Decision Making in Mice (*Mus musculus*) Using Two-Dimensional Binary Choice Sets

Philipp Burt, Clara Jongen[†]and Julia Joos[‡]

Humboldt-Universität zu Berlin*

29

30

31

32

33

34

35

36

Abstract

1

Models of decision making have 2 traditionally assumed a rational 3 decision maker who will always try 4 to maximize the return currency. 5 However, various findings breach 6 with the idea that decisions are 7 made solely on the basis of rational, 8 economic principles. One possible 9 explanation for this breach is that 10 the cognitive process of translating 11 perceived values of an option from a 12 physical to a cognitive scale happens 13 in a nonlinear fashion. In this study 14 we analyzed choice behavior in mice 15 by investigating reward evaluation 16 with respect to the dimensions 17 of reward" "amount and 18 "propability to receive a reward". To 19 this end, we designed a two 20 alternative forced choice experiment 21 presenting individual mice with 22 differently rewarding options using 23 water from two water feeders as 24 reward. We exposed the mice to four 25 with incongruent contexts and 26 neutral setups of reward dimension 27 parameters to test if noneconomical 28

behavior could be observed. Our results show that the mice did not use absolute reward evaluation. Furthermore, the mice were only efficient in making economically correct decisions when exposed to options that varied in volume but not in probability.

1 Introduction

he study of animal decision making 2 is a useful method for the study of 3 L economic decision making in humans 5 (Kalenscher and van Wingerden, 2011). 6 Traditionally, decision making models have 7 assumed a rational decision maker who 8 will always opt for the most profitable In this context, profitability is 9 option. 10 understood as an optimization process of 11 maximizing benefits and minimizing costs 12 (Schuck-Paim and Kacelnik, 2002). In 13 natural environments, options usually vary 14 in multiple dimensions. For example, an 15 animal might have to decide between a 16 foraging option A offering vast amounts of 17 food on an infrequent basis and a foraging 18 option B offering few amounts of food with 19 certainty.

20 A common approach that allows 21 comparisons between options varying in

^{*}philippburt@googlemail.com

[†]clara.jongen@student.hu-berlin.de

[‡]julia.joos@web.de

22 multiple dimesions is the assumption that 23 animals use value based decision making. 24 In this model, the decision maker assigns 25 weights to each dimension and derives a 26 single value for each option. Options are 27 thereby reduced to a common currency 28 referred to as utility. Assuming a rational 29 decision maker this concludes that the 30 common currency will be maximized 31 within the decision process. In evolutionary 32 terms the common currency for an animal 33 has been assumed to be Net Energy Gain 34 (NEG) or Fitness Level. Therefore, an 35 animal will always try to optimize its 36 energy intake or reproductive opportunities 37 (Stephens and Krebs, 1986).

38 However, recent studies have questioned 39 the idea that humans and animals use 40 rational based decision making. Various 41 observations show that humans as well as 42 other animals do not always make 43 economical decisions (Cnaani et al., 2006; 44 Kahneman and Tversky, 1979; Shafir and To understand how 45 Yehonatan, 2014). 46 noneconomical behavior can be explained, 47 it is necessary to look at the cognitive 48 aspects involved in the reward evaluation 49 process. In order for an animal to evaluate 50 rewards by value, it needs the ability to 51 store obtained values in memory and it 52 needs the ability to discriminate between 53 options by the sensory information 54 obtained. This requires a translation from 55 the physical quantities of a reward to 56 cognitive information (Nachev et al., 100 caloric value into account, its decision 57 2013a,b). The relationship between physical 101 might differ from the optimal decision due 58 and cognitive scales has been a major 102 to the impact of the priority dimension. For 59 research area within the field 60 psychophysics and is has been found that 104 beween nectar rewards in bumblebees is 61 the translation is often nonlinear (Nachev 105 priorily influenced by sucrose concentration 62 and Winter, 2012). Comparisons between 106 rather than by NEG (Cnaani et al., 2006). 63 options could occur on a physical or a 107 One advantage of comparative decision 64 cognitive scale which has to be accounted 108 making 65 for, when forming theories of decision 109 computational

66 making. Context can have a strong impact 67 on the value assigned to an option on a 68 cognitive scale, while context would not 69 affect the physical quantities of an option. 70 For example, a food deprived animal 71 presented with a specific food reward 72 might later prefer this specific reward over 73 a food reward of higher caloric potential. 74 The information obtained in the food 75 deprivation context might have been 76 processed in a way so that the animal will 77 continue to prefer this reward over other 78 more rewarding options in the future. This 79 example illustrates, that physical reward 80 information are not sufficient to fully 81 understand the processes involved in 82 decision making. Context-dependent 83 reward evaluation has been intensively 84 studied in starlings as well as in 85 hummingbirds and honey bees (Bateson 86 et al., 2003; Kacelnik and Marsh, 2002; 87 Pompilio and Kacelnik, 2010; Shafir et al., 88 2002).

89 Due to the insufficiency of the absolute 90 reward evaluation model, various have *91* alternatives been proposed. 92 Comparative reward evaluation assumes, 93 that animals base their decisions on a 94 priority dimension and only use in 95 dimension comparisons (Shafir et al., 1993; 96 Shafir and Yehonatan, 2014). Comparative 97 reward evaluation would explain 98 noneconomic even behavior because 99 though the animal might take overall of 103 example, it was shown that deciding

is that it requires less thus effort, reducing 110 processing costs which could be beneficial 154 absolute reward evaluation and were able 111 for an animal. Comparative and context 155 to 112 dependent reward evaluation offer possible 156 intensities chosen for each dimension they 113 explanations why objectively economic 157 should prefer the option that yielded the 114 behavior not always is 115 (Kahneman and Tversky, 1979; Shafir et al., 159 condition was tested for one day, followed 116 1993; Shafir and Yehonatan, 2014).

117 Since we cannot directly measure subjective 161 results are in accordance with 118 cognitive representations 119 researchers have instead 120 measuring behavioral output (Nachev et al., 164 mice decisions were only economically 121 2013b). In order to broaden our knowledge 165 efficient when forced to decide between 122 of when and how 123 uneconimically, it is necessary to study a 167 dimension. 124 broad range of species.

125 Mice are fairly closely related to humans, 126 show similar brain organization and 127 economic behavior. Therefore, studies with 128 mice could provide valuable insights to decision processes 129 human making 130 (de Visser et al., 2011; Zschummel, 2014).

131 The hypothesis that we test in the present 132 study is that mice do not use absolute 133 reward evaluation as it has been observed 134 in bumblebees, starlings, humans and other To this end, we designed a 135 species. 136 two-alternative forced choice (2AFC) 137 experiment presenting the mice with two 138 differentially rewarding options. The 139 rewards were provided by two water 140 feeders that differed in the probability to 141 give water and the water volume of a single 142 reward. Naive mice have been observed to 143 prefer probability over volume (Nachev, 144 personal communication). In the present 145 study we used non-naive mice that had 146 previously similar been used in 147 experiments. Assuming a learned certainty 148 of eventual food rewards within the 149 laboratory context we expected the mice's 150 preference of probability over volume to 151 decrease. We exposed the mice to four 152 different contexts creating incongruent and 153 neutral parameter conditions. If mice used

distinguish between the relative observed 158 better average volume output. Each 160 by a reversal to avoid side biases. Our our of rewards, 162 hypothesis and show that mice do not use focused on 163 absolute reward evaluation. Furthermore, animals behave 166 options that varied only within the volume

1 Methods

2 Experimental Setup

3 In our experiment we used 8 female 4 non-naive laboratory mice of the strain 5 C57Bl6/NHsd. The mice, which were 20 6 weeks of age, had been used for similar 7 behavioral experiments before.

8 The mice were housed isolated in 9 individually ventilated cages (IVCs). Each 10 cage contained two water feeders which 11 would be activated through nose pokes, 12 while the water volume and reward 13 probability could programmed be 14 individually. The recorded information 15 comprise the nose pokes on each feeder, 16 together with a time stamp, the duration of 17 each event and whether a reward was given 18 or not. Further details on the cage setup as 19 well as on the handling of the mice are 20 found in Becker et al. (2016) and Clos et al. Differing from the experiments 21 (2016). 22 performed in those studies, we did not add 23 any time delay or timeout. We also 24 removed any separating walls between the 25 feeders as we had observed them to cause 26 strong left side biases.

27 Our experiment was designed, executed

28 and pre-evaluated as a collaborational work29 together with Sophie Leineweber, Falk30 Mielke and Nicola Vallon.

31 The experiment was designed so that the 32 reward volumes differed between the two However, relative volume 33 feeders. 34 intensities were kept constant throughout 35 the experiment and only the reward 36 probabilities were varied instead. For the 37 reverse experiments we swapped the 38 parameters between the left and right 39 feeder. The general idea was to subject the 40 mice to four different setups in regard of ⁴¹ the relative intensity ratio for volume $I_r(v)$ ⁴² and probability $I_r(p)$. In all our setups the 43 probability dimension opposed the volume 44 dimension so that the greater reward 45 volume was combined with the lower 46 probability and vice versa. We created three 47 incongruent setups, where the $I_r(p)$ 48 differed from the $I_r(V)$ and one neutral 49 setup where the $I_r(p)$ was equal to the 50 $I_r(V)$ (Table 1). The relative intensities were 51 calculated on the basis of equation 1.

$$I_r(x) = \frac{|x_1 - x_2|}{\frac{x_1 + x_2}{2}} \tag{1}$$

with x: conditions on the differentfeeders

⁵⁴ We decided on the relative intensities to use
⁵⁵ in accordance with a psychometric curve
⁵⁶ obtained from previous experiments
⁵⁷ (Nachev and Rivalan, personal
⁵⁸ communication), fitted with a Weibull
⁵⁹ distribution (Weibull, 1951) (Figure 1).

60 Experimental Schedule

61 The mice were split into two groups of four
62 mice, participating on our experiment for
63 nine days one group at a time. Before the
64 actual experiment started, the mice were
65 given one day to adapt to their cages,
66 without any differences on the reward



Figure 1: Psychometric function based on which the relative intensities were chosen. The relative intensities were chosen to cover the slope of the function, chosen values are indicated by different symbols for both used dimensions.

Table 1: Experimental setup, chosen values for the relative dimensions for volume and probability.

$I_r(V)$	$I_r(p)$	$I_r(p)/I_r(V)$	Setup	
0.8	0.0	0.0	incongruent	
0.8	0.5	0.6	incongruent	
0.8	0.8	1.0	neutral	
0.8	1.1	1.4	incongruent	

⁶⁷ volume between the feeders and a
⁶⁸ probability of one on both. Afterwards, the
⁶⁹ four setups were applied in a random order
⁷⁰ thus that ascending and descending orders
⁷¹ of relative intensities were avoided and no
⁷² mouse would get the same setup as another
⁷³ on the same day. Each setup was followed
⁷⁴ by its reversal the next day, to avoid side
⁷⁵ biases.

76 For the first group of mice, reward
77 probabilities between 0.26 and 0.9 were
78 chosen. Since we observed a lack of
79 learning behavior we lowered the
80 probabilities for the second group to values

81 between 0.1 and 0.35, hoping to thereby82 enforce learning behavior. The exact values83 are listed in Table 2.

Table 2:	Values f	or volum	e and	probability	for
both gro	ups of mi	се			

Feeder	Volume	Group 1	Group 2
	[ml]	Probability	Probability
1	6	0.3	0.15
2	14	0.3	0.15
1	6	0.5	0.25
2	14	0.3	0.15
1	6	0.7	0.35
2	14	0.3	0.15
1	6	0.9	0.35
2	14	0.26	0.1

84 At 4 pm each day the new set of 85 experiments was started, the mice then had 86 water access under the listed conditions for 87 18 hours, during their nocturnal phase. To 88 better understand the behavior of our mice, 89 we captured two mice on video under 90 infrared light during one night.

91 Data Analyses

⁹² We collected and distributed our data using
⁹³ an SQLite database (Hipp et al., 2015) as
⁹⁴ well as a GitHub account (GitHub Inc.,
⁹⁵ 2015). Data Analysis has been done using R
⁹⁶ (R Core Team, 2015).



Figure 2: Structure of the database used for data analysis, which has been set up by Falk Mielke. The data as well as our analysis are accessible through GitHub as referenced below.

97 The collected data can be accessed via 98 https:

99 //github.com/falkm/mus_oeconomicus.

100 The structure of the database is presented 101 in Figure 2.

1 Results

2 Throughout the experiment all mice showed
3 strong side biases while the side preferences
4 varied for different mice. The alteration of
5 the settings for the second group of mice
6 even increased those biases. Mathematically,
7 we broadly eliminated them by averaging
8 over reverse experiments. However it is not
9 possible to fully dispose of other influences
10 besides the different rewarding options.

¹¹ As can be seen on our video footage, the ¹² mice regularly poked repeatedly at the ¹³ same feeder or sometimes switched freely ¹⁴ between feeders, as there were no walls to ¹⁵ hinder them. This behavior has been ¹⁶ captured on video (see Appendix). In ¹⁷ consequence we excluded events which ¹⁸ occurred within a threshold of 4 seconds ¹⁹ from the prior event.

20 Learning behavior

21 We had planned to analyse the learning 22 behavior by calculating the cumulated 23 water intake over time or trials for the
24 different mice under the varying settings.
25 However, in the majority of cases, our
26 results do not indicate a clear learning
27 behavior over one testing period (one day
28 each).

29 Instead, we did a changepoint analysis, 30 using the approach proposed by Gallistel 31 et al. (2004), by firstly calculating the 32 cumulated sum of events at the feeder with 33 the higher water volume (V_+) over trials, 34 then calculating the change points and 35 subsequently the slopes between them 36 (Gallistel et al., 2004). A changepoint in this 37 context is the point where the behavior 38 changes, indicated by a change in the slope. 39 It is calculated for each point as the earlier 40 point that deviates maximally from the 41 straight line between the start of the record 42 and the latest point. For this calculation the 43 R function "cp_wrapper" from the package 44 "cpdetectorr" has been used (Nachev, 2015). 45 We applied a binominal test with a decision $_{46}$ criterion of p=0.15. The slope between the 47 last two change points (the last relevant 48 slope) was used for further analysis. As an ⁴⁹ event at the feeder V_+ counts plus one and 50 an event at the feeder V_{-} counts as zero, 51 ideally a steep slope would be expected if 52 the volume favored side provides the 53 (objectively) better option and a flat slope 54 otherwise. An exemplary fit is illustrated in 55 Figure 3.

⁵⁶ For further analysis, we averaged the ⁵⁷ respective last slopes over those from the ⁵⁸ reversed experiments and then plotted our ⁵⁹ data for the $I_r(p)$ (Figure 4). Even if single ⁶⁰ mice adapted diversely to the different ⁶¹ conditions, overall no significant variance ⁶² can be detected (using ANOVA, binominal). ⁶³ A mean slope around 0.5 indicates that the ⁶⁴ feeders on average had been chosen ⁶⁵ randomly. There is no exception for any ⁶⁶ condition. However, the data are widely



Figure 3: Exemplary changepoint analysis with equal probability on both feeders, cumulated sum of events at volume favored feeder. In this case, a change in the mouse's behavior after approximately 100 trials can be observed. This is reflected in the stepwise learning curve.

67 scattered for any condition that was tested,68 and individual mice reacted differently to69 the same conditions.

70 The absence of a clear learning effect in
71 conjunction with the strong side biases led
72 us to examine the explorative behavior of
73 our mice over an expanded period of time,
74 supposing they might integrate over longer
75 timescales than the duration of one
76 experimental setting (one day).

77 Therefore, for each day and each mouse, we 78 calculated the ratio of events at the less 79 frequented feeder to events at the preferred 80 one. Then for each day, counting the day a 81 mouse started to participate in the 82 experiment as day one, we averaged over 83 the event ratios from the different mice. 84 Figure 5 illustrates how these mean ratios 85 changed over the days of the experiment.

86 A higher mean events ratio means that the
87 mice were more explorative that day. As
88 illustrated by Figure 5(a), if averaged over
89 all 8 mice, the mean events ratio decreases
90 over the days of experiment, meaning that
91 the mice explored less over time. In Figure



Figure 4: Slope analysis for different $I_r(p)$. Dots represent single datapoints, each color represents one mouse. The economical choices would have been: Feeder V_+ for $I_r(p) = 0.0$ and $I_r(p) = 0.5$ (slope > 0.5), feeder V_- for $I_r(p) = 1.1$ (slope < 0.5) and both feeders equally for $I_r(p) = I_r(V) = 0.8$ (slope \approx 0.5). Nonetheless no significant variance could be detected (tested with ANOVA). A mean slope around 0.5 indicates that the feeders on average had been chosen randomly.

92 5(b) and 5(c) the two groups of mice are 93 presented separately. Since there were only 94 4 mice in each group, no statistical 95 approaches can be made for those two 96 separate groups. Even so, we wanted to 97 examine the behavior of each group 98 because the lower probabilities, which have 99 been used as parameter settings in the 100 second group, might have influenced the 101 mice's behavior crucially. The plots indeed 102 indicate that group 1 is mainly responsible 103 for the decrease over time in 5(a) while no 104 clear conclusion on the explorative 105 behavior over time for group 2 is possible. 106 All in all, the mean ratios for group 2 are 107 lower than in group 1 and the explorative 108 behavior possibly even increased over time.



(c) Averaged over group 2

Figure 5: Exploration behavior over days of the experimental phase, illustrated by the ratios of events and their standard deviation. (a) Events ratio - averaged over all 8 mice - decreases over the days of experiment. (b) Events ratio averaged over the 4 mice from group 1, who seem to be mainly responsible for the decrease over time in (a). (c) Events ratio averaged over the 4 mice from group 2. No clear tendency over time, mean ratios are lower than in group 1.

109 Efficiency

¹¹⁰ Due to the lack of a clear learning effect, we
¹¹¹ decided against a psychometrical anaysis.
¹¹² Instead we calculated the efficiency of the
¹¹³ mice under the different reward parameter
¹¹⁴ conditions, regarding the dimensions
¹¹⁵ Volume and Probability as well as the
¹¹⁶ combination of the two dimensions,
¹¹⁷ Volume×Probability.

118 To calculate the efficiencies, we first 119 calculated the sum of the infimum, 120 supremum and actual drinking the 121 performance over the events for volume, 122 probability and the combination of both 123 (volume×probabiliy). The infimum being 124 the lowest possible value the mouse might 125 have chosen, the supremum being the 126 highest possible value and the actual 127 drinking performance being the option the We then 128 mouse actually did choose. 129 calculated the efficiency index using A high efficiency index 130 equation 2. 131 indicates that the mice did prefer the better 132 option in regard to the chosen dimension, a 133 negativ index indicates that the mice 134 prefered the other one while an index 135 around 0 indicates that the mice treated 136 both options equally.

$$\eta(x) := 2 \times \frac{x - inf(x)}{sup(x) - inf(x)} - 1 \quad (2)$$

137 with $\mathbf{x} \subset \{V, p, Vp\}$

138 The results are presented in Figure 6.

139 While there is no significant difference in 140 the efficiency index, in regard to the 141 dimension probability for each 142 $I_r(p)/I_r(V)$ the index stays around 0 -143 there is a difference in regard to the 144 dimensions volume and 145 volume×probability. The smaller the 146 $I_r(p)/I_r(V)$, which means an $I_r(p)$ near 0, 147 the more efficient were the mice in regard 148 to the dimension of volume, while they



(c) regarded dimension: volume×probability

Figure 6: Efficiencies for different $I_r(p)/I_r(V)$, regarding (a) probability, (b) volume and (c) volume×probability. The results indicate that the mice treat the dimension of probability randomly and only distinguish for volume if $I_r(p)/I_r(V) \approx 0$. Regarding the combined dimensions, the mice are highly inefficient, when $I_r(p)/I_r(V)$ is highest. 149 started choosing randomly if the $I_r(p)$ 150 increased. Regarding the combined 151 dimensions volume×probability this means 152 the mice have been efficient for a 153 $I_r(p)/I_r(V)$ around 0 but are highly 154 inefficient for a $I_r(p)/I_r(V)$ around 1.4 155 where the $I_r(p)$ is largest. Nonetheless, the 156 data again are widely scattered and single 157 mice performed differently.

1 Discussion

2 Our findings support the initial hypothesis 3 that mice do not use absolute reward 4 evaluation. If so, they would have been 5 expected to choose the altogether more 6 profitable option frequently more 7 throughout all tested conditions. However, *s* as our efficiency analysis shows (see Figure 9 6), this was not the case. Not choosing the 10 economically correct option more often 11 than other options based on a universal 12 "currency" has also been observed in other 13 species (Bateson et al., 2003; Cnaani et al., 14 2006; Shafir et al., 2002). The universal 15 currency to compare different options 16 across various dimensions is usually NEG, 17 as is the case for our experiments, because 18 the mice only eat when having access to 19 water.

20 Slope analysis revealed that, on average, all 21 mice did choose both available reward 22 options as if by chance and independently 23 from relative intensity of probability. This 24 observation was also apparent in the 25 efficiency analysis, solely when 26 probabilities of both feeders where equal 27 did the mice choose the economically more 28 profitable option more frequently and thus 29 achieved an above average total water 30 intake. This behavior implies that, for equal 31 probabilites, they were able to discriminate 32 between the offered options and identify 33 the more rewarding choice. As this was not 34 the case for the other settings, we could 35 assume that our mice were not able to 36 discriminate the offered choices when 37 probability came into play. This unability 38 could be due either to the introduction of 39 another dimension or, in particular, that 40 this dimension was probability. However, 41 in earlier experiments mice were able to 42 differentiate between choices that differed 43 in probability (Zschummel, 2014; Nachev 44 and Rivalan, personal communication). explanation for 45 Another the lower 46 efficiencies associated with the probability 47 dimension could be that the mice were able 48 to discriminate between the offered options, 49 but the differences were not relevant to However, it should seem more 50 them. 51 reasonable to assume that discriminating 52 between probabilities rather than differing 53 volumes would be important to mice, as the 54 water sources encountered in natural 55 environments do not require a good ability 56 to discriminate volume due to their usually 57 large amount of water (Zschummel, 2014). 58 Alternatively, the observed behavior could 59 have been driven by influences unrelated to 60 our setup and thus uncontrollable by us. 61 Such influences can rarely be ruled out 62 completely when studying mice, as they 63 are complex animals, though well-studied, 64 and their behavior is often obscure.

65 It is noteable that the mice tested in the first 66 week explored the offered choices more in 67 the earlier days of testing, with an 68 increasing side bias towards the end of the 69 experimentation phase (Figure 5b). The 70 mice tested in the second week were less 71 explorative altogether and did not show a 72 decrease or increase in their exploration 73 behavior over time. The higher exploration 74 habit in the mice of week 1 might indicate 75 that they integrated the rewards over a 76 longer period than one day and came to 77 choose one favorite feeder after some time.

79 exploration behavior between the two 123 physical effort for the mice to reach the 80 groups could have been the altered 124 feeders could be considered, e. g. placing 81 conditions. In the first week, the mice 125 the feeders further apart or making them 82 might not have felt pressured enough to 126 less accessible by placing them higher up. 83 choose a preferred feeder, because they 127 This way the mice would have to climb up 84 received sufficient water from both feeders 128 first (which they are able to, as can be seen 85 regardless of treatment. In the second 129 in the video footage) and therefore would 86 group, however, due to much lower 130 require much more effort and energy to 87 probabilities the pressure to select an 131 access the feeder, which could presumably 88 option was considerably higher and 132 lead to a greater desire to make the 89 therefore the mice from week 2 might have 133 economically right choice. Additionally, to 90 been forced to reconsider their choice more 134 prevent repeated nose pokes, a delay of 91 often. Another strategy which could be 135 rewards rather than probability could be 92 considered influential here is win-stay; a 136 introduced, or, an activation key added, 93 more explorative behavior during the 137 resultinh in the necessity to carry out 94 beginning of an experimental phase, as has 138 another activity first to activate either one 95 been observed for the mice from week 1, 139 of the feeders, e. g. another poke hole 96 has been found for rats in an earlier study 140 located somewhere else in the cage. 97 (Moustgaard and Hau, 2009). For the mice 141 Furthermore, future studies should include 98 of the second week, which had already 142 congruent settings, as this might shed light 99 been exposed to another choice-experiment 143 on the discrimination ability of mice 100 in the prior week, it could be possible that 144 regarding different dimensions. If mice still 101 they had already developed a win-stay 145 do not perform above average with 102 strategy during the preceding experiment, 146 congruent settings, this would mean that 103 which they applied in our experiment. 147 the lower efficiency for all settings 104 However, as the mice in general did not 148 including a relative intensity of probability 105 perform well in discriminating between 149 over zero in this study, is due to the 106 offered options and thus choosing the more 150 introduction 107 rewarding one, other factors have to be 151 dimension. Since we do not know if the 108 considered. Side preferences were apparent 152 underlying reason for the lacking efficiency 109 in all mice, but do not generally distort the 153 regarding all settings including a relative 110 results as long as sampling still occured - 154 intensity of probability over zero, is the 111 assuming, of course, that the mice based 155 introduction of the dimension 'probability' 112 their decisions on the used dimensions.

114 stronger need to choose between options, 158 several different dimensions. To conduct a 115 the initial short walls between the nose 159 psychometric 116 poke-holes could be reintroduced to 160 dimensions 117 separate each hole and another short wall 161 congruent conditions, with the relative 118 could be added instead of the long wall 162 intensity for one dimension set to zero 119 from the initial setup. This way, the mice 163 constantly, while varying the I_{rel} of the 120 would not be able to just sit in front of the 164 other. 121 feeders and switch between them without 165 Keeping the mice in single cages could

78 A possible reason for the differing 122 much effort. Other changes to increase the

of another (random) 156 or only the introduction of another 113 Still, to reduce side bias and enforce a 157 dimension, the mice should be tested with analysis, both used should be tested with

20

21

22

23

24

have also influenced them in some way; on
the one hand, they were not in competition
with other mice for the water rewards,
which might have led them to decide more
freely. On the other hand, they could still
see the neighboring mice through the
plastic walls of their cages which might
have had an influence. Furthermore, mice
are social animals, therefore keeping them
in single cages might affect their (choice)
behavior.

177 Summary

178 As hypothesized earlier, our results show 179 that mice do not use absolute reward 180 evaluation. To find out, if mice can 181 superiorly discriminate volume rather than 182 probability or if incongruent conditions or 183 the mix of two dimensions blocked the 184 ability to discriminate proability, further 185 research is necessary.

1 References

- 2 Bateson M, Healy SD, Hurly TA (2003). Context-
- 3 dependent foraging decisions in rufous
- 4 hummingbirds. P Roy Soc London
- 5 270:1271-1276

⁶ Becker E, Eltner F, Kraft J, Mieske P (2016). Mice
⁷ exhibit side-biased behavior in a decision-

8 making task under risk. Gruppe 1B

9 Clos C, Haas K, Jusyte M, Púčiková V (2016). Assessment of immediate and long-term 10 advantages and disadvantages of mice on 11 a RGT-inspired gambling task. Gruppe 1A 12 13 Cnaani J, Thomson JD, Papaj DR (2006) Flower choice and learning in foraging 14 bumblebees: effects of variation in nectar 15 volume and concentration. Ethology 16 112:278-285 17

18 de Visser L, Homberg JR, Mitsogiannis M, Zeeb19 FD, Rivalan M, Fitoussi A, Galhardo V,

van den Bos R, Winstanley CA, Dellu-Hagedorn F (2011) Rodent versions of the iowa gambling task: opportunities and challenges for the understanding of decision-making. Front Neurosci 5:109

25 Gallistel CR, Fairhurst S,Balsam P (2004)
26 The learning curve: implications of a
27 quantitative analysis. P Natl Acad Sci USA
28 101:13124-31

29 GitHub Inc. (2015) GitHub. https://github. 30 com/

- 31 Hipp R, Kennedy D, Mistachkin J (2015) SQLite32 (Version: 3.10). SQLite Development Team
- 33 Kacelnik A, Marsh B (2002) Cost can increase
 preference in starlings. Anim Behav 63:245–
 250

36 Kalenscher T, van Wingerden M (2011) Why
37 we should use animals to study economic
38 decision making - a perspective. Front
39 Neurosci 5:82

- 40 Moustgaard A, Hau J (2009) Introduction of
 41 habits in rats by a forced-choice procedure
 42 in T-maze and the effect of pre-test free
 43 exploration. Behav Process 81:104-107
- 44 Nachev V (2015) cpdetectorr: Change point45 estimation from sequences of choices.
- 46 Nachev V, Stich KP, Winter Y (2013) Weber's law,
 47 the magnitude effect and discrimination
 48 of sugar concentrations in nectar-feeding
 49 animals. PloS one 8:e74144
- Nachev V, Thomson JDJ, Winter Y (2013)
 The psychophysics of sugar concentration
 discrimination and contrast evaluation in
 bumblebees. Anim Cogn 16:417-427
- 54 Nachev V, Winter Y (2012) The psychophysics
 55 of uneconomical choice: non-linear reward
 56 evaluation by a nectar feeder. Anim Cogn
 57 15:393–400

58 Pompilio L, Kacelnik A (2010) Contextdependent utility overrides absolute 59 memory as a determinant of choice. P Natl 60 Acad Sci USA 107:508-12 61 Kahneman D, Tversky A (1979) Prospect 62 theory: an analysis of decision under risk. 63 Econometrica 47:263-291 64 65 R Core Team (2015) R: A language and environment for statistical computing. 66 R Foundation for Statistical Computing, 67 Vienna, Austria 68 Schuck-Paim C, Kacelnik A (2002). Rationality in 69 risk-sensitive foraging choices by starlings. 70 Anim Behav 64:869-879 71 72 Shafir EB, Osherson DN, Smith EE (1993) The Advantage Model: A Comparative 73 Theory of Evaluation and Choice under 74 Risk. Organ Behav Hum Dec 55:325–378 75 Shafir S, Waite TA, Smith BH (2002). Context-76 dependent violations of rational choice 77 in honeybees (Apis mellifera) and gray 78 jays (Perisoreus canadensis). Behav Ecology 79 Sociobiol 51:180-187 80 81 Shafir S, Yehonatan L (2014) Comparative evaluations of reward dimensions in honey 82 bees: evidence from two-alternative forced 83 choice proboscis-extension conditioning. 84 Anim Cogn 17:633-644 85 Stephens DW, Krebs JR (1986) Foraging theory. 86 87 Princeton University Press Weibull, WA (1951) Statistical Distribution 88 Function of Wide Applicability. J Appl 89 Mech 90

91 Zschummel, M (2014) Discrimination of
92 reward-volumes and -probabilities in *Mus*93 *musculus*.

1 Appendix

2 Video

3 http://amor.cms.hu-berlin.de/~mielkefa/Sem9/CEB/20151208_165418_Mouse83all.mp4

• At 10:40 repeated nose poking behavior and feeder changing can be observed.

5 Source Code

```
6 The
         relevant
                    source
                              code
                                      for
                                             this
                                                                         through
                                                    paper
                                                             accessed
7 https://github.com/Claartje/ceb_paper_1/tree/master/paper/relevant%20Code
9 The code for the calculation of the mean events ratios is given as an example below:
10
12 ## in this example, the dplyr way is chosen.
13 require('dplyr')
14
15 ##### database connection #####
16 ## go to the folder of the current file
17 setwd(dirname(parent.frame(2)$ofile))
18
19 ## load the SQL interface helpers
20 source('../../database/SimplerSQLQuery.r')
21
22 ## connect the database, in this case you choose to return a dplyr tbl object
23 sql_connection <- SQL_TBL$new(drv = RSQLite::SQLite(),</pre>
24 dbname = "../../database/data.db")
25 if (!sql_connection$connected) print ("something went wrong! no connection.")
26
27 # print(sql_connection$tables)
28
29 ## load the tables with master data
30 experiments = sql_connection$LoadTable("Experiments")
31 schedule = sql_connection$LoadTable("Schedules")
32 days = sql_connection$Run("SELECT day_nr,
33 start_date,
34 block FROM Days;") # alternative: run an SQL query
35
36 ## load the data table
37 events = sql_connection$LoadTable("Events")
38 events$date_time <- as.POSIXct(strptime(events$date_time, "%Y-%m-%d %H:%M:%S"))
39 # (unfortunately, SQLite is incapable of reliable date/time handling.
40 # Was saved as string.)
```

```
41
42 mice = sql_connection$LoadTable("Mice")
43
44 ## when everything's done with SQL:
45 sql_connection$Close()
46
48 #merge tables
49 alldata <- merge (experiments, schedule) %>%
50 merge(days)%>%
51 merge(events)%>%
52 merge(mice)
53
54 #Count Number of events
55 data<-alldata%>%
56 filter(exclude==F)%>%
57 group_by(day_nr,mouse_nr,side)
58
59 eventsSummary<-summarise(data, length(event_duration_s))
60
61 #filter for events on left and right side
62 eventsLeft<-eventsSummary%>%
63 filter(side=="1")%>%
64 group_by(day_nr,mouse_nr)
65
66 eventsRight <- eventsSummary %>%
67 filter(side=="r")%>%
68 group_by(day_nr,mouse_nr)
69
70 ####Calculate ratio events
71 # divide number of events on less prefered side
72 # through number of events on prefered side
73
74 eventsRatio<-(ifelse(eventsLeft$`length(event_duration_s)`>
75 eventsRight$'length(event_duration_s)';
76 eventsRight$'length(event_duration_s)'/eventsLeft$'length(event_duration_s)',
77 eventsLeft$'length(event_duration_s)'/eventsRight$'length(event_duration_s)') )
78
79 eventsRatio<-data.table(cbind(eventsLeft$day_nr,eventsLeft$mouse_nr,eventsRatio))
80 names(eventsRatio)[1]<-c("day_nr")</pre>
81 names(eventsRatio)[2]<-c("mouse_nr")</pre>
82
83 #split tables for mice of first and second week
84 eventsRatio_mice1<-eventsRatio%>%
```

```
85 subset(mouse_nr==1|mouse_nr==2|mouse_nr==3|mouse_nr==4)%>%
86 mutate(day_nr=day_nr-1)
87 eventsRatio_mice2<-eventsRatio%>%
88 subset(mouse_nr==5|mouse_nr==6|mouse_nr==7|mouse_nr==8)%>%
89 mutate(day_nr=day_nr-9)
90
91 ###calculate mean events ratios
92 #for mice of first week
93 mean_mice1<-eventsRatio_mice1%>%group_by(day_nr)%>%
94 summarise(mean=mean(eventsRatio),
95 st_deviation=sd(eventsRatio))%>%
96 mutate(lower=mean-st_deviation,
97 upper=st_deviation+mean)
98
99 #for mice of second week
100 mean_mice2<-eventsRatio_mice2%>%group_by(day_nr)%>%
101 summarise(mean=mean(eventsRatio),
102 st_deviation=sd(eventsRatio))%>%
103 mutate(lower=mean-st_deviation,
104 upper=st_deviation+mean)
105
106 #calculate mean ratio over mice of all weeks
107 meanMice<-full_join(eventsRatio_mice1,eventsRatio_mice2)%>%
108 group_by(day_nr)%>%
109 summarise(mean=mean(eventsRatio),
110 st_deviation=sd(eventsRatio))%>%
111 mutate(lower=mean-st_deviation,
112 upper=st_deviation+mean)
113
115 require('ggplot2')
116
117 # Plot for all mice
118
119 meanMice %>% ggplot(aes(day_nr,mean)) +
120 xlab("Day number") +
121 ylab("Mean ratio of events") +
122 scale_x_continuous(breaks = 1:9) +
123 geom_point()+
124 geom_errorbar(aes(ymin = lower,
125 ymax = upper))->meanMicePlot
126 print(meanMicePlot)
127 ggsave( sprintf("meanMice.pdf")
128 , plot = meanMicePlot
```

```
129, width = 16
130, height = 12
131 , units = "cm"
132, dpi = 150
133 , device = cairo_pdf
134 )
135
136 #Plot for mice of first week
137
138 mean_mice1 %>% ggplot(aes(day_nr,mean)) +
139 xlab("Day number") +
140 ylab("Mean ratio of events") +
141 scale_x_continuous(breaks = 1:9) +
142 geom_point() +
143 geom_errorbar(aes(ymin = lower,
144 ymax = upper))->meanMice1Plot
145 print(meanMice1Plot)
146 ggsave( sprintf("meanMice1.pdf")
147 , plot = meanMice1Plot
148, width = 16
149 , height = 12
150 , units = "cm"
151, dpi = 150
152 , device = cairo_pdf
153)
154
155 #Plot for mice of second week
156
157 mean_mice2 %>% ggplot(aes(day_nr,mean)) +
158 xlab("Day number") +
159 ylab("Mean ratio of events") +
160 scale_x_continuous(breaks = 1:9) +
161 geom_point() +
162 geom_errorbar(aes(ymin = lower,
163 ymax = upper)) -> meanMice2Plot
164 print(meanMice2Plot)
165 ggsave( sprintf("meanMice2.pdf")
166 , plot = meanMice2Plot
167 , width = 16
168, height = 12
169 , units = "cm"
170, dpi = 150
171 , device = cairo_pdf
172)
```

List of Figures

1	Psychometric function
2	Database
3	Exemplary changepoint analysis
4	Slope analysis
5	Exploration behavior over time
6	Efficiencies for different $I_r(p)/I_r(V)$
List of 7	Tables

1	Experimental setup	4
2	Values for volume and probability for both groups of mice	5

Role Assignment

	Author	1. Reviewer	2. Reviewer
Abstract & Introduction	Philipp Burt	Clara Jongen	Julia Joos
Methods & Results	Clara Jongen	Julia Joos	Philipp Burt
Discussion & References	Julia Joos	Philipp Burt	Clara Jongen