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

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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. Orbitofrontal cortex (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 60Hz; 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. Further, coherence between prefrontal cortex 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 prior to successful tactile detection.

Keywords: barrel cortex, cortical oscillations, detection, rat, orbitofrontal cortex

Considerable evidence supports the role of prefrontal cortex in higher-order sensory processing including stimulus categorization and the top-down control of sensory inputs (Fritz et al., 2010; Everling et al., 2006; McKee et al., 2014; Fritz et al., 2007; Ding, 2015). Rodent orbitofrontal cortex (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 and Price, 2000; Reep et al., 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 et al., 2009; Passingham and Ettlinger, 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 (Bouret and Richmond, 2010; Kringelbach, 2005; Takahashi et al., 2009; Cooch et al., 2015; Neubert et al., 2015).

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 non-cortical regions (Hawking and Gerdjikov, 2013; Panzeri et al., 2015; Castro-Alamancos, 2009; Ding, 2015). 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 pre-stimulus cortical oscillatory activity modulates detection of near-threshold stimuli comes primarily from human EEG studies in regions other than OFC (Pleger and Villringer, 2013; Schubert et al., 2009; Linkenkaer-Hansen et al., 2004). For example, pre-stimulus 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 pre-stimulus 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 and 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 pre-stimulus 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 overtrained 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 pre-stimulus coherence between the two regions.

Materials and Methods

Animals and Surgery

Male Sprague Dawley rats (n = 4), obtained from Charles River (Margate, Kent, UK), weighing between 200 and 250 g on arrival were housed in pairs on a 12-h reversed light–dark cycle (lights on at 1900 hour) 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 UK 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_2O) were given daily for 3 days before surgery in the drinking water. Rats were anaesthetised with isoflurane (2-3%). Core temperature was monitored rectally and maintained at 37 ˚C using a homeothermic pad (Harvard Apparatus, Boston, MA, USA). For fluid replacement, 5% glucose was continuously administered via an infusion pump (3 mL/hour, s.c.; Instech, K. D. Scientific, Holliston, MA, USA). Glycopyrronium bromide (40 μL/kg, i.m.; 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, Wesport, 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, Massachusetts, USA, 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 (Fig. 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). Illumination was provided by three high-brightness deep-red LEDs (655 nm; product nr. LXM3-PD01; Philips Lumileds, San Jose, CA, USA) mounted directly on the objective. The software acquired 75 x 75 resolution images at 20 Hz over ten 5 s 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 s stimulation-free baseline. For mapping, the intrinsic optical signal was compared to 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, USA) 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, Melville, NY, USA). OFC implantation coordinates were: AP +3.2, ML 2 to 4, DV -4 (Paxinos and Watson, 2007) (Fig.1C). Antibiotic ointment (Fuciderm; Dechra vetinary products, Uldum, Denmark) was applied to the wound and the skin was sutured around the implant. Analgesia (Carprieve, 5 mg/kg; s.c; Norbrook Laboratories Ltd, Corby, UK) was administered 2-3 hours before recovery and twice daily for 3 days post-surgery or longer as needed. Glucose solution (5%, 5 mL/day; i.p.) 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 headpost clipped to a metal bracket extruding from the front of the tunnel. The apparatus and general behavioral approach has been described previously (Schwarz et al., 2010; Gerdjikov 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 the spout (Part nr. FS-2513P; Farnell, Leeds, UK). Water delivery was controlled by a magnetic valve (Takasago Electric Inc, Nagoya, Japan; WTA-2R-N3F). A data acquisition board (National Instruments PCI-6229) and custom-written software were used for experimental control and behavioral data acquisition (Labview, National Instruments, Austin, TX, USA).

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 (Mathworks, Natick, MA) and delivered using custom-written LabVIEW software. The stimuli consisted of brief pulsatile deflections (single-period π/2-shifted cosine wave, 100 Hz, duration 10 ms) presented to the right C1 whisker for 2 s at interpulse intervals of 17 ms 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 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°-175° 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 1-2 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 (Fig. 1 A&B). If needed, daily water intake was supplemented after testing to prevent drops in body weight. Rats were trained to associate a 2 s 0.5 mm stimulus with water reward (inter-trial interval 15-20 s). To discourage licking during the inter-trial interval, a 5 s time-out was introduced if the animal emitted a lick in the 5 s prior to stimulus presentation. The time-out clock was reset with every subsequent lick, so that a stimulus never followed a lick by less than

5 s. 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 s of stimulus presentation. Stimuli were always presented in blocks of ten and stimulus order was chosen randomly within each block and across blocks. One block consisted of 5 stimuli at 0.5 mm amplitude and 5 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 (LFPs) were acquired continuously via an op-amp-based headstage amplifier (HST/8o50-G1-GR, 1 x gain; Plexon, Dallas, TX) and passed through a preamplifier (PBX2, 1,000 x gain; Plexon). Recording electrodes consisted of quartz glass-coated platinum/ tungsten wires pulled and ground to custom shapes in our laboratory (shank diameter 80 µm; diameter of the metal core 23 µm; free tip length < 10 µm; Thomas Recording, Giessen, Germany). The signal was low-pass filtered using a 300 Hz cut-off Butterworth filter and downsampled offline to 2000 Hz. Raw power spectral densities (PSD) 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 an FFT algorithm with a Hanning window (Neuroexplorer, Nex Technologies, Littleton, MA) in a 4 s window preceding the presentation of the 0.1mm stimulus; this was the stimulus intensity which produced near-threshold psychophysical detection during behavioral testing (Fig. 2 A&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. ANOVA 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 Fig. 2A. The apparent double peak in the histogram corresponding to the .5 mm stimulus represents an initial operant lick to the tactile stimulus (compare Fig. 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 for each of the tested tactile stimulus amplitudes revealed clear psychometric curves for each rat (Fig. 2B). Responding was robust for the 0.5 mm stimulus amplitude for all 4 animals tested and was progressively lower for stimuli of lower amplitudes. This was confirmed by a one-way within-subjects ANOVA [$F(4, 64) = 51.14$, $p < .001$]. Based on these 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 behavioural 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 behavioural 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 non-significant both across animals (rho = -.14, p = 0.327359) and for each individual animal (rho = -.56, p = 0.187496, rho = .13, p = 0.617367, rho = .07, p = 0.737537, rho = -.38, p = 0.402602). These calculations suggest that the behavioural 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 pre-stimulus 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 s prior to the onset of near-threshold 0.1 mm vibro-tactile stimuli. The analysis indicated that successful detection of near-threshold stimuli was associated with increased delta power in OFC but not barrel cortex (Fig. 3 A-E). This interpretation was confirmed by structure (OFC vs. barrel cortex) x response (hit vs. miss) ANCOVA at each frequency band (with other bands as covariates). For the delta band this produced a response x structure interaction [$F(1, 256) = 5.069$, $p = .025$] and no main effects 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 [$F(1, 126)= .98$, $p= .32$]. This effect was specific to delta power: We observed no response, structure or structure x 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 [$F(1, 256) =.33$, $p = .56$, $F(1, 256) =.02$, $p = .90$, $F(1, 256) =.60$, $p = .44$], beta [$F(1, 256) =3.63$, $p = .06$, $F(1, 256) =.26$, $p = .61$, $F(1, 256) = 2.04$, $p = .15$] or gamma [$F(1, 256) =.87$, $p = .35$, $F(1, 256) =.07$, $p = .79$, $F(1, 256) =1.15$, $p = .29$] bands. We also assessed whether the rat variable influences the overall conclusions by reruning the analysis using animal as a covariate. In this analysis, we obtained the exact same pattern of results: namely a significant structure x frequency band interaction for delta: $F(1, 255) = 5.03$, $p = 0.025708$, reflecting higher hit delta power in OFC but not in BCx. 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 x 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 non-significant, mirrored the findings observed with a 4 second interaction window (data not shown).

Thus cortical power analysed 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 LFPs. This analysis revealed that indeed periods of lower synchrony between the two structures are associated with higher detection probability (Fig. 4). This was confirmed by a frequency x response type (5 x 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.

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 vibro-tactile 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 prior to 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; Petersen et al., 2003; Poulet and Petersen, 2008). 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 and Nicolelis, 2003). Interestingly, the latter finding contrast with increased theta locking in barrel cortex during an active discrimination task, highlighting the different neurophysiological representations of detection vs. discrimination behavior (Ollerenshaw et al., 2014; Grion et al., 2016).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 (Fanselow and Nicolelis, 1999; Castro-Alamancos, 2004). 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 orbitofrontal cortex, a structure previously implicated in sensory integration and attention (Ongur and Price, 2000; Frey et al., 2009). It should be noted that OFC has been implicated in a variety of behavioural 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 et al., 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 pre-stimulus 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 (Mathewson et al., 2009; Lundqvist et al., 2013; 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 et al., 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 (Cardin et al., 2009; Carlen et al., 2012; Cho et al., 2015); 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’ vs ‘bottom-up’ attentional processing of sensory input in relation to discrimination vs. detection performance (Buschman and

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 et al., 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 vs. 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 (Sherman, 2001; Ollerenshaw et al., 2014; Harris and Thiele, 2011); however, this remains an open question requiring further investigation.

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Figure Captions

Figure 1. Overview of experimental paradigm and behavioral results. 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 0.01-0.5mm. Each lick during the no-lick period shifted stimulus onset by 5 sec. C: Bright-field photomicrograph (x5) of a coronal section indicating orbitofrontal cortex 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 centre of the image.

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: 2sec). Amplitude of the tactile stimulus is indicated on each lick histogram. Responses to the 0.5mm 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 17 sessions. Error bars represent SEM.

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 orbitofrontal (OFC) and barrel cortex (BCx) power in delta through to gamma frequency bands in a 4 second pre-stimulus time intervals separated by hits and misses for detection of a 0.1 mm stimulus. Error bars represent SEM.

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

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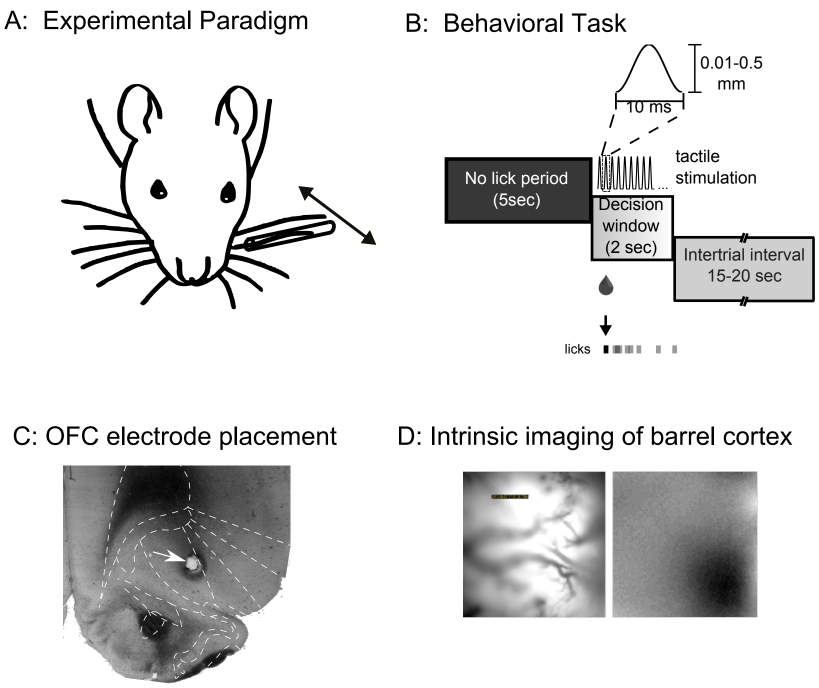

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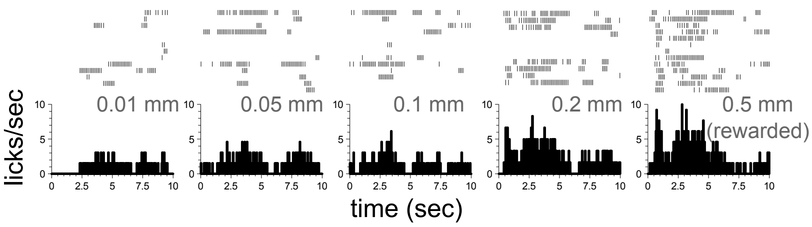
Figure 1

A: Tactile detection behavior



B: Psychophysical response curves

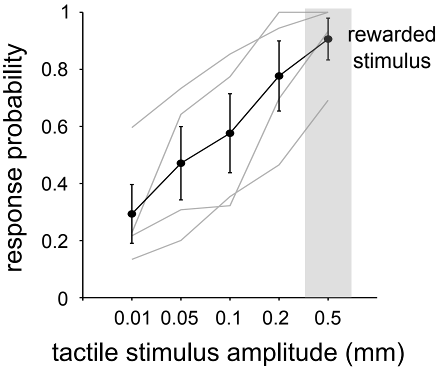


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Figure 2

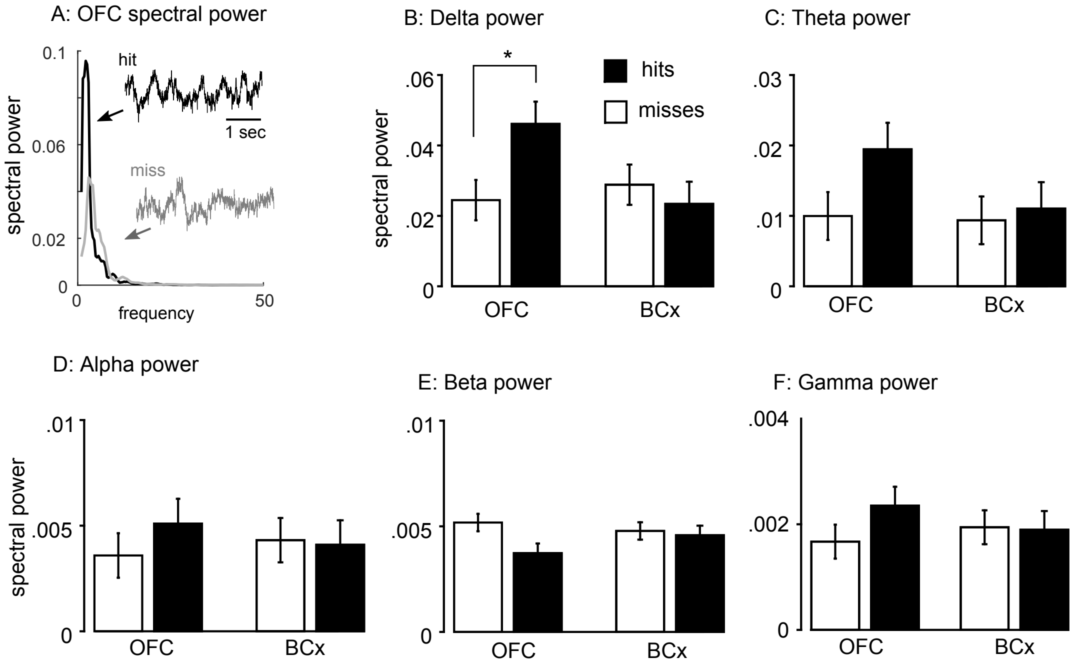

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Figure 3

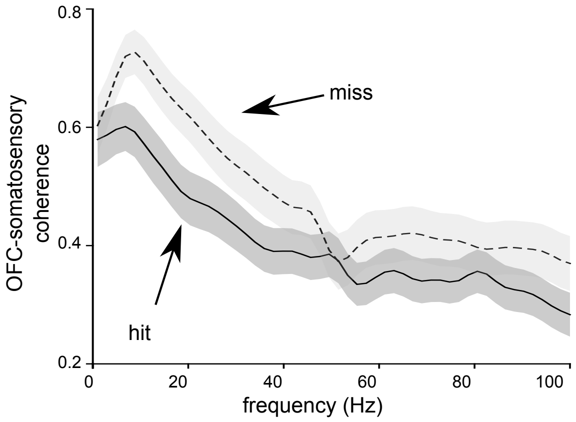

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Figure 4