Computational Neuroethological Approaches to Problems in Social Neuroscience
Robert Liu and Elizabeth Buffalo, Emory University, Atlanta, GA, USA

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Wednesday, July 25
9:00 am - 5:30 pm
Agnes Scott College: Bullock Room 210E

Free Parking is available at the West Parking Deck
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Schedule

9:10-9:15  Elizabeth Buffalo, Emory University and Yerkes National Primate Research Center
          Introduction to the Workshop

9:15-9:30  Larry Young, Emory University and Yerkes National Primate Research Center
          Introduction to Social Neuroscience

9:30-10:00 Hans Hofmann, University of Texas at Austin
          Modules, Circuits, and Networks: Making Sense of Data across Levels of Organization and over Evolutionary Time

10:00-10:30 Robert Liu, Emory University
             Neural Mechanisms of Communication from the System to Sub-Cellular Scale

10:30-10:50 Coffee Break: Bullock Hall Atrium

10:50-11:20 Bruce Carlson, Washington University
             Decoding of Temporal Information in Social Communication Signals

11:20-11:50 Eric Fortune, Johns Hopkins University
             Wired to Cooperate: Neural Mechanisms of Duet Singing in Wrens

11:50-12:20 Asif Ghazanfar, Princeton University
             Vocal Communication Emerges and Evolves Through Coupled Oscillations

12:20-2:00 Lunch – on your own

2:00-2:30 Michael Platt, Duke University
           Neuronal Basis of Giving and Receiving

2:30-3:00 Katalin Gothard, University of Arizona
           Decoding Social Signals from Neural Activity in the Monkey Amygdala

3:00-3:20 Coffee Break: Bullock Hall Atrium
Poster Abstracts

*In vivo* electrophysiology in a prairie vole model of social bonding

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The ability to form positive social relationships is key to mental health [1], and yet the neural circuitry underlying social learning remains poorly understood. Prairie voles, a rodent species that forms life-long bonds with mates, are a canonical animal model of social learning. Much progress on the underlying neurobiology has been made through pharmacological, genetic, anatomical, and behavioral approaches [2], and yet *how brain regions dynamically work together as functional neural circuits during bonding in voles* remains unclear. As first steps towards answering this question, we have 1) exploited the Neurologger (NewBehavior) technology to record neural activity in naturally behaving, socially interacting voles and 2) found preliminary evidence of enhanced functional connectivity between social information processing and reward areas during social interactions leading to bonding. Future work will involve manipulation of neuropeptides implicated in bonding (e.g. oxytocin) to determine their role in modulating functional connectivity. The work emphasizes the prairie vole as a powerful functional-behavioral model in which quantitative neuroethological approaches can be applied to probe the neural mechanisms underlying social interactions.

Acknowledgements
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References
Is the monkey auditory cortex pre-tuned to human speech rhythms?

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Speech has characteristic amplitude modulations (AM) with 3-8 Hz rhythmicity [1], which entrain neuronal theta oscillations in same frequency range in human auditory cortex [2]. Selective abolishment of this low-frequency component of speech AM impairs both the intelligibility of speech [3] and phase-locking of MEG theta (3–8 Hz) signals recorded from auditory cortex [2], suggesting that the common rhythmic structure is important for discretizing packets of acoustic information and pacing inputs to the auditory system. To what extent is this rhythmic coordination between speech and the auditory cortex reflect a human-specific versus general property of the auditory cortex? While the importance of low-frequency acoustic AM for the coding of high-frequency fine structure of synthetic stimuli is known [6], it is not known whether the influence of AM structure on encoding fine structure is limited to a particular frequency band. Here, we investigated the encoding of human speech by the macaque monkey auditory cortex. We used multielectrode recordings from the primary auditory cortex of passively-listening monkeys. The auditory signals were natural human speech and phase-vocoded speech whose rhythm was sped up or slowed down (that is, faster and slower than 3 or 8 Hz) but retained normal fine structure. Multi-unit activity (MUA) from auditory cortex showed the greatest temporal precision and inter-trial reliability for natural versus sped up or slowed speech, in agreement with human behavior and MEG phase-locking results [2]. In contrast, firing rates increased proportionally with speech rate. These data not only provide insights into the local circuit dynamics underlying human speech processing that can’t be measure by neuroimaging techniques, but also suggest that human speech exploited pre-existing auditory cortical processes that are perhaps general to primates or even all mammals.

Figure 1. Auditory cortex MUA during speech perception at varying rates. A. MUA responses to natural speech. The acoustic stimulus waveform is shown in black. Single-trial responses are shown below. B. Population summary of inter-trial correlations (Pearson’s r) as a function of speech rate. Higher (lower) rates indicate sped up (slowed down) speech. Brackets indicate significant differences (p<0.05, t-test).

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References

Neuronal Reference Frames for Social Decisions in Primate Prefrontal Cortex

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One of the most fundamental distinctions in biology is between self and non-self. In humans and some other animals, social interactions further depend on the distinctions between self, non-self, and another individual. Using a reward donation task involving two monkeys [1,2], we investigated the encoding of juice rewards delivered to oneself, another, or no one by neurons in the anterior cingulate gyrus (ACCg), the anterior cingulate sulcus (ACCs), and the orbitofrontal cortex (OFC) of rhesus macaques. In some contexts, monkeys preferred to deliver rewards to the second monkey, whereas in others they preferred to deliver rewards to themselves. These preferences were magnified when the rewards at stake were larger. All three regions contained a substantial number of neurons that were sensitive to reward magnitude independent of who received the reward. Despite these commonalities, neurons in OFC selectively signaled the decision to reward oneself, neurons in ACCs selectively signaled the decision to reward non-self, and neurons in ACCg signaled the decision to reward oneself or another individual. Notably, neuronal responses to self-reward were inversely proportional to non-self-reward in OFC, and self reward responses in ACCg were context-dependent. The coefficient of variation (CV) in firing rates in each area largely corresponded to the reward outcome for which each area was most responsive. These findings reveal distinct neuronal reference frames—self, other, shared—in prefrontal cortical circuits mediating reward-guided decision-making.

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References
Reciprocal circuit between hypothalamic oxytocin and forebrain CRF system: 
Implications for anxiety-like behavior

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Oxytocin is a hypothalamic peptide that is thought to facilitate social behavior, decrease anxiety, and attenuate stress response; as such, it is being considered as a possible treatment for multiple psychiatric disorders including autism, depression, and schizophrenia. Recent work in our lab has revealed the existence of a novel circuit involving a direct interaction between the hypothalamic oxytocin (OT) system and the forebrain corticotropin releasing factor (CRF) system of the bed nucleus of the stria terminalis [1] (BNST). The BNST is involved in stress adaptation and is known to mediate behavioral and autonomic responses to stressors. We have shown that OT neurons of the paraventricular nucleus of the hypothalamus (PVN) express CRF receptor type 2 (CRFR2), and that these OT neurons send oxytocinergic projections to the BNST, where they make broad perisomatic contacts with local CRF neurons, which in turn express high mRNA levels of the oxytocin receptor (OTR). Using whole cell patch-clamp recording in conjunction with single cell RT-PCR, we have data showing that in rats and mice, oxytocin receptor mRNA is also found in another class of electrophysiologically distinct neurons in the BNST that express the mRNA for either enkephalin or neuropeptide Y. Previous single-unit recording studies have shown that local application of OT increased the firing rate of BNST neurons [2], and it is possible that activation of OTR in the BNST may cause a paradoxical increase in anxiety-like behavior due to a direct excitation of CRF neurons. To address this issue we infused the selective OT agonist, [Thr4-Gly7]OT (TGOt), directly into the mouse BNST through bilaterally implanted cannulas prior to behavioral testing in an open field. Our preliminary data suggests that OTR activation in the BNST may indeed increase anxiety-like behavior. Furthermore, to determine whether the circuit is fully reciprocal, we examined whether the CRF neurons in the BNST project to the hypothalamic OT neurons using cell-type specific neuronal tracing. Here, we injected a “floxed” anterograde tracer (rAAV5/EF1a-DIO-mCherry) into the oval nucleus of the BNST (BNSTov) of CRFp3.0CreGFP transgenic mice, which show Cre-dependent expression of a green fluorescent protein (GFP) under the control of the CRF promoter. Two weeks later serial brain sections were analyzed for the presence of dual-labeled fibers in potential projection sites using confocal microscopy. As expected, high GFP-mCherry co-expression was observed in cell bodies of the BNSTov, while dual-labeled fibers were observed in the dorsal raphe nucleus, ventral tegmental area, as well as the PVN. Significantly, CRF-GFP terminals arising from the BNSTov of CRFp3.0CreGFP mice were seen to make contacts with dendrites and cell bodies of OT neurons in the PVN. The reciprocal connection between CRF neurons of the BNST and OT neurons of the PVN suggest that the two neuropeptides can regulate the release of one another. Future studies aim to determine if CRF release from the BNST effects OT release in the PVN and vice versa. Additionally, we aim to explore the behavioral consequences of this reciprocal connection in both anxiety and social interaction paradigms.

Acknowledgements
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Predicting Viewing Patterns in Macaques using Salience Detection and a Random Walk Process

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Natural scenes are complex and composed of many objects. When macaques view natural scenes they choose to focus or fixate on certain objects but not others. Two prominent determinates of object fixation are thought to be social content (e.g. faces) and salience. Salience is defined as object features that are distinct from their background and include color, orientation, and intensity contrast [1]. In order to examine the extent to which macaques’ viewing patterns correlate with regions of high salience in natural scenes, we implemented a salience model to describe each scene. Salience was calculated using a linear combination of color, orientation, and intensity contrast on different spatial scales. An analysis of salience values at each fixation location revealed that fixations occurred in regions with high salience significantly more often than what would be expected by chance (p < 0.05). These effects were strongest towards the beginning of each trial, suggesting that salient objects attract attention and guide the first few fixations in a natural scene. However, salience alone does not fully predict viewing behavior especially towards the end of each trial. In particular, some images contain large regions that are void of salience, yet macaques still show several fixations in these areas. In other images macaques fail to fixate on all of the salient objects. Thus, we propose that a better model of viewing behavior might be to first detect the salient objects in the natural scene and then use the salience to create an environment for a biased, correlated random walk (BCRW). Bias is determined by the local salience gradient and correlation refers to the persistence of movement in the same direction. Features including saccade angles, saccade magnitude, and intra-saccade intervals derived from the behavioral data are modeled as probability distribution functions and integrated into the random walk process to better reflect macaque behavior. Predicting viewing patterns of macaques can help us determine what monkeys find relevant in images, help in the design of images for memory tasks, and inform measures of memory based on where subjects look in a repeated scene.

References
Towards a behavioral and physiological method for validating treatments for autism spectrum disorders

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Dysfunction in the extended amygdala is believed to play an important role in the etiology of emotional and social deficits observed in Autism Spectrum Disorders (ASD). Here we will be working with a rodent model of Fetal Valproate Syndrome, a human condition in which prenatal exposure to the anti-seizure medication valproic acid (VPA, aka Depakote) can cause an ~18-fold greater incidence of ASD than in the general population. Administration of a single dose of VPA to a pregnant rat induces an array of behavioral deficits in her offspring, including delays in social approach and reduced novelty preference consistent with the presentation of ASD in humans. Interestingly, these behavioral changes are accompanied by several physiological hallmarks of ASD, such as increased gamma frequency electrocortical activity, heightened sensitivity to stressful stimuli, and dysregulation of the serotonin (5-HT) system.

Using this model, our lab has already observed major disruptions to the expression of neurotransmitter receptors in the basolateral amygdala (BLA). In particular, pronounced, ectopic expression of the 5-HT1B receptor was seen in BLA principal neurons. We were motivated to explore this observation in our behavioral tests, and discovered an intriguing interaction between the 5-HT changes and anxiety behavior in these VPA rats. While there were no group differences in elevated plus maze behavior at baseline, the mild stress of a saline injection was enough to bring out significantly higher anxiety in the VPA rats. Paradoxically, a 5-HT1B agonist that is usually anxiogenic in control rats was able to normalize the heightened anxiety of the stressed VPA rats, presumably related to the altered expression profile.

We are interested in further exploring the neural correlates of these differences in stress reactivity and anxiety behavior, as well as the reduced preference for novelty in a social interaction test and whether administration of oxytocin may rescue normal social behaviors in VPA-exposed rats. Toward this aim, we are applying two more sophisticated tools: in vivo electrophysiology and recording of ultrasonic vocalizations (USVs). As proof of principle, we will show some simultaneous recordings we have made of USVs and BLA local field potentials (LFPs) in freely moving control rats interacting in this social novelty test. As expected, we have detected an increased number of frequency modulated 50-60 kHz “chirps” during the social interaction phases of the test. However, we have thus far had difficulty identifying a neural correlate of these vocalizations in the time-locked amygdala LFPs. We will present examples and elicit feedback on our analysis methods.
Eye contact, a fundamental building block of social behavior, engages single unit activity in the monkey amygdala

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In primates, the meaningful use of facial signals and eye contact is a prerequisite for normal social behavior. Just by looking at the face of another monkey, an individual can determine its age, sex, dominance status, health, etc. Facial expressions are useful to determine the emotional state and possible intentions of others. Eye contact facilitates affiliative behaviors such as facial mimicry in the context of mother-infant interactions, but also conveys threats and dominance status in adult-adult interactions. The neural circuitry that underlies these behaviors is largely unknown. One goal of our research is to determine the role of the primate amygdala in basic aspects of social communication that involve looking at the eyes of other individuals. To achieve this goal we developed an experimental paradigm that elicits reliably and reproducibly several aspects of social behavior including eye contact, facial mimicry, and gaze following [1]. Additionally, we recorded single unit activity from the monkey amygdala to determine which of these social components (if any) reliably induce neural responses. Species-specific and socially meaningful behaviors were elicited using naturalistic videos that depicted unknown monkeys displaying neutral, agonistic, or affiliative behaviors. Each video contained segments of displays when the movie monkey's eye gaze was directed toward the viewer monkey. The eye movements of the viewer monkey were co-registered with each movie frame and with multiple channels of single unit activity recorded from the amygdala.

We found that 23/123 (19%) of neurons in the amygdala discharged selectively or exclusively when the viewer monkey looked at the eyes of the movie monkey (Figure 1). These neurons had a response latency of 100-150ms from the start of fixation on the movie monkey’s eyes. They exhibited either excitatory (13/23, 57%) or inhibitory responses to looking at the eyes, and either no response (or a polar opposite response) to looking at other parts of the face or body. Higher responses occurred when the movie monkey's eye gaze was directed at the viewer (eye contact) than for averted gaze. A subset of neurons showed phasic responses indicating that eye contact had been established, whereas others showed tonic, sustained changes in firing for the entire duration of the fixation. We conclude that the amygdala is likely an important center for the elaboration of a fundamental building block of social behavior: looking at the eyes of others and establishing eye contact.

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References
Oxytocin selectively reduces attentional bias to negative facial expressions in rhesus monkeys

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Because of its known effect in promoting social behavior, including pair bonding, social recognition and maternal attachment, the neuropeptide oxytocin (OT) has emerged as a leading pharmacotherapy for treating social impairments, such as those seen in autism. However, preclinical studies are necessary to evaluate the long-term effects of chronic OT treatment and its administration efficacy. We examined the effect of OT on social perception in rhesus monkeys using an attentional priming task (dot-probe) that measures subjects’ reaction time (RT) to contact a target when it is either congruent or incongruent with the location of an image (prime) presented 500 ms prior. Three categories of prime pairs were shown in this study, nonsocial images (clip art), neutral faces, and negative facial expression versus scrambled versions of each. Five monkeys were given a 48IU dose of OT or placebo (saline) intranasally, after which they performed 100 trials of the dot-probe task. Similar to humans, subjects demonstrated an attention bias (faster RT) to both the neutral faces and expressions in the placebo condition. Oxytocin had no impact on RT to the neutral faces or nonsocial images, but it significantly slowed monkeys’ RT to the negative facial expressions, p< 0.05. Therefore, OT appears to selectively reduce the automatic attentional bias to negative emotional images in rhesus monkeys, like humans, suggesting a prosocial function.

Early orbital frontal cortex damage alters the way rhesus macaques process species-specific audio-visual vocalizations

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The orbital frontal cortex is a heteromodal association area that receives converging projections from multiple sensory systems and has been implicated in processing affective information. Here, we examined the role of the orbital frontal cortex in processing bimodal species-specific vocalizations using eye tracking in rhesus macaques. The looking behaviors of four adult rhesus monkeys that received neonatal lesions of the orbital frontal cortex (group Neo-Oasp; 2M, 2F) were compared to those of six previously characterized adult, sham-operated rhesus macaques (group Neo-C; 3M, 3F). Two side-by-side videos of unknown male conspecifics emitting different vocalizations were presented with the audio signal matching one video. The percentage of time spent looking at each video was used to assess crossmodal integration ability and the percentages of time spent looking at a priori ROIs (eyes, mouth, rest of each video) were used to characterize scanning patterns. Group Neo-Oasp failed to show a preference for one of the videos when the onsets of the auditory and visual components were synchronized ($p = 0.153$), indicating impairment in crossmodal integration. However, the percentage of time animals looked towards their preferred stimulus video did not vary across groups ($p = 0.286$), and group Neo-Oasp did exhibit a preference when the onset of the auditory component was delayed relative to the visual component ($p = 0.050$). Post-hoc indicated that integration ability was sensitive to the relative identity of the stimulus animals, but not the relative valence of the vocalizations. Group Neo-Oasp showed integration ability in trials comprised of two videos of the same stimulus animal (Identity Same; $p = 0.054$), but not in trials with videos of two different stimulus animals (Identity Different; $p = 0.319$). Analyses of scanning patterns revealed that both groups preferentially attended to the eyes over the mouth and rest of the stimulus videos in Identity Same and Identity Different trials, yet displayed striking differences in overall scanning strategies across trial types. Like group Neo-C, the preference observed in Identity Same trials was associated with a preference for the eyes over the mouth ($p = 0.036$) and the rest of the stimulus video ($p = 0.006$), with a slightly greater preference for the eyes of the congruent stimulus video ($p = 0.064$). The lack of preference in Identity Different trials was characterized by a strong preference for the eye regions of both stimulus videos (congruent = incongruent), which resulted in Neo-Oasp monkeys looking more to the eye regions than group Neo-C ($p = 0.042$). This greater salience for the eyes was consistent with increased aggression, a common trait following damage to the orbital frontal cortex [1-3], and indicated that group Neo-Oasp interpreted the stimuli differently than group Neo-C (e.g. more threatening). Their interpretation of and response to the complex social signals likely interfered with the expression of integration ability. The current results parallel the looking behavior of human children with high aggression [4], and are consistent with a role of the orbital frontal cortex in creating appropriate representations of complex social signals [5].

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References
A Novel Behavioral Task for Assessing Social Attention and Memory in Rhesus Macaques

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Disruptions in attention and memory for socially relevant stimuli are distinctive features of numerous psychiatric disorders, including autism spectrum disorders [1] (ASD), social anxiety disorder [2] and schizophrenia [3]. Particularly in ASD, eye tracking methodologies have proved to be a sensitive way to assess these disruptions, with the time spent fixating faces and objects strongly predicting levels of social competence [4] and cognitive development [5]. By using the same approach in rhesus monkeys, we can begin to investigate the neurophysiological and hormonal mechanisms of social attention and memory that may be disrupted in autism. Previous studies have illustrated the importance of maintaining high ecological validity with realistic social scenes [6], however, studies using realistic scenes also suffer from a number of stimulus confounds that can impair the ability to draw firm conclusions [6].

Here we present a novel variant of a scene memory task that assesses attention and memory for social and non-social items while controlling for item size, number, gaze direction and facial expression. In this task, monkeys freely viewed static scenes comprised of novel objects and unfamiliar rhesus monkeys displaying averted and direct gaze with neutral facial expressions. In each session, ninety novel scenes were each shown twice, with thirty scenes repeated without change, and sixty scenes featuring a manipulation of one scene item. Thirty of these manipulated scenes replaced one monkey in the scene with a different monkey and thirty scenes replaced one object in the scene with a different object.

During the first presentation of scenes, subjects showed a significant preference for viewing monkeys in the scene compared to novel objects ($p<.01$), and spent significantly more time viewing monkeys gazing directly at the subject than monkeys with averted gaze ($p<.05$). Subjects also displayed memory for the scenes by spending more time viewing a novel monkey ($p<.01$) or object ($p<.01$) in the manipulated scenes. This experience-dependent change in eye movements occurred within the first two seconds of viewing, indicating that the subjects rapidly appreciated the change in the scene. The quantitative analysis of these behaviors form the baseline for future experiments investigating the role of oxytocin in social attention and memory, and the neurophysiological correlates of this relationship.

References