Neural Mechanisms of Bias and Sensitivity in Animal Models of Decision Making

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ABSTRACT

Animals perceive stimuli in their environment and are required to make motor responses according to this perception. The perception-to-action mechanisms rely on the accumulation of neural activity in specific areas of the brain that need to reach a threshold in order for the action to be initiated. These mechanisms can be influenced by various types of information and prospective outcomes; that is, contextual factors can speed up or slow down the processes. Here we describe how behavioral paradigms coupled with neural recordings can illustrate two basic features of the speeding up (or slowing down) of the perception-to-action mechanisms. The features are bias (a general increase in decision activity prior to stimulus onset) and sensitivity (a change in the cumulative firing rate up to a decision point). We then propose the direction for future research emphasizing the need to examine bias and sensitivity with a focus on dynamics.

Keywords: Decision-Making, Bias and Sensitivity, LATER Model, Signal Detection Theory, Monkey, Rat

1. INTRODUCTION

There are many opportunities to make decisions in daily life as we choose between several possibilities to gain desirable outcomes. Psychophysics aims to develop mathematical functions that can account for the relation between stimuli and responses in a variety of decision-making contexts. Two well established psychophysical approaches to the study of decision making are Signal Detection Theory [1] and reaction-time models [2]. One important challenge to understanding the neural mechanisms of decision making is to combine these psychophysical models with measurements of neural activity. Predictions from the theoretical models can be tested against what is actually happening within the decision-making areas of the brain. Correlates between neural activity and behavioral measures can then be observed, adding converging validity to theories of decision making. The present paper reviews how several contextual factors (e.g., the prospect of reward) influence decision-making processes, introducing theoretical models, experimental paradigms and neural recordings that form a picture of these processes. The review focuses on two important animal models - monkeys and rats - that afford scientific investigation at a level of detail that, for ethical reasons, cannot be achieved in humans. These animal models of decision making are the focus of translational research, aimed at providing fundamental insights for neuroscience as a whole and for various domains of application (e.g., biomedical engineering, from brain-machine interfacing to neurofeedback).

2. THEORETICAL APPROACHES TO DECISION MAKING

2.1 Signal Detection Theory

One of the most simple decision tasks imaginable is a forced-choice task to determine whether there is a sensory stimulus (signal) or not. For instance, a subject may need to indicate whether a pure tone is present or not against a background of noise [3]. The task employs a simple instruction but often may be hard to perform. In this instance, the subject must answer either “yes” or “no”. The outcome produces an unambiguous measurement of accuracy; the subject is either correct or incorrect. Stating “yes” when there is a signal (i.e., a hit) and stating “no” when there is no signal (i.e., a correct rejection) are the two possible correct responses. Stating “yes” when there is no signal (i.e., a false alarm) and stating “no” when there is a signal (i.e., a miss) are the two types of incorrect responses.

With Signal Detection Theory we can propose that, in order to perceive a stimulus as being present, neural activity that represents the perception of the signal needs to reach a required threshold. However, noise (from the environment or from internal influences) can also produce a degree of neural activity. Importantly, there is a distribution of activity when the stimulus is present that is normally distributed (so in any given trial the activity produced in response to noise could reach a level that overlaps with this distribution). There is also a distribution of activity for noise (again, presumably normally distributed, with a mean less than that of the signal dis-

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tribution). This scheme is illustrated in Fig. 1 (top panel). Signal Detection Theory proposes that the overlap in neural activity in response to noise and signals creates the prospect of incorrect responses. This occurs when a criterion is set so that a certain amount of neural activity will produce a "yes" response. As seen, on some occasions the neural activity will be higher than the criterion in the presence of noise (4), thus creating a false alarm. On other occasions the neural activity in the presence of a signal will be below the criterion for a "yes" response (3), thus creating a miss.

Introducing a reward into this simple paradigm can have two different effects. One effect is that a reward improves the discrimination between signal and noise, either increasing the neural activity in the presence of the stimulus, reducing the neural activity in the presence of noise, or both. All of these options act to increase the sensitivity to the signal and thus increase the likelihood of correct responses (as illustrated in Fig 1; bottom left).

A second potential effect of reward is that it changes the threshold required for a yes response to be stated. That is, the subject becomes 'trigger happy' needing less evidence in order to make the "yes" response (as illustrated in fig 1. bottom right). Theoretically, this can be achieved either by setting the criterion at a lower level, or by increasing the signal and noise distributions equally (i.e., the criterion stays fixed, but both distributions shift to higher levels, creating a general increase; this possibility may be more plausible in terms of neurophysiology). In this instance, although the likelihood of hits increases, there is also an increased likelihood of false alarms. The situation amounts to a general bias in favor of responding "yes".

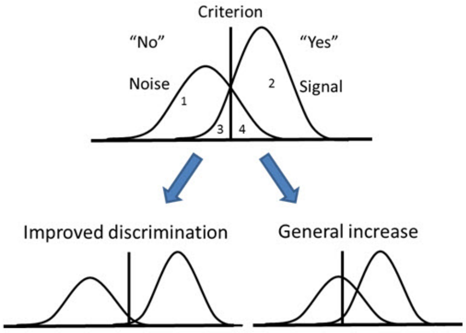

Fig.1: *Signal Detection Theory and the mechanisms of sensitivity ("improved discrimination") and bias ("general increase").*

2.2 A linear model with a cumulative decision signal for the analysis of reaction time

Although Signal Detection Theory has the merits of simplicity, specificity, and testability, it is also limited in its scope, unable to make predictions about reaction time during decision making. An important merit of reaction-time analysis is that it increases the statistical power, especially when considering neural activity on a trial-by-trial basis. The Linear Approach to Threshold with Ergodic Rate model (LATER model) is one model for the analysis of reaction time [4-7] that has proven to be fruitful in studying the mechanisms of bias and sensitivity.

In neural computational models of decision making, every option during a decision task is considered to be represented by a respective node of neural activity [8-11]. This decision-related activity has two distinctive components: a) an accumulation of activity, and b) a decision threshold for the activity to overcome in order for the choice to be made [12-14]. The LATER model is in line with such computational models of decision making, using reaction-time analysis (usually of eye movements) to examine cumulative properties of the decision process (with respect to how reward influences bias and sensitivity mechanism).

Reaction time is defined as the difference in duration between the stimulus onset and the behavioral act (e.g., eye movement towards the stimulus). The important constants affecting reaction time in this model are the cumulative slope of activity leading up to the decision threshold and the starting point of the activity upon stimulus onset (Fig 2. top panel)

There are two possibilities when reaction time becomes clearly faster than in another condition. One is that the slope becomes steeper than in the alternative condition; the other is that the starting point moves closer to the threshold (Fig. 2, bottom left and right, respectively). These two possibilities reflect the hypotheses of sensitivity and bias in the LATER model, respectively [12-14]. The cumulative signal can be inferred from examining the nature of the Gaussian distributions of reaction times across many trials. A reduction in reaction time without a change in the shape of the distribution is indicative of a general bias for choosing one option (due to a general increase in firing even before initiation of the accumulation). A reduction in reaction time with an accompanying change in the shape of the distribution (the proportion of quick trials increasing in relation to slow trials) occurs when the rate of accumulation becomes steeper. Such a shift is indicative of improved sensitivity of the information processing. The LATER model has been shown to predict reaction-time distributions in accordance to bias and sensitivity manipulations, thus providing a reliable approach to investigating cumulative decision mechanisms. Such models are an effective way to infer differences in cumulative signals during various decision tasks.

3. EXPERIMENTS IN MONKEYS

To study the mechanisms of decision making, many neurophysiological experiments have been con-

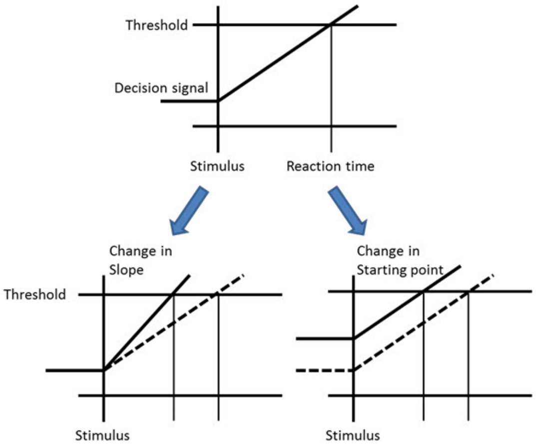

Fig.2: *Decision signal accumulation model and the effect of sensitivity ("change in slope") and bias ("change in starting point").*

ducted with saccade eve movement and manual response paradigms in monkeys. Here, we introduce several methods and paradigms.

3.1 Neural evidence of cumulative decision signals and reward-oriented bias

There is compelling evidence for cumulative decision mechanisms from single cell recordings in the lateral parietal area (LIP) and the frontal eye field (FEF) of monkeys performing perceptual decision-making tasks. Such evidence comes from monkeys that are required to make a saccadic eye movement to target locations in visual space (e.g., a location that is determined by the direction of moving dots [15][16]; or a static target that differs from several distracters [17]). The activity rates of LIP and FEF neurons correspond to specific locations in visual space, with the location-specific firing occurring while an object falls into the receptive field of the neuron. During the decision process of looking toward target locations, a cumulative firing rate occurs in the same location-specific neurons.

Neurophysiological evidence for the existence of a signal decision criterion has been obtained with monkeys in simple perceptual decision-making tasks, involving an oculomotor response to a visual target [18][19]. Hanes and Schall (1996) recorded single-unit activity from the FEF while the monkeys performed a task in which they had to make an eye movement from a central circle to a peripheral target (appearing after a variable interval). The results showed a cumulative firing rate in the FEF. The cumulative firing rate continues until a threshold is reached, at which time the eye movement is generated; that is, movements are always initiated at the moment when the activity level reaches a certain level (e.g., 100 spikes per second), no matter how long it takes for the brain to reach that level (whether it takes 200 or 400 ms). This neural evidence agrees with the LATER model and shows that analyses of reaction times and neurophysiological measures can be used as convergent operations in the study of the mechanisms underlying decision making.

A further component that influences the amount of initial sensory firing is the quantity of stimuli in the visual array. Using single cell recordings in the LIP of monkeys, Churchland, Kiani and Shadlen (2008) found that as the amount of stimuli in the visual array increased, the neural representations of the items were characterized by a smaller firing rate [20]. In terms of a computational decision mechanism, the researchers also found the increase in quantity of stimuli resulted in a slower accumulation of neural activity up to the decision threshold. The accumulation rate correlated with the reaction time for the saccade towards the target in such trials, therefore providing further evidence that a threshold of activity needs to be reached before the movement is initiated. The researchers proposed that the slower accumulation was a result of a requirement to accumulate more evidence over time to accurately decide where to look out of the many competing stimuli.

The basal ganglia have a neural circuit which predicts the availability of reward during the behavioral task [21-23]. Lauwereyns et al. (2002a) recorded single-unit activity from the caudate nucleus during a visually-guided saccadic eve movement task to illustrate a reward-related bias mechanism in decision making [24]. As shown in Fig. 4, the monkey was required to orient the gaze toward the target that appeared. The researchers found that caudate neurons change their discharge rate systematically, even before the appearance of the visual target, usually showing more activity when the contralateral position is associated with reward (Fig. 5). Strong anticipatory activity of caudate neurons with a contralateral preference correlated with decreased latency for eye movements in the contralateral direction. With the LATER model, it can be thought that this anticipatory firing reflects the increased level of activity prior to the onset of the stimulus, so that the cumulative activity takes less time to reach the threshold (as per Fig. 2, bottom right).

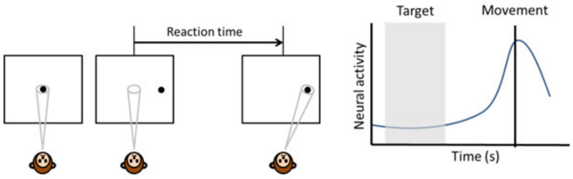

Fig.3: *Experimental design and schematic result of visually-guided saccadic eye movement tasks in monkeys. The neural activity accumulates toward the moment when the movement is initiated.*

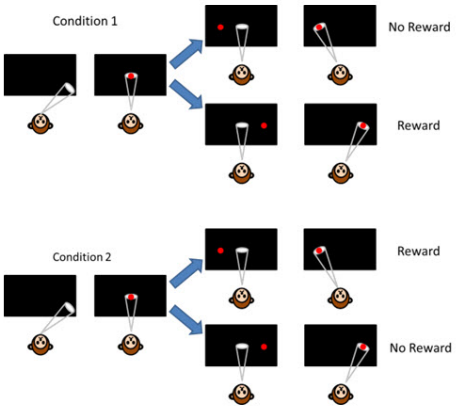

Fig.4: *Experimental design of visually-guided saccadic eye movement tasks with asymmetric reward. Depending on the condition, the monkeys can receive either a reward (Condition 1) or no reward (Condition 2) for a rightward eye movement, while the opposite mapping applies for a leftward eye movement.*

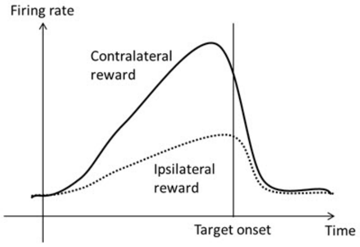

Fig.5: *Schematic illustration of anticipatory activity of caudate neurons, in advance of target onset, reflecting a reward-oriented bias.*

3.2 Effects of relevant and irrelevant information on sensitivity

One way to investigate sensitivity in decision making is to manipulate the significance of noise in the environment. This can be achieved by giving more weight to the items in the environment that are to be ignored. Lauwereyns et al. trained monkeys in a task that required a go/no-go response to stimuli that consisted of different colors and different directions of motion [25][26]. In some trials, when the color was green (for example), the monkey was required to make a go response (manual response) while ignoring the motion direction of the stimulus. On other trials, when the motion direction of the stimulus was up (for example), the monkey was required to make the go response while ignoring the color. The type of trial (color discrimination or motion discrimination) was known to the monkey prior to the trial, via a central task cue. This paradigm produced congruent and incongruent trials (as per fig. 6) such that the color and motion direction implied either matching (congruent) or mismatching (incongruent) responses.

The behavioral results showed that reaction times were slowed and error rates increased during incongruent trials. Furthermore, neural activity from neurons in prefrontal cortex showed three types of coding with respect to go/no-go responses. Some neurons would code for color discrimination only, others for motion discrimination only, and a further set for both color and motion discrimination (i.e., integration cells). Prefrontal neurons have been shown to code for the interpretation of visual information to determine a future action (e.g. where to look or where to move a hand to) [18][27][28]. The prefrontal cortex is therefore a prime area to detect neural evidence of sensitivity mechanisms. Of the three types of neurons in Lauwereyns et al.'s study, the activity of the integration cells correlated with the behavioral response to the stimulus. The slope of the cumulative activity in these cells appeared to be steeper in congruent trials compared to incongruent trials (Fig 7).

It is possible to interpret the slower reaction times and slower accumulation of firing as an increase in noise (due to salient, but conflicting irrelevant information). The features that were supposed to be ignored influenced the decision-making activity of the prefrontal cortex, inhibiting the cumulative activity for the required response. This is a sensitivity mechanism, as the base rate activity is the same at the onset of stimulus presentation, but the cumulative firing toward the response initiation is affected by the noise within the environment.

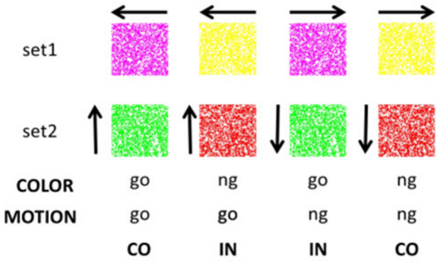

Fig.6: *Experimental design of the Stroop paradigm; monkeys make a go or no-go (ng) response based on either the color or the motion direction, while ignoring the alternative feature. This paradigm produces congruent (CO) and incongruent trials (IN).*

4. EXPERIMENTS IN RATS

Experiments with rats for the purpose of investigating the neuroscience of decision making are advantageous in many ways. Rats imply smaller ethical and economical costs as compared to monkeys; rats represent an animal model compatible with studies that require a large sample (e.g., pharmacology) and with studies that aim to connect to molecular and genetic avenues of investigation. The present section turns to decision-related paradigms that can be employed with rats.

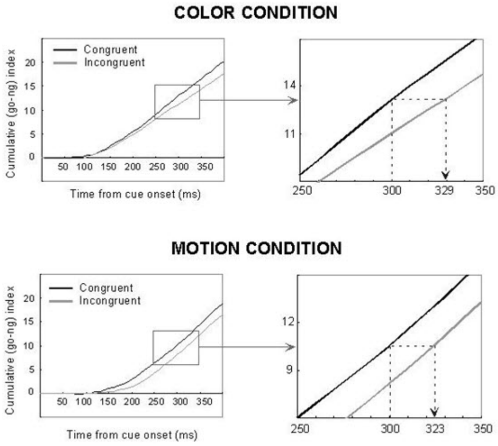

Fig. 7: *The population activity response of integration cells in congruent and incongruent trials, showing different gradients of accumulation as a function of the signal-to-noise ratio. More noise (i.e., competition from irrelevant information) leads to reduced sensitivity, less efficient accumulation, and slower reaction times.*

4.1 Nose-poke paradigm to analyze reaction time

For reaction-time analysis to investigate bias and sensitivity mechanisms in animals, it is important to maintain a starting point of behavior before the response to the stimulus. In eye movement tasks with monkeys, it is easy to control this by fixating the head and eye position before the onset of the stimulus, whereas these fixations are difficult to achieve with rats. However, a nose-poke paradigm is adequate for the purpose of controlling the behavior of rats. Tasks using nose-poke paradigms have successfully been conducted in several experiments (e.g. location-cueing tasks [29], five-choice serial reaction-time tasks [30]).

Lauwereyns et al. developed an asymmetric reward paradigm including nose-poking fixation (Fig. 8) to examine how reward magnitude affects reaction time [14]. In all trials, the rats had to poke their noses into the hole to the left or to the right of center, corresponding to the side at which 4 lights were illuminated, while ignoring distracters on the other side (Fig. 8). Reaction times were faster for large-reward trials compared to small-reward trials (Fig. 9, left). In large-reward trials, there was no influence of the number of distracters, whereas in small-reward trials, a greater number of distracters produced an increase in reaction time. The results suggest that the rats' reaction times were at maximum speed in the direction associated with a large reward, regardless of the level of visual stimulation on the other side. For the further reaction-time analysis, the researchers drew a reciprobit plot (Fig. 9, right). This analysis provided evidence of a swivel in the slope of the linear line; the swivel was indicative of a bias effect.

Thus, this paradigm has successfully combined reaction time and the LATER model as a technique to illustrate the influence of bias (as a result of reward magnitude) on the decision-making process in rats.

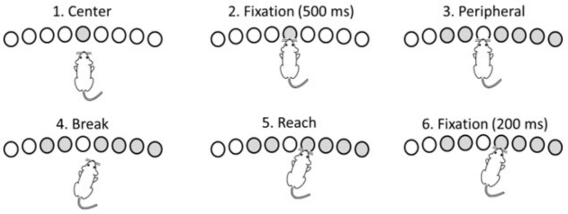

Fig. 8: *Experimental design of the asymmetric reward task in a nose-poke paradigm for rats; the rats are required to choose the side where 4 LEDs are illuminated regardless of the number of illuminated LEDs on the other side. The reward schedule is independent of the visual stimulation, with one side designated as the large-reward side, the other as the small-reward side.*

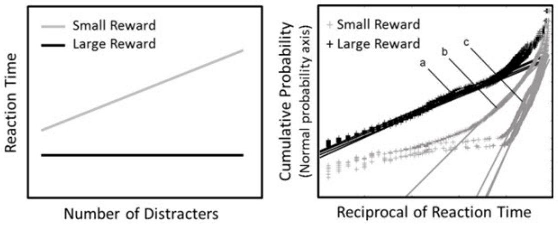

Fig. 9: *Reaction-time data (left) and LATER analysis (right) obtained with the asymmetric reward task in rats.*

4.2 Hippocampal activity during fixation in a memory-guided spatial alternation task

It has long been established that the hippocampal memory system plays a crucial role in the organization and maintenance of episodic information in spatially defined contexts [31]. Researchers have focused on the function of "place cells" in the hippocampus, whose activity levels track locations and signal physical changes in the spatial environment [32-34]. However, Ainge and his colleagues provided data of hippocampal animals showing memory deficits in a spatial alternation task with a T-maze paradigm that included a forced waiting period between trials [35]. The result implied that the hippocampal activity during this period might be crucial for spatial choice, and suggest a crucial difference in the hippocampal neural mechanisms between an active exploratory (i.e., mobile) stage and a fixated waiting (i.e., immobile) stage [36-38].

For the purpose of analyzing the neural activity during this immobile waiting period, Takahashi et al. developed a memory-guided spatial alternation task including a fixation period during nose poking [39][40]. The paradigm can effectively control factors affecting the hippocampal activity (motion, position and head angle [32]), and thus provides a unique opportunity to study covert spatial processing. Takahashi and his colleagues recorded single-unit activity and local field potentials (LFPs) from hippocampal area CA1 during fixation in the spatial alternation task.

The researchers observed fixation-dependent neurons in hippocampal CA1 that showed a preference in their firing rates for a specific behavioral sequence (from-LEFT-to-RIGHT or from-RIGHT-to-LEFT trials). The activity of these neurons may code covert spatial information of the behavioral sequences, and shows commonalities with the anticipatory activity observed in caudate neurons during the saccadic eye movement task [24]. Furthermore, the relationship between the spike timing of these neurons and theta rhythms (8 to 10 Hz in rats) showed a phenomenon reminiscent of theta phase precession [41][42]. The spikes tended to occur at the positive peaks of the ongoing theta oscillation at the beginning of the fixation period, whereas they shifted about 180 degrees and occurred at the negative trough toward the end of fixation [43]. It is known that two major, mutually exclusive streams of input reach CA1: from entorhinal cortex (EC) and from CA3, corresponding to the peak and trough of the theta cycle, respectively [44-46]. Thus, the theta phase shift of the spike timing may indicate that the hippocampus propagates different types of information toward downstream structures during the fixation period.

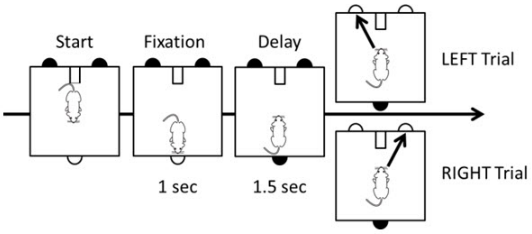

Fig.10: *Experimental design of the memory-guided spatial alternation including a fixation period.*

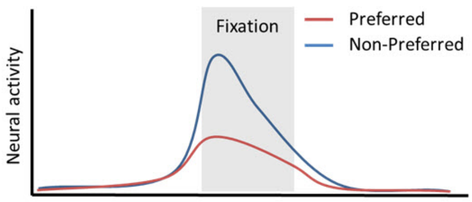

Fig.11: *Population histogram of sequence-dependent fixation neurons in hippocampal area CA1.*

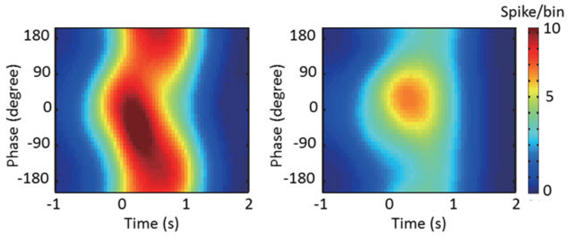

Fig.12: *The relationship between fixation neuron spikes and the theta phase.*

5. FUTURE WORK

The findings described in this paper have illustrated how bias and sensitivity mechanisms can be measured, coupling behavioral paradigms with neural recordings. The future research now needs to closely examine just how sensitivity and bias is dynamically formed.

To study such dynamics, we recently devised a behavioral paradigm consisting of an initial learning phase, followed by a "transition test," which included a novel stimulus (Nishida et al., *in press* [47]). Two groups of rats were trained to perform a nose poke into a central hole upon the illumination of an LED inside the nose-poke hole. One group would receive a food pellet as a result of a correct nose poke ("App-Only"; appetitive conditioning only). The other group would also receive a food pellet but would additionally avoid a foot shock as a result of a correct response ("App-Av"; appetitive and avoidance conditioning). Once this task had been learned, the rats were subjected to a new context: A second LED would illuminate inside a peripheral hole at the same time as the central LED. Any subsequent nose poke into the central hole would have the same result as before. However, if that rat was to nose poke into the peripheral hole, it would be rewarded with 3 food pellets (and avoidance of a foot shock for the second group). Traditional operant-conditioning models would predict that the S-R bond for the central LED will be stronger for the second group as they are receiving two types of reinforcement (food delivery and shock avoidance); therefore they should be less likely to explore the peripheral hole. However, our findings showed that the second group shifted their preference to the peripheral hole sooner than group 1, who worked only for food delivery (Fig. 13).

Rats in Group 2 were exposed to a more complex environment (with the food rewards and foot shock avoidance). Thus it was advantageous for these rats to disambiguate the uncertain properties of their environment. This may have motivated them to seek additional information in order to build a coherent cognitive map of the environment. This paradigm, coupled with the existing neural findings of hippocampal activity during decision making, can

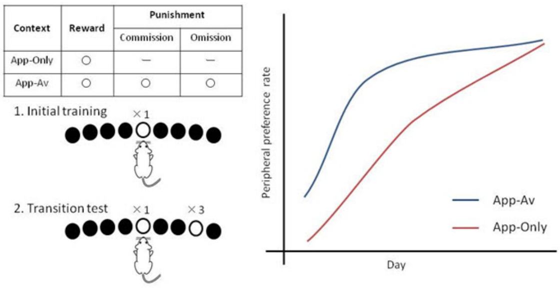

Fig.13: *Experimental design and result of transition test. Rats who worked for food delivery as well as foot-shock avoidance (App-Av) were faster to make the transition to the peripheral option than rats who worked only for food delivery (App-Only).*

be used to assess the dynamics of bias and sensitivity as they are formed from trial to trial. Preference will shift from the central hole to the peripheral hole, at which point the neural signature of this shift can be captured. Findings from such a study will provide detailed online analysis of bias and sensitivity mechanisms and could prove to be fruitful in the development of further paradigms using rats, reaction time, and neural recordings as correlates of decision-making mechanisms.

Future research will benefit from converging rat behavioral paradigms with neural recordings. Animal models offer the opportunity to examine single unit recordings in carefully controlled laboratory settings. Specifically rat models afford an increase in subject size while lowering the cost (both financially and ethically) compared to monkey studies. The end goal is to provide a framework of bias and sensitivity mechanisms during dynamic decision making in a changing environment. This will build on existing models of bias and sensitivity mechanisms while increasing the external validity of these models in accordance to real-life, dynamics environments.

6. ACKNOWLEDGMENT

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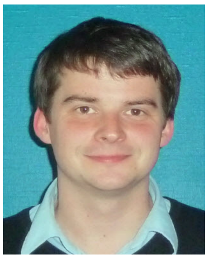

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