EC 490

Lecture 9: Neural observations during games

1. Neuroeconomists have examined neural activity while agents played the range of 'classic' 2-person generic games: Ultimatum games, Dictator games, Trust games, Prisoner's Dilemmas, Inspection games and Matching Pennies. Experimenters have used monkeys, so as to be able to take single cell recordings, and people (under fMRI and TMS).

2. The basic paradigm for observing game play in monkeys was developed at Paul Glimcher's lab at NYU. Monkeys are trained to implement choices by directing their gaze to one member of a set of colored flashes on a computer screen. These choices are sometimes moves in simple games. While the monkeys do this, activity in the lateral intraparietal area (area LIP) is recorded. Neurons in this area encode salience of visual targets, and thereby direct attention to them. They deliver output to parts of the visuomotor system that plan and execute eye saccades. Thus it is hypothesized that area LIP neurons do not compute, but are closely correlated with, the monkeys' decisions about where to look.

3. One of the early breakthrough experiments in neuroeconomics found that, when monkeys played the inspection game, firing rates of LIP neurons were equal for each pure strategy that was mixed in Nash equilibrium. If the neurons were tracking probabilities of movement instead of expected utility, this should not have been observed.

	Inspect	Don't inspect
Work	2, 2	2, 4
Shirk	-2, -2	4, -4

NE = (randomize, randomize)

4. This interpretation of the observations was greatly strengthened by a 2004 experiment in which monkeys learned changing reward values. Trial-by-trial fluctuations in LIP activity correlated with trial-by-trial behavioral estimates of expected utility.

5. Given recent skepticism from behavioral economists about NE as a solution concept that people actually implement – skepticism sounded in the chapter by Sanfey and Dorris – it is striking to find evidence of monkey neurons directly computing it.

6. By looking elsewhere in the visuomotor system, at superior colliculus, convergence to the selected saccade was observed while monkeys played Matching Pennies. Thus the time course of the neural decision can be estimated.

	H	T
H	-2, 2	2, -2
T	2, -2	-2, 2

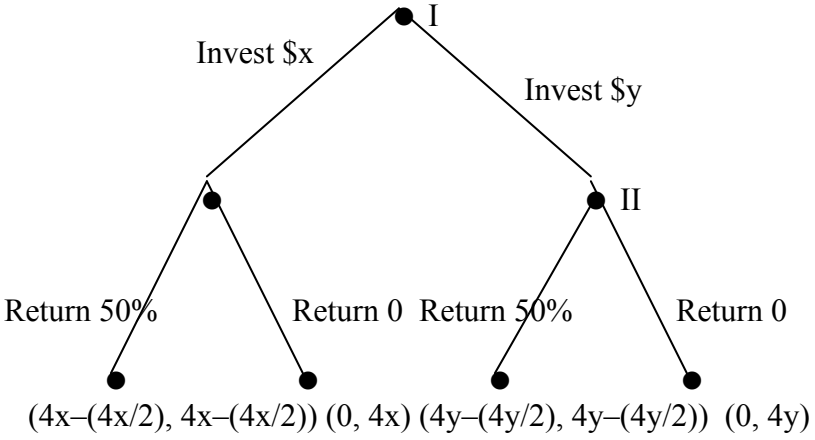
NE = (randomize, randomize)

7. Daeyeol Lee's group have identified dlPFC neurons that fire in correlation with, respectively, choices, consequences of choices, and particular combinations of choices and consequences when monkeys play Matching Pennies. Because these groups of neurons are distributed rather than topographically concentrated, this discovery may be difficult to test in humans.

8. fMRI work with humans indicates that responses of midbrain dopamine neurons scale with reward magnitudes. Thus this is usually a part of the brain that is monitored when people play games in the scanner.

9. Striatum shows increased activation when people experience cooperation (i.e., non-Nash play) in one-shot PDs, and decreased activation when people encounter Nash play. In addition, striatal activity on a given round is associated with higher probability of non-Nash play by that person on subsequent rounds.

10. In a trust game, caudate activity in trustees' brains was found to be correlated with the degree of reciprocity the investor had shown in previous rounds. Most interestingly, in early trials this activity followed investors' decisions, but then a learning effect was observed: the onset of activity shifted, until by later trials it preceded investors' decisions.



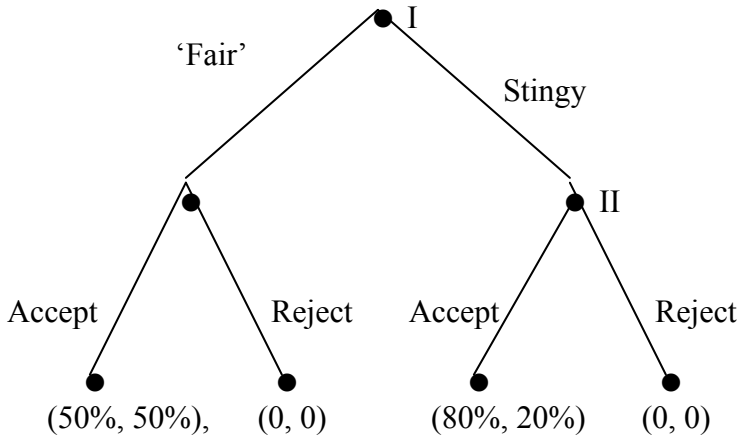
11. In another experiment, investors given an opportunity to pay to punish non-reciprocating trustees showed increased caudate activity when they did so.

12. What is the value of knowing where in the brain some response is coded? It allows one to then watch that area while experimental manipulations are performed. So, in another experiment, TG players were divided into three groups. One group were told morally positive things about their partners, another were told morally neutral things, and the third heard morally damaging stories. Players in groups 1 and 3 showed reduced caudate activity relative to baseline during play, but group 2 did not. Perhaps caudate is involved in processing moral evaluation, something the group 1 and 3 subjects

didn't need to do once they'd been alerted by the stories.

13. In two experiments, striatum was engaged when subjects received money and when they decided to donate money to charity. Activation was enhanced when donations were voluntary rather than forced.

14. Sanfey *et al* examined the brain's response to fair and unfair offers in Ultimatum games. Each participant was introduced to 10 people who would be their partners. 5 offered \$5:\$5 splits. The other 5 offered \$9:\$1, \$9:\$1, \$8:\$2, \$8:\$2 and \$7:\$3 respectively. Players also received 10 offers from a partner they were told was a computer. Players showed significantly greater activation to stingy offers from people than to 'fair' offers and to stingy offers from computers in anterior insula, dlPFC and anterior cingulate. Anterior insula also showed correlation between activity levels and degree of offer stinginess (e.g., more activation in response to \$9:\$1 than to \$8:\$2). Anterior insula has consistently been associated with pain, distress, hunger and thirst. In another experiment, its activation levels predicted retaliation by players who suffered defection in a repeated PD. In the TG, anterior insula activity was correlated, in pooled data, with decisions by subjects to reject offers.



15. Another group of subjects watched films before playing UG. One group watched a sad film, one watched a happy film, and one watched a neutral film. The group that watched the sad film had a significantly higher rate of rejection of stingy offers than either of the other two groups.

16. Two studies used TMS to disrupt processing in dlPFC – associated with goal maintenance and executive control – while subjects played UG. The authors say that "stimulation" increased the rate of acceptance of unfair offers. This would make sense as a result, since we could interpret it as indicating that cognitive reflection helps to suppress responses based on anger. But it doesn't make sense given the experimental procedure, which involved *suppressing*, not stimulating, dlPFC.

17. These experiments we've been reviewing seem clearly relevant to the task of building functional maps of the brain. Do they tell us anything about economics?