software. The stimuli consisted of brief pulsatile deflections (single-period  $\pi/2$ -shifted cosine wave, 100 Hz, duration 10 msec) presented to the right C1 whisker for 2 sec at interpulse intervals of 17 msec corresponding to a frequency of 60 Hz. Displacement amplitude was 0.01, 0.05, 0.1, 0.2, and 0.5 mm delivered at a 5-mm distance from the whisker base. The length of the glass capillary and the point of attachment of the piezo element were optimized to remove ringing of the stimulator. Calibration with a phototransistor (HLC1395, Honeywell, Morristown, NJ) showed that differences in amplitude and peak velocity between individual pulses due to ringing of the stimulator were smaller than 3%. The capillary tip was tilted at an angle of  $155^\circ$ – $175^\circ$  against the whisker, such that the vibrissa rested against the inside wall of the

capillary, ensuring that the stimulator engaged the whisker immediately. Stimuli were applied in the rostral direction.

### Behavioral Procedure

Rat housing, handling, habituation to head fixation, and water control were performed as described previously (Schwarz et al., 2010). Training sessions were scheduled one to two times a day, 5 days a week, followed by 2 days of free access to water. Rats underwent a systematic habituation protocol ensuring they were comfortable with head fixation and willing to retrieve the water reward. During testing, water intake was restricted to the apparatus where animals were given the opportunity to earn water to satiety (Figure 1A and B). If needed, daily water intake was supplemented after testing to prevent drops in body weight. Rats were trained to associate a 2-sec 0.5-mm stimulus with water reward (intertrial interval = 15–20 sec). To discourage licking during the intertrial interval, a 5-sec time-out was introduced if the animal emitted a lick in the 5 sec before stimulus presentation. The time-out clock was reset with every subsequent lick, so that a stimulus never followed a lick by less than 5 sec. Once responding on this task was stable, stimuli of lower amplitudes were introduced (see Tactile Stimuli), and reward was contingent on licking the spout during the 2 sec of stimulus presentation. Stimuli were always presented in blocks of 10, and stimulus order was chosen randomly within each block and across blocks. One block

consisted of five stimuli at 0.5-mm amplitude and five stimuli of lower amplitudes. Response probabilities were calculated as the number of responses to each stimulus amplitude divided by the number of presentations.

### Electrophysiological Recordings and Analysis

Recordings commenced when each rat achieved stable asymptotic behavior (0.8 response probability for the highest amplitude stimulus – 0.5 mm), and the data set consisted of a total of 132 trials (60 hits). Local field potentials were acquired continuously via an op-amp-based headstage amplifier (HST/8050-G1-GR,  $1 \times$  gain; Plexon, Dallas, TX) and passed through a preamplifier (PBX2,  $1,000 \times$  gain; Plexon). Recording electrodes consisted of quartz glass-coated platinum/tungsten wires pulled and ground to custom shapes in our laboratory (shank diameter =  $80 \mu\text{m}$ , diameter of the metal core =  $23 \mu\text{m}$ , free tip length  $< 10 \mu\text{m}$ ; Thomas Recording, Giessen, Germany). The signal was low-pass filtered using a 300-Hz cutoff Butterworth filter and down-sampled offline to 2000 Hz. Raw power spectral densities for each power band (delta, 0–4 Hz; theta, 4–7 Hz; alpha, 8–13 Hz; beta, 12–30 Hz; gamma, 30–100 Hz) were extracted using a fast Fourier transform algorithm with a

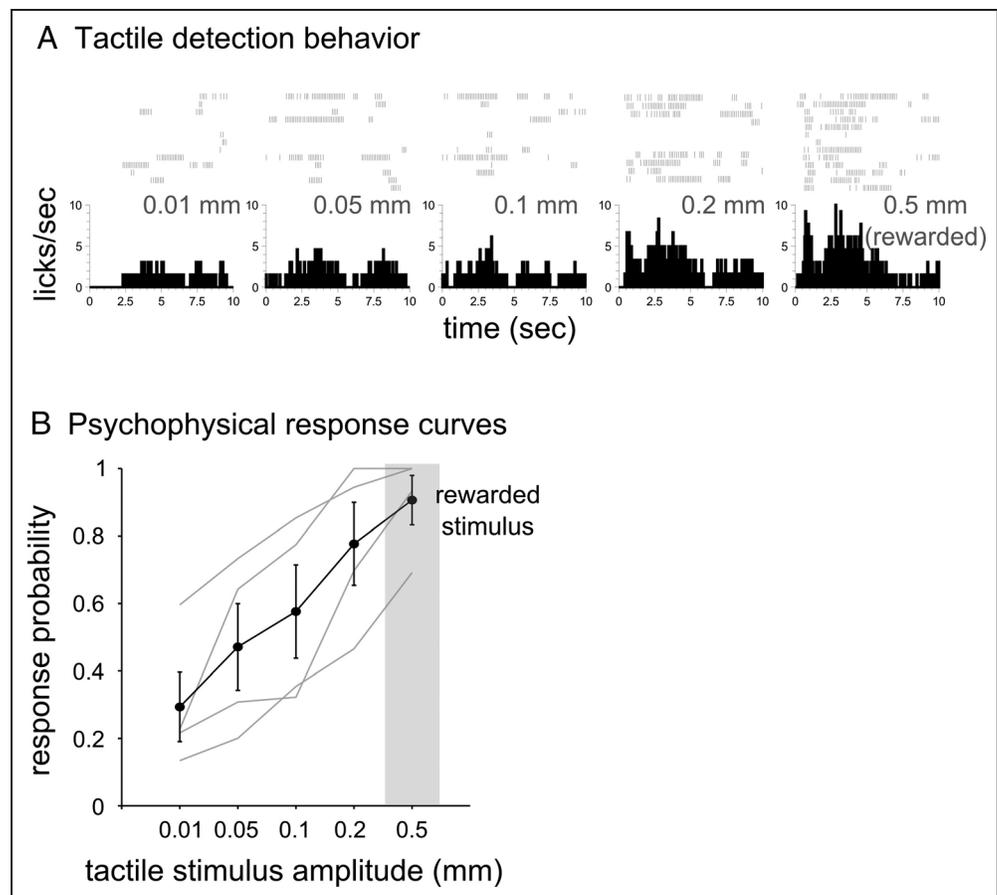
Hanning window (Neuroexplorer, Nex Technologies, Littleton, MA) in a 4-sec window preceding the presentation of the 0.1-mm stimulus; this was the stimulus intensity that produced near-threshold psychophysical detection during behavioral testing (Figure 2A and B). Responses to near-threshold stimuli are most likely to be affected by attentional fluctuations, and they produce roughly equal numbers of hits and misses. Analyses were calculated using Neuroexplorer and custom-written Matlab routines. ANOVAs were performed using SPSS (IBM SPSS, Somers, NY).

## RESULTS

### Psychometric Performance

Example licking rasters and histograms during the presentation of each stimulus intensity are presented in Figure 2A. The apparent double peak in the histogram corresponding to the 0.5-mm stimulus represents an initial operant lick to the tactile stimulus (cf. Figure 1B) and a train of consummatory licks when the rat retrieves the reward, which was triggered by the first operant lick. Overall, response likelihood was higher for higher-amplitude stimuli and highest for the reference (rewarded) 0.5-mm stimulus. Response probability calculated

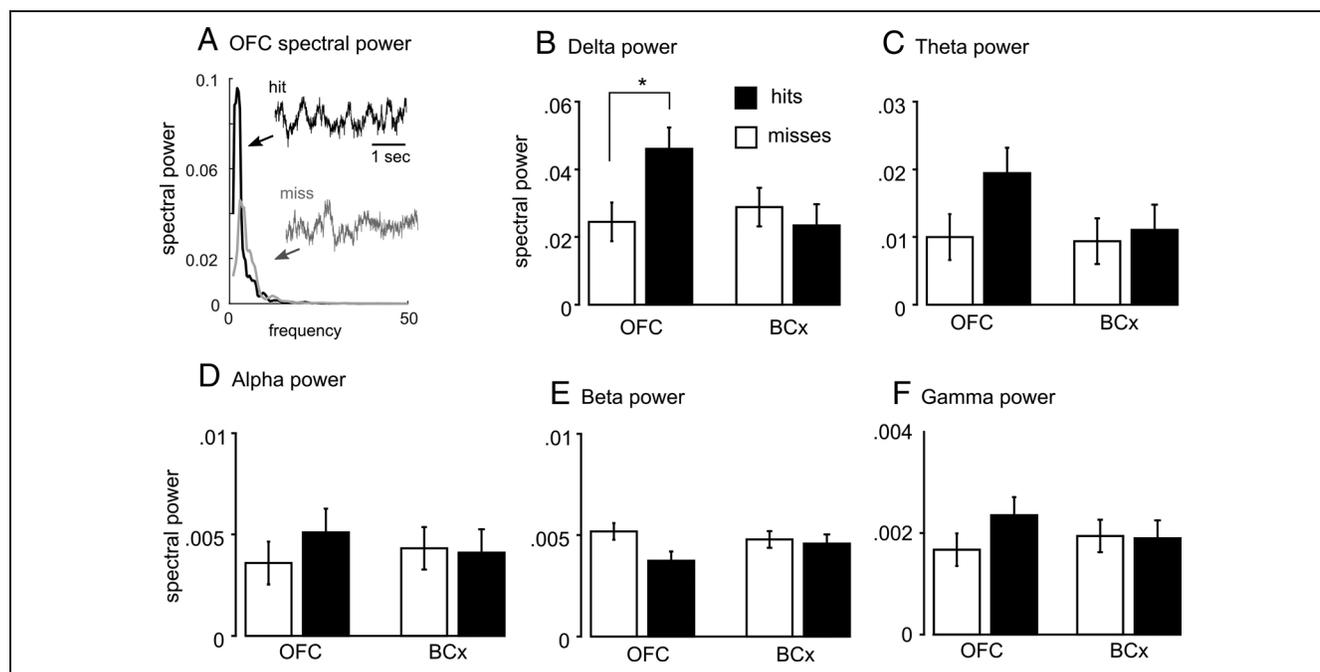
**Figure 2.** Psychophysical detection of vibrotactile whisker stimuli. (A) Example lick raster plots and histograms from one representative session. Data are locked to tactile stimulus onset (stimulus duration = 2 sec). Amplitude of the tactile stimulus is indicated on each lick histogram. Responses to the 0.5-mm amplitude produced a liquid reward. (B) Psychophysical detection performance in four rats. The 0.1-mm stimulus showed near-threshold detection performance. The black line represents the average performance of all rats in a total of 17 sessions. Error bars represent *SEM*.



for each of the tested tactile stimulus amplitudes revealed clear psychometric curves for each rat (Figure 2B). Responding was robust for the 0.5-mm stimulus amplitude for all four animals tested and was progressively lower for stimuli of lower amplitudes. This was confirmed by a one-way within-subject ANOVA,  $F(4, 64) = 51.14, p < .001$ . On the basis of this observation, the 0.1-mm amplitude was chosen for electrophysiological analyses, as it represented a clear threshold with approximately 50% response probability. Next, we investigated whether the behavioral results shown here may be due to discrimination between lower and higher amplitude stimuli. We reasoned that if animals are using a discrimination strategy, the behavioral data would show the evolution of discrimination learning as improved performance across sessions. On the other hand, performance would not vary systematically across sessions if it depends on detection. We indexed the performance of the animals as the difference between response probability for the highest and lowest amplitude stimuli and calculated the Spearman correlation coefficient between this index and session number. The correlation coefficient was nonsignificant both across animals ( $\rho = -.14, p = .33$ ) and for each individual animal ( $\rho = -.56, p = .19, \rho = .13, p = .62, \rho = .07, p = .74, \rho = -.38, p = .40$ ). These calculations suggest that the behavioral results presented here are unlikely to be driven by discrimination between lower and higher amplitude stimuli but rather are consistent with the view that they depend on detection.

### Detection of Near-threshold Stimuli Is Associated with Increased Prestimulus OFC Slow Oscillation Power

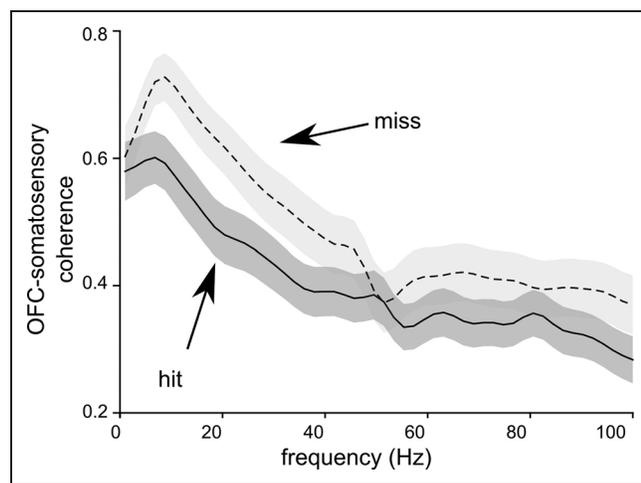
To assess the relationship between brain state and the detection of vibrotactile stimuli to single whiskers, we used local field potentials in OFC to measure spectral power in the delta to gamma frequency bands. We recorded and integrated spectral power in the respective frequency bands for the 4 sec before the onset of near-threshold 0.1-mm vibrotactile stimuli. The analysis indicated that successful detection of near-threshold stimuli was associated with increased delta power in OFC but not barrel cortex (Figure 3A–F). This interpretation was confirmed by Structure (OFC vs. barrel cortex)  $\times$  Response (hit vs. miss) ANCOVA at each frequency band (with other bands as covariates). For the delta band, this produced a Response  $\times$  Structure interaction,  $F(1, 256) = 5.069, p = .025$ , and no main effect of Structure or Response,  $F(1, 256) = 2.31, p = .13$  and  $F(1, 256) = 1.79, p = .18$ , respectively. Following this up with simple main effects of Response for each structure revealed increased delta for hits in OFC,  $F(1, 126) = 4.91, p = .03$ , but not in barrel cortex,  $F(1, 126) = 0.98, p = .32$ . This effect was specific to delta power: We observed no effects of Response, Structure, or Structure  $\times$  Response interaction for the theta,  $F(1, 256) = 2.41, p = .12, F(1, 256) = 1.58, p = .21, F(1, 256) = 1.17, p = .28$ , alpha,  $F(1, 256) = 0.33, p = .56, F(1, 256) = 0.02, p = .90, F(1, 256) = 0.60, p = .44$ , beta,  $F(1, 256) = 3.63, p = .06, F(1, 256) = 0.26, p = .61$ ,



**Figure 3.** Association between cortical spectral power and detection probability of near-threshold stimuli. (A) Example hit and miss trial OFC field potential traces (4 sec before stimulus onset) and corresponding power spectra. Bar graphs (B–F) demonstrate the amount of OFC and barrel cortex power in delta through to gamma frequency bands in a 4-sec prestimulus time intervals separated by hits and misses for detection of a 0.1-mm stimulus. Error bars represent SEM.

$F(1, 256) = 2.04, p = .15$ , or gamma,  $F(1, 256) = 0.87, p = .35$ ,  $F(1, 256) = 0.07, p = .79$ ,  $F(1, 256) = 1.15, p = .29$ , bands. We also assessed whether the rat variable influences the overall conclusions by rerunning the analysis using animal as a covariate. In this analysis, we obtained the exact same pattern of results, namely, a significant Structure  $\times$  Frequency band interaction for delta:  $F(1, 255) = 5.03, p = .025708$ , reflecting higher hit delta power in OFC, but not in barrel cortex. The interaction was not significant for any other frequencies (data not shown). This pattern of effects suggests that the subject (i.e., rat) variable does not unduly influence our conclusions. To rule out more transient effects on gamma, we repeated the above analysis for a relatively short baseline period of 1 sec. The Structure  $\times$  Response interaction revealed no significant main effects or interactions ( $ps > .6$ ), except for the effect on delta where we noted the interaction,  $F(1, 256) = 2.88, p = .091$ , which, even though nonsignificant, mirrored the findings observed with a 4-sec interaction window (data not shown).

Thus, cortical power analyzed separately for each structure revealed dissociable patterns of activity in relation to detection probability. To directly test whether correlated activity between the two structures was decreased on a trial-by-trial basis for success detection, we calculated cortical coherence between prefrontal and barrel cortex local field potentials. This analysis revealed that indeed periods of lower synchrony between the two structures are associated with higher detection probability (Figure 4). This was confirmed by a Frequency  $\times$  Response type ( $5 \times 2$ ) ANOVA, which revealed a main effect of Response type,  $F(1, 130) = 4.24, p < .05$ , on coherence, but no significant frequency band effect. Thus, reduced synchrony across frequencies was associated with improved detection.



**Figure 4.** Association between OFC–somatosensory cortical coherence and detection probability of near-threshold stimuli. Coherence was lower for hit versus miss trials for 0.1-mm amplitude detection. Error band represents SEM.

## DISCUSSION

Background cortical oscillations are related to psychophysical performance in a number of tactile tasks. OFC appears to be involved in the top–down modulation of sensory processing; however, the specific contribution of ongoing OFC oscillations to perception has not been characterized. Here we studied for the first time how ongoing OFC and somatosensory cortical activity relate to the detection of near-threshold vibrotactile stimuli in head-fixed rats. We found that higher OFC but not somatosensory delta power was associated with increased detection probability. Furthermore, detection was associated with significantly lower coherence between the two regions. Consistent with the role of OFC in attention, this dissociation identifies a cortical network whose activity shows differential modulation before successful tactile detection.

We found that increased OFC delta band activity is associated with higher psychophysical detection probability. Slow wave oscillations across cortex are typically associated with deep sleep; however, delta band activity is also observed in awake, head-fixed mice (Ito et al., 2014; Poulet & Petersen, 2008; Petersen, Hahn, Mehta, Grinvald, & Sakmann, 2003). Delta band activity is reduced during active and alert states (Buzsaki et al., 1988). However, our current result that periods of increased OFC delta are associated with higher tactile detection probability is consistent with previous observations that quiet wakefulness, which is associated with high-amplitude slow oscillations, may serve to heighten sensitivity to sensory input and decrease detection thresholds (Castro-Alamancos, 2009). Notably in the current study, this effect did not extend to oscillations recorded in barrel cortex. Previous work has not looked specifically at rodent tactile psychophysical performance as a function of OFC oscillation state; however, negative detection findings on prestimulus oscillations in somatosensory cortex have been reported in the theta range (Wiest & Nicolelis, 2003). Interestingly, the latter finding contrasts with increased theta locking in barrel cortex during an active discrimination task, highlighting the different neurophysiological representations of detection versus discrimination behavior (Grion, Akrami, Zuo, Stella, & Diamond, 2016; Ollerenshaw, Zheng, Millard, Wang, & Stanley, 2014). That detection is enhanced during periods of cortical activation linked to quiet immobility is consistent with extensive previous findings on enhanced sensory responses during quiet immobility (Castro-Alamancos, 2004; Fanselow & Nicolelis, 1999). Thus, ongoing cortical activity modulates behavioral performance presumably by optimizing the representations of behaviorally relevant perceptual parameters (e.g., detection vs. processing of finer stimulus detail). Adding to these previous findings, we now link such modulation specifically to OFC, a structure previously implicated in sensory integration and attention (Frey et al., 2009; Ongur & Price, 2000). It should be noted that OFC has been implicated in a variety of behavioral functions in addition to attentional control. These

include value encoding and response inhibition. Recent results suggest that the role of OFC in these processes may have to be understood in terms of more fundamental functions, including salience and a cognitive map of the associative structure of the environment (Stalnaker, Cooch, & Schoenbaum, 2015). These roles are not inconsistent with a role of OFC in detecting salient reward-paired stimuli. Our results specifically suggest that rodent tactile perception is related to frequency ranges lower than those reported in humans. We identified prestimulus slow oscillations in the delta band as the primary correlate of psychophysical detection. Delta power appears to play a fundamental neurophysiological role in rodents related to alertness and wakefulness, but also to lower-level processes such as respiration (Ito et al., 2014). In humans, alpha oscillation and phase, as well as higher oscillations in some studies, relate to tactile or visual detection probability (Lundqvist, Herman, & Lansner, 2013; Mathewson, Gratton, Fabiani, Beck, & Ro, 2009; Linkenkaer-Hansen et al., 2004). Human gamma band oscillatory activity is widely associated with visual attention, and ongoing gamma oscillations relate to visual task performance (Akimoto et al., 2014; Fries, Reynolds, Rorie, & Desimone, 2001). We found no evidence that ongoing gamma power is associated with behavioral detection probability. Rodent cortical gamma oscillations can be manipulated optogenetically and using constitutive mutants (Cho et al., 2015; Carlen et al., 2012; Cardin et al., 2009); however, interestingly increased baseline gamma power in the mutants was associated with poorer performance on cognitive tasks. These differences may reflect task, modality, or species-specific mechanisms and warrant further investigation.

Recording OFC and somatosensory oscillations concurrently allowed us to directly measure the extent to which network activity between the two regions relates to detection. We found that, on average, coherence between the two regions was reduced preceding successful detection. We have thus identified a cortical network whose suppression may facilitate tactile detection in rats. This uncoupling between OFC and somatosensory cortex activity may relate to the proposed distinction between mechanisms governing “top-down” versus “bottom-up” attentional processing of sensory input in relation to discrimination versus detection performance (Buschman & Miller, 2007). This may potentially explain why, during a higher-level tactile matching-to-sample task in primates, delta coherence between sensory and prefrontal areas is enhanced, unlike the result on decreased coherence in the current study employing a detection task (Nacher, Ledberg, Deco, & Romo, 2013). The relationship between OFC–somatosensory coherence and psychophysical performance observed here was not specific to the delta band. However, it contributes to the observation that increased corticocortical coherence is associated with higher-level decision-making tasks but seems to impair tactile detection. It is also consistent with the proposed dissociation and trade-off between cortical processes associated with

detection versus discrimination performance as a function of ongoing behavioral demands (Ollerenshaw et al., 2014). Current hypotheses regarding the implementation of this dissociation include modulations of thalamocortical projections by either cortical or subcortical modulatory afferents (Ollerenshaw et al., 2014; Harris & Thiele, 2011; Sherman, 2001); however, this remains an open question requiring further investigation.

## Acknowledgments

We thank the University of Leicester Biomedical Workshop for excellent technical support. This study was funded in part by the Royal Society (UK). R. R. was in receipt of a University of Leicester postgraduate studentship.

Reprint requests should be sent to Todor V. Gerdjikov, Department of Neuroscience, Psychology and Behaviour, University of Leicester, University Road, Leicester LE1 9HN, United Kingdom, or via e-mail: tvg3@le.ac.uk.

## REFERENCES

- Akimoto, Y., Nozawa, T., Kanno, A., Ihara, M., Goto, T., Ogawa, T., et al. (2014). High-gamma activity in an attention network predicts individual differences in elderly adults' behavioral performance. *Neuroimage*, *100*, 290–300.
- Aronoff, R., Matyas, F., Mateo, C., Ciron, C., Schneider, B., & Petersen, C. C. (2010). Long-range connectivity of mouse primary somatosensory barrel cortex. *European Journal of Neuroscience*, *31*, 2221–2233.
- Bouret, S., & Richmond, B. J. (2010). Ventromedial and orbital prefrontal neurons differentially encode internally and externally driven motivational values in monkeys. *Journal of Neuroscience*, *30*, 8591–8601.
- Buschman, T. J., & Miller, E. K. (2007). Top-down versus bottom-up control of attention in the prefrontal and posterior parietal cortices. *Science*, *315*, 1860–1862.
- Buzsaki, G., Bickford, R. G., Ponomareff, G., Thal, L. J., Mandel, R., & Gage, F. H. (1988). Nucleus basalis and thalamic control of neocortical activity in the freely moving rat. *Journal of Neuroscience*, *8*, 4007–4026.
- Cardin, J. A., Carlen, M., Meletis, K., Knoblich, U., Zhang, F., Deisseroth, K., et al. (2009). Driving fast-spiking cells induces gamma rhythm and controls sensory responses. *Nature*, *459*, 663–667.
- Carlen, M., Meletis, K., Siegle, J. H., Cardin, J. A., Futai, K., Vierling-Claassen, D., et al. (2012). A critical role for NMDA receptors in parvalbumin interneurons for gamma rhythm induction and behavior. *Molecular Psychiatry*, *17*, 537–548.
- Castro-Alamancos, M. A. (2004). Absence of rapid sensory adaptation in neocortex during information processing states. *Neuron*, *41*, 455–464.
- Castro-Alamancos, M. A. (2009). Cortical up and activated states: Implications for sensory information processing. *Neuroscientist*, *15*, 625–634.
- Cho, K. K., Hoch, R., Lee, A. T., Patel, T., Rubenstein, J. L., & Sohal, V. S. (2015). Gamma rhythms link prefrontal interneuron dysfunction with cognitive inflexibility in *Dlx5/6* (+/−) mice. *Neuron*, *85*, 1332–1343.
- Cooch, N. K., Stalnaker, T. A., Wied, H. M., Bali-Chaudhary, S., McDannald, M. A., Liu, T. L., et al. (2015). Orbitofrontal lesions eliminate signalling of biological significance in cue-responsive ventral striatal neurons. *Nature Communications*, *6*, 7195.

- Ding, L. (2015). Distinct dynamics of ramping activity in the frontal cortex and caudate nucleus in monkeys. *Journal of Neurophysiology*, *114*, 1850–1861.
- Everling, S., Tinsley, C. J., Gaffan, D., & Duncan, J. (2006). Selective representation of task-relevant objects and locations in the monkey prefrontal cortex. *European Journal of Neuroscience*, *23*, 2197–2214.
- Fanselow, E. E., & Nicolelis, M. A. (1999). Behavioral modulation of tactile responses in the rat somatosensory system. *Journal of Neuroscience*, *19*, 7603–7616.
- Frey, S., Zlatkina, V., & Petrides, M. (2009). Encoding touch and the orbitofrontal cortex. *Human Brain Mapping*, *30*, 650–659.
- Fries, P., Reynolds, J. H., Rorie, A. E., & Desimone, R. (2001). Modulation of oscillatory neuronal synchronization by selective visual attention. *Science*, *291*, 1560–1563.
- Fritz, J. B., David, S. V., Radtke-Schuller, S., Yin, P., & Shamma, S. A. (2010). Adaptive, behaviorally gated, persistent encoding of task-relevant auditory information in ferret frontal cortex. *Nature Neuroscience*, *13*, 1011–1019.
- Fritz, J. B., Elhilali, M., David, S. V., & Shamma, S. A. (2007). Auditory attention—Focusing the searchlight on sound. *Current Opinion in Neurobiology*, *17*, 437–455.
- Gerdjikov, T. V., Bergner, C. G., Stüttgen, M. C., Waiblinger, C., & Schwarz, C. (2010). Discrimination of vibrotactile stimuli in the rat whisker system: Behavior and neurometrics. *Neuron*, *65*, 530–540.
- Grien, N., Akrami, A., Zuo, Y., Stella, F., & Diamond, M. E. (2016). Coherence between rat sensorimotor system and hippocampus is enhanced during tactile discrimination. *PLoS Biology*, *14*, e1002384.
- Harris, K. D., & Thiele, A. (2011). Cortical state and attention. *Nature Reviews Neuroscience*, *12*, 509–523.
- Hawking, T. G., & Gerdjikov, T. V. (2013). Populations of striatal medium spiny neurons encode vibrotactile frequency in rats: Modulation by slow wave oscillations. *Journal of Neurophysiology*, *109*, 315–320.
- Ito, J., Roy, S., Liu, Y., Cao, Y., Fletcher, M., Lu, L., et al. (2014). Whisker barrel cortex delta oscillations and gamma power in the awake mouse are linked to respiration. *Nature Communications*, *5*, 3572.
- Kringelbach, M. L. (2005). The human orbitofrontal cortex: Linking reward to hedonic experience. *Nature Reviews Neuroscience*, *6*, 691–702.
- Langer, D., van 't Hoff, M., Keller, A. J., Nagaraja, C., Pfaffli, O. A., Goldi, M., et al. (2013). HelioScan: A software framework for controlling in vivo microscopy setups with high hardware flexibility, functional diversity and extensibility. *Journal of Neuroscience Methods*, *215*, 38–52.
- Linkenkaer-Hansen, K., Nikulin, V. V., Palva, S., Ilmoniemi, R. J., & Palva, J. M. (2004). Prestimulus oscillations enhance psychophysical performance in humans. *Journal of Neuroscience*, *24*, 10186–10190.
- Lundqvist, M., Herman, P., & Lansner, A. (2013). Effect of prestimulus alpha power, phase, and synchronization on stimulus detection rates in a biophysical attractor network model. *Journal of Neuroscience*, *33*, 11817–11824.
- Mathewson, K. E., Gratton, G., Fabiani, M., Beck, D. M., & Ro, T. (2009). To see or not to see: Prestimulus alpha phase predicts visual awareness. *Journal of Neuroscience*, *29*, 2725–2732.
- McKee, J. L., Riesenhuber, M., Miller, E. K., & Freedman, D. J. (2014). Task dependence of visual and category representations in prefrontal and inferior temporal cortices. *Journal of Neuroscience*, *34*, 16065–16075.
- Nacher, V., Ledberg, A., Deco, G., & Romo, R. (2013). Coherent delta-band oscillations between cortical areas correlate with decision making. *Proceedings of the National Academy of Sciences, U.S.A.*, *110*, 15085–15090.
- Neubert, F. X., Mars, R. B., Sallet, J., & Rushworth, M. F. (2015). Connectivity reveals relationship of brain areas for reward-guided learning and decision making in human and monkey frontal cortex. *Proceedings of the National Academy of Sciences, U.S.A.*, *112*, E2695–E2704.
- Ollerenshaw, D. R., Zheng, H. J., Millard, D. C., Wang, Q., & Stanley, G. B. (2014). The adaptive trade-off between detection and discrimination in cortical representations and behavior. *Neuron*, *81*, 1152–1164.
- Ongur, D., & Price, J. L. (2000). The organization of networks within the orbital and medial prefrontal cortex of rats, monkeys and humans. *Cerebral Cortex*, *10*, 206–219.
- Panzeri, S., Macke, J. H., Gross, J., & Kayser, C. (2015). Neural population coding: Combining insights from microscopic and mass signals. *Trends in Cognitive Sciences*, *19*, 162–172.
- Passingham, R. E., & Eitlinger, G. (1972). Tactile discrimination learning after selective prefrontal ablations in monkeys (*Macaca mulatta*). *Neuropsychologia*, *10*, 17–26.
- Paxinos, G., & Watson, C. (2007). *The rat brain in stereotaxic coordinates*. Cambridge, MA: Academic Press.
- Petersen, C. C., Hahn, T. T., Mehta, M., Grinvald, A., & Sakmann, B. (2003). Interaction of sensory responses with spontaneous depolarization in layer 2/3 barrel cortex. *Proceedings of the National Academy of Sciences, U.S.A.*, *100*, 13638–13643.
- Pleger, B., & Villringer, A. (2013). The human somatosensory system: From perception to decision making. *Progress in Neurobiology*, *103*, 76–97.
- Poulet, J. F., & Petersen, C. C. (2008). Internal brain state regulates membrane potential synchrony in barrel cortex of behaving mice. *Nature*, *454*, 881–885.
- Reep, R. L., Corwin, J. V., & King, V. (1996). Neuronal connections of orbital cortex in rats: Topography of cortical and thalamic afferents. *Experimental Brain Research*, *111*, 215–232.
- Schubert, R., Haufe, S., Blankenburg, F., Villringer, A., & Curio, G. (2009). Now you'll feel it, now you won't: EEG rhythms predict the effectiveness of perceptual masking. *Journal of Cognitive Neuroscience*, *21*, 2407–2419.
- Schwarz, C., Hentschke, H., Butovas, S., Haiss, F., Stüttgen, M. C., Gerdjikov, T. V., et al. (2010). The head-fixed behaving rat—Procedures and pitfalls. *Somatosensory & Motor Research*, *27*, 131–148.
- Sherman, S. M. (2001). Tonic and burst firing: Dual modes of thalamocortical relay. *Trends in Neurosciences*, *24*, 122–126.
- Stalnaker, T. A., Cooch, N. K., & Schoenbaum, G. (2015). What the orbitofrontal cortex does not do. *Nature Neuroscience*, *18*, 620–627.
- Takahashi, Y. K., Roesch, M. R., Stalnaker, T. A., Haney, R. Z., Calu, D. J., Taylor, A. R., et al. (2009). The orbitofrontal cortex and ventral tegmental area are necessary for learning from unexpected outcomes. *Neuron*, *62*, 269–280.
- Wiest, M. C., & Nicolelis, M. A. (2003). Behavioral detection of tactile stimuli during 7–12 Hz cortical oscillations in awake rats. *Nature Neuroscience*, *6*, 913–914.
- Zhang, Y., & Ding, M. (2010). Detection of a weak somatosensory stimulus: Role of the prestimulus mu rhythm and its top-down modulation. *Journal of Cognitive Neuroscience*, *22*, 307–322.