Bachelor thesis

State dependent valuation

August 2009
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Introduction

Choices are made constantly and numerous times every day. But how are these decisions made? How and why are there sometimes suboptimal choices made?

If there is a choice made, there is a preference for one of the options. But why would there be preference for something? If you think about the evolutionary purpose of preference there must be preference for the thing that is the best option for you. So can you use preference to determine the most valuable reward for the animal? Or can preference be fooled? Can preference be an irrational thing?

In state dependent valuation a preference changes towards the sometimes suboptimal choice. The studies I have compared deal with these kind of state changes and preferences. My criteria for using the articles where, only animal studies, non- pharmaceutical behavioral studies and in the experimental design the state had to be changed in training and in the choice situation.

Conventional learning

Before state dependent learning or valuation can be discussed the question "what is learning?" has to be answered.

There are a lot of examples of learning and of the purpose of learning.

If there is not a lot of food available it becomes useful to learn to find food and to learn this quickly. If there is a lot of food is not very necessary to learn to find food and to learn this quickly. This is a case of variable in motivation. If the motivation is high the animal will be more eager to learn.

Another kind of learning is habituation, learning not to respond or respond different to a stimulus. If the stimulus is learned not to be threatening the fright response will not be present after some trails. Imprinting is also a kind of response altering learn experience. A chick response in first instinct with signs of fear to a salient object but after a while this response is replaced with another very different response, following and pecking at the object.

These three kinds of learning are direct stimulus response effects. There is also another way of learning the pairing of events.

The Pavlov reaction is an example of classical conditioning. The reaction that does not require special training is the unconditioned response, UR. The stimulus that triggers the UR is the unconditioned stimulus, US. If the animal in the case of the Pavlov reaction begins to secrete saliva not because the US but because the light is on, the light is the conditioned stimulus, CS, and the response is conditioned response, CR, because it is an conditioned reaction. The animal does not have to do anything. With the other type of conditioning, instrumental or operant conditioning the actions of the animal are very important for learning. (Bolhuis 2005)

State dependent valuation

Work ethics, sunk costs, Concorde fallacy and state dependent preference are terms for preferences based on the link between the options history and preference instead of only the expected payoffs. In state dependent valuation is the past state dependent gain more important than the actual properties of the possibility (Pompilio 2005). This kind of valuation can be a mechanism to deal with the different kinds of information, the information about the state gain and the properties of the option (Pompilio 2008). The outcome of this decision is sometimes suboptimal because of the conflicting information about the option. Reward X is e.g. bigger but reward Y has more previous gains because this one was given under higher deprivation. Which one is the best one? This is not a very easy decision to make, the mechanism underlying state dependent valuation is maybe the best way to deal with this kind of decision making, despite the occasional suboptimal choice(Pompilio 2005).

An example to make the hypothesis more clear is if you have two individuals, one is rich, the other is poor and give them both 1000 euro. The fitness gain for the poor person is much bigger than the gain for the richer person(Pompilio 2005 crossreff Bernouilli 1738) . The actual properties of the reward do not differ between the two subject but the gain, the remembered value, is significantly different. If you can vary the state within one person to the rich and poor condition and than give him or her the 1000 euro. If you than later give them the choice between the two rewards, it is likely he or she will choose the one with the higher fitness gain. With money it is a bit difficult to do this because a human being knows what he or she gets when given 1000 euro. Also the state manipulation is not ideal because for the training and learning the individual needs to be in the two different states, and to make someone believe he or she is rich or poor when this is not really the case can be challenging. But it is a simple example to show how the curve (figure 1) and remembered value works.

If you use the same principle in animals the easiest way to manipulate state is to change de energy reserves.
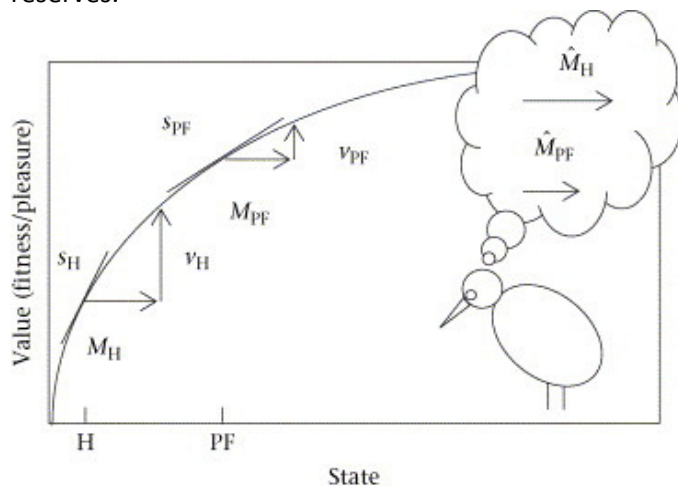

Figure 1. state and value curve (Pompilio 2005)

Figure 1 shows the state gain value (V_h for hungry V_{pf} for prefed), the state gains (S_h and S_{pf} for hungry and prefed) and the food source (M_h and M_{pf}). The remembered value is presented as M_h and M_{pf} above the bird in the inset.

Results.

Most of the studies I compared obtain results supporting the state dependent valuation mechanism hypothesis. Only two studies both done by Capaldi suggest the opposite (Capaldi 1982, 1983). One of the really interesting results is the results for a starling study, the starlings preferred a longer delay over a shorter one if this was learned under high deprivation. The result was not explained with perception distortion, the starlings did know the difference between the delays (Pompilio 2005). Another interesting result is the long lasting effects of coffee preferences, 10 days even if the rats where exposed to both substances constantly (Revusky 1974). The preferences for wintergreen and cinnamon persisted even 28 days (Capaldi 1983). The effects of a learn preference is long lasting. The various experiments show that the found results are not due to; calorie density (Capaldi 1983), a very small meal during high deprivation (Capaldi 1983), preference for hard work instead of the reward (Marsh 2003) or the familiarity with the substance (Revusky 1974).

The difference between the flavor preference, low deprivation cue preferred, and the position preference, high deprivation cue preferred, is remarkable (Capaldi 1982). The hypothesis stated by Capaldi (1982) is that the position is instrumental learning, stronger learning with high deprivation, and the flavor cues are not.

There are effects of learning, when starlings have one more day of training the effects are stronger (Marsh 2003).

Pompilio (2005) proposed 4 hypothesis for the outcome of the experiments.

- magnitude priority
    - if this is the case there will be no difference in preference because the magnitude of the rewards is the same.
- Value priority
    - The choice is based on past gains, so the low state (high food deprivation) will be preferred
- State priority
    - The choice is based on past states, so then the high state (low food deprivation) will be preferred more.
- State option association
    - The choice will be the choice associated with the same state during training. So if the animal is in low state during testing it will choose the option learned in training linked to the low state.

Only the second one was not rejected in the 2005 and 2006 study (Pompilio 2005,2006).

Results in different presentation

All the following figures are for the date obtained by Capaldi (1982) in the 2nd experiment in the paper.
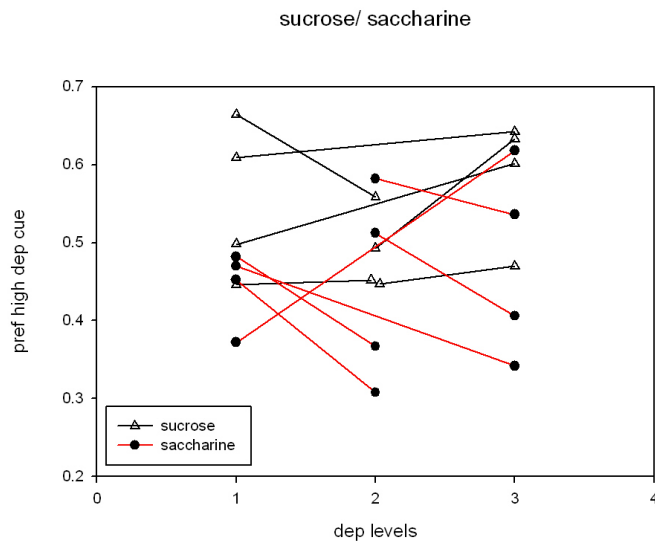

Figure 2. preferences for high deprivation cue in 1:low 2:medium 3:high deprivation for cues dissolved in sucrose or saccharine. Data for Capaldi 1982.

In figure 2 the preferences are shown for saccharine and sucrose, what is striking is that all the saccharine, except one, preference decline if the deprivation level increases. In the sucrose this is not the case, some increase the preference others the preference is lower and in two cases there is not much difference.
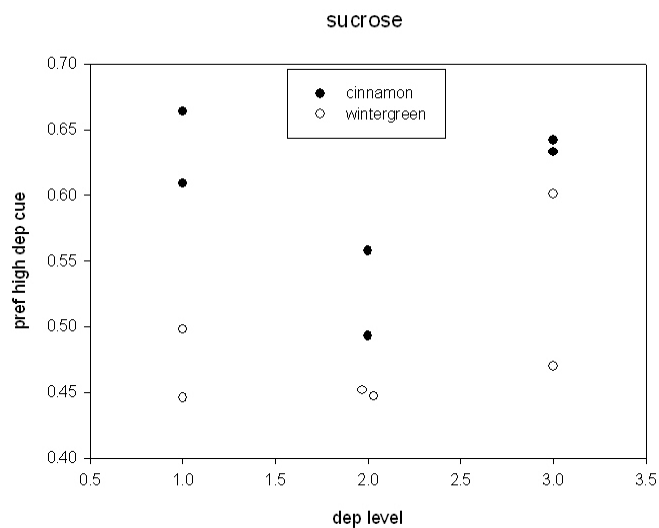

Figure 3. the preferences for the different flavors high deprivation cue dissolved in sucrose in 1:low 2:medium 3:high deprivation.

In figure 3 the preferences for the different flavors dissolved in sucrose are plotted, the preference for cinnamon is higher in all the cases, so this can influence the preferences in the choice test. The preference has to be learned, if there is a strong preference for one of the two flavors this can be difficult. The effects of learning must overrule the preference in the beginning. And if one of the flavors is disliked to get a preference can also be difficult, so if there is a taste bias the results are not totally reliable.

Discussion

The 4 hypothesis

If you test the state dependent valuation with rewards that have equal calories, there are 4 different predicted outcomes in preference (Pompilio 2005, 2006).

- magnitude priority
    - if this is the case there will be no difference in preference because the magnitude of the rewards is the same.

This is only true if the animal does not alter the digestion to the state where the animal is in. if the animal can get more nutrients out of the same reward if the animal is more deprived this hypothesis is not correctly rejected.

- Value priority
    - The choice is based on past gains, so the low state (high food deprivation) will be preferred

If the curve as suggested by Pompilio (2005,2006) see figure 1. is not the correct one this is maybe also not the case.

- State priority
    - The choice is based on past states, so then the high state (low food deprivation) will be preferred more.

If the animal links the saccharine, non-nutritive, solution with the state instead of with the state change gain this can explain the results found in Capaldi's study (1982).

- State option association
    - The choice will be the choice associated with the same state during training. So if the animal is in low state during testing it will choose the option learned in training linked to the low state.

Preference for hunger cue was higher when test deprivation was also higher in the Capaldi (1982) study. This is the only result that suggest matching of the state when the preference is learned and state when the choice is given.

Other remarks

Capaldi (1982) hypothesized that the preference for the low deprivation cue could be due to the fact that a small taste of food while high deprived had more averse effects than a small taste during low deprivation. In the 1983 publication the hypothesis is rejected because the same preference was found if the rats got 13 calories instead of a small taste. The calorie density of the cues is also of no influence on the preference. If poly glucose was added to the solutions the preference did not change (Capaldi 1983).

Another problem with the way the experiments are done is that it is know that if the animal is higher deprived the animal learns better and faster (Marsh 2003).So this can be a problem because the cues have to be learned equally well. But if learning is asymptotic the differences are very little if the animals are trained enough (Marsh 2003). Also consumary learning of the flavors is probably not instrumental and has the higher deprivation no influence on the learning (Capaldi 1982).

In the model proposed by Marsh in 2003 the remembered gain in fitness is more important than the actual gain. If the animal is in poorer conditions the gain of a reward is bigger than when the animal is in richer conditions (Pompilio 2005 crossref Marsh 1999).

The problem with the experiment done so far is the link between the cue and the deprivation level is not clear. It is not clear if the cue is linked to the state (Capaldi 1982) or to the fitness gain (Pompilio

2001, 2005, 2006, Aw 2008) or to the after effects (Revusky 1967). Also how the cue is linked to the one or more of these hypotheses are not clear.
 Maybe it is a combination of all 3, and the proportion can be changed in various situations.
The different outcomes of Capaldi (1982, 1983) and others (e.g. Revusky and Pompilio) cannot be explained by a methodic difference. Maybe it has something to do with the biology of the animal. That in some conditions it is preferred to use state dependent valuation and in others it is preferred to link not the state change but the actual state at the time of learning. Another explanation can be that the fitness-state curve as describe in Pompilio (2005, 2006) is different than assumed. I think that that is not very likely but there is no proof to discard this possibility.
If the after effect can be linked to the cue given earlier (Revusky 1967, Revusky cross linked Holman 1974), it is almost impossible to determine which cue is linked to what and if this is the same as the experimenters think. Is the high deprivation cue really the high deprivation cue or not.

State dependent valuation is seen in different taxa, this suggest a mechanism that is developed on its own and not co-developed with another trait (Pompilio 2008). The mechanism in the grasshopper and the starling are probably different but the outcome is the same (Pompilio 2006). This is very interesting because state dependent valuation can lead to suboptimal choices. An explanation for the so called suboptimal choices is that the choices as proposed in different experiments are choices that are not common in nature (Pompilio 2008). Or the costs of the suboptimal choices are less than the development a complex mechanism that makes sure always the optimal choice is made (Pompilio 2006). Then there is the fundamental discussion about what is an irrational or suboptimal choice and why is it not the optimal choice. As said earlier, a reward yields different kinds of information, the actual properties and the properties of the previous gains. But what is the more important one, and why is this one seen as the more important one, is something you can argue about. What is important can change per situation, as said before this could be an explanation for the different outcomes of the different studies.

In nature the past gains and future gains can not been seen separate (Kacelnik 2002). So the experiment cannot be done in natural environment, so the real use of the mechanism cannot be examined in nature. So the purpose of the mechanism in natural environments is not known.

If state dependent valuation is looked at from the conventional learning state of view, the unconditioned stimulus cannot be the deprivation level in it self. If that was the case there would be no differences found between flavor dissolved in saccharine or sucrose (Capaldi 1983). So the learning effects are due to something else than the deprivation level alone.

The palatability of sucrose can mask the effect of state dependent valuation (Capaldi 1983). The preferences for other properties of the rewards used can also influence the results. The milk and grape juice experiment shows strong preferences for milk (Revusky 1967). The preferences for grape juice are higher when it was the high deprivation cue, but this is not the ideal testing situation.

Starlings prefer rewards given after hard work. The question is if they prefer the hard work or if they prefer the effect of the reward. The latency of hard work is longer than the latency during easy trails, due to these findings there can be concluded that the preference shown is not due to the hard work but due to something else (Kacelnik 2002).
Another explanation for preferring the hard work is the release of build up tensions during hard work, the more tension is build up the higher the satisfaction when this is released.

The preference for high deprivation cue is only seen with nutritive cues, the saccharine cue during high deprivation may have an aversive effect (Capaldi 1982). How this works is not know jet, maybe its like chewing gum, you eat something but do not get any nutrition. Another remark to make when using cues with calories (sucrose solutions) is that this may change the state where the animal is in. if

under high deprivation the animal has access to a large quantity of a cue with calories the question is, if the animal is nearly satiated after eaten the cue, is the cue in that case still linked to the high deprivation cue or is it linked to the nearly satiated state.

It is counterintuitive that starlings prefer a longer delay over a shorter one. But what I found even more interesting about these results is that if the delay became to long the birds were indifferent (Pompilio 2005). This shows that the birds make suboptimal choices but is has its limits.

The maintaining of preferences in the Revusky and Capaldi experiment are very strong. The first one in preference for the high deprivation cue and the latter for the low deprivation cue (Revusky 1974, Capaldi 1983). These results show that the preference is a learned and the effect is long lasting.

Future research

In new research there are a few point of interest.
In the grasshopper in the experiments of Pompilio in 2006 the taste receptors become more sensitive if the deprivation level increases. Also in the forebrain of a rat and in other primates state dependent modulation occurs (Pompilio 2008 crossreff Giza and Scott 1983 Rolls 1999). Due to the changes the perception of the cues is possibly not the same. And maybe not only is the perception different also the gain can be different, if there is high deprivation it is likely that more of the nutrients of a food reward are used. If this is the case the first thing to do is trying to understand how this works and to what extend this can change. When an animal get more nutrient out of the high deprivation cue, it is interesting to see if when the cues are changed so that the nutrient value is the same for the cues there is still a preference for one of the cues.
Also the deprivation levels can be changed, to see what kind of difference there has to be to have the state dependent valuation. If this can be accomplished with very little changes in state or only with large differences in state. In a natural environment small changes in state are more common than the large changes.
It is also important to see if other properties of the cue could influence the result. Capaldi stated in 1983 that the palatability of sucrose can mask the effect of preference (Capaldi 1983). If an effect is maybe masked by a property of the cue the outcomes are not as reliable as they should be. In the results of Capaldi 1982 experiment 2 there was a difference in flavor and preference, see results, so not only the sucrose taste has influence on the results, also the artificial flavors. The preference for one kind of food or flavor could be because of the preference for that kind of flavor but it could also be the effect of the aversion against the other (Capaldi 1982). This is also something to consider when choosing an flavor for testing. Because in Revusky 1967, Capaldi 1983, Revusky 1974 there was a taste bias, and if this is preference for one or aversion against the other can influence the results.
Maybe the state dependent valuation is also present in other aspects of an animals life, not only food related. Shelter in hot and cold environments is one of the things that come to mind. This would be interesting to test.
Another problem with the way the experiments are done is that it is know that if the animal is higher deprived the animal learns better and faster (Marsh 2003). To tackle this problem the method can be changed flowing the example of Aw, the fish in this experiment needed to make very little mistakes before they stopped the training. The learning was adapted to the individual fish (aw et al 2008). If this is used for the different deprivation levels as well the problem is solved.
In the delay study with starlings Pompilio showed that starlings prefer the high deprivation delay, but when the delay is very long the bird become indifferent (Pompilio 2005). This is something to integrate in future research to check how strong the effect is. If the high deprivation cue has a less ideal reward, e.g. less calories, when will the animal become indifferent. This is interesting because this can be of very great importance in nature, the rewards found in nature are not equal, for example caterpillars are not all the same size.

Conclusion

There is a lot not known about choices why they are made and how this can change in different situations. I think the animal adapts his decision-making mechanism to the situation he is in. Also the preferences before the training can influence the results obtained during a choice trail.
A lot of research can be done on the subject of state dependent valuation. How the animal uses the mechanics in his natural environment is one of the very interesting questions to be answered.

References

Aw J.M. et al 2009. State-dependent valuation learning in fish: banded tetras prefer stimuli associated with greater past deprivation. *Behavioural Processes*, 81, 333–336

Bolhuis J.J. & Giraldeau 2005. the behavior of animals, mechanisms, function, and evolution. *Blackwell publishing,* isbn 0631231250

Capaldi E.D. et al 1983. Conditioned flavor preferences based on hunger level during original flavor exposure. *Animal Learning &Behavior* , 11 (1}, 107-115

Capaldi E.D. et al 1982. Taste preferences as a function of food deprivation during original taste exposure. *Animal Learning & Behavior*, 10 {2), 211-219

Kacelnik A. et al 2002. Cost can increase preference in starlings. *Animal behaviour*, 63, 245–250

Marsh B. et al 2004. Energetic state during learning affects foraging choices in starlings. *Behavioral Ecology*, 15 {3}: 396–399

Pompilio L. et al 2006. State-Dependent Learned Valuation Drives Choice in an Invertebrate. *Science,* 311, 1613-1614

Pompilio L. et al 2005. State-dependent learning and suboptimal choice: when starlings prefer long over short delays to food. *Animal behaviour*, 70, 571–578

Revusky S. H. 1974. Retention of a Learned Increase in the Preference for a Flavored Solution. *behavioral biology*, 11,121-125

Revusky S.H. 1968. Effects of thirst level during consumption of flavored water on subsequent preference. *Journal of Comparative and Physiological Psychology,* 66 {3}, 777-779

Revusky S.H. 1967. Hunger level during food consumption: effects on subsequent preference. *psychonomic society,* 7 {3}, 109-110