Seminar

The Role of Memory in Decision Making

Sep 9-11, 2010

Bernstein Focus Neuronal Basis of Learning (bfnl)
Freie Universität Berlin

Organizers:
Dorothea Eisenhardt, Randolf Menzel, Martin Nawrot

Seminar/Module 23903 | SS 2010 | FU Berlin
Final Program

The Role of Memory in Decision Making

Venue Seminar Room, KL 32-102, Silberlaube Habelschwerdter Allee 45, Entry Habelschwerter-Allee

Date Sep 9-11 (Thu - Sat)

Organization

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The Role of Memory in Decision Making, Sep 9 – Sep 11

Seminar Room, KL 32-102, Silberlaube Habelschwerdter Allee 45

Thursday, Sep 9 *(10:00 – 17:00)*

Reward encoding and reward prediction error

10:00 Introductory remarks

Session 1

10:15 Svenja Specovius (M)

10:45 Christian Hoppe

11:15 Coffee Break

11:30 Rithwik Mutyala

12:00 Anna Galicka

Discussion

12:45 – 14:00 Lunch Break

Decision making: Behavior & Neurophysiology

Session 2: ***Working memory – a prerequisite for perceptual decisions***

14:00 Christoph Standfuß

14:30 Adriana Schatton

Discussion

15:00 Coffee Break

Session 3: ***Perceptual decision making***

15:30 Matthias Kluge (M)

16:10 (M.N.)

Discussion

16:45 - 17:15 Summary

18:30 Social Decision Making over Dinner:

'Piazza Michelangelo', Breitenbachplatz 4

http://www.piazza-michelangelo.de/

Friday, Sep 10 *(10:00 – 17:00)*

Session 4: ***Value-based decision making***

10:00 Marcus Schröder (M)

10:40 Bastian Kayser

11:15 Coffee Break

Session 5: ***Social decision making***

11:30 Maria Kramarek

12:00 Jia Shen Guo

Discussion

12:45 – 14:00 Lunch Break

Session 6: ***Neural correlates and neuronal circuits of decision making***

14:00 Johanna Stärk (M)

14:40 Kersten Döring

15:15 Coffee Break

15:30 Katharina Grauel

Discussion

16:00 – 16:30 Summary

Saturday, Sep 11 *(10:00 – 12:30)*

Decision making: computational models and artificial agents

Session 7

10:00 Anna Kosenko

10:40 Hatice Celik

11:15 Nico Güttler

Discussion

11:45 - 12:15 Summary and Conclusions, Feedback

List of Topics

1 Reward encoding and reward prediction error

[1 **Svenja Specovius**] [Tutor: M Nawrot]

Prediction error in dopaminergic neurons

Schultz W, Apicella P, Ljungberg T (1993) Responses of monkey dopamine neurons to reward and conditioned stimuli during successive steps of learning a delayed response task. J Neurosci. 13(3):900-13.

Here, Schultz and colleagues describe the encoding of a reward in dopaminergic neurons of in the monkey brain.

Mirenowicz J, Schultz W (1994) Importance of unpredictability for reward responses in primate dopamine neurons. J Neurophysiol 72(2):1024-7. (*physiology*)

This paper shows for the first time that phasic dopamine responses to a liquid reward occur only if that reward is unexpected, i.e. after learning the response to the reward stimulus is lost. This is the basis for the idea of encoding a prediction error.

Schultz W, Dayan P, Montague PR (1997) A neural substrate of prediction and reward. Science 275: 1593-1599

[2 **Christian Hoppe**] [Tutor: Evren Pamir]

Temporal difference (TD) learning model with prediction error (PRE)

Montague PR, Dayan P, Sejnowski TJ (1996) A framework for mesencephalic dopamine systems based on predictive Hebbian learning. J Neurosci. 16(5):1936-47 (*modeling*) [Temporal difference learning algorithm].

Schultz W, Dayan P, Montague PR (1997) A neural substrate of prediction and reward. Science 275: 1593-1599 (*modeling*)

Two original papers on modeling the use of the prediction error in Hebbian-type learning. Relation to temporal difference learning algorithms in machine learning. The basic model idea of temporal difference learning must be explained.

[3 **Rithwik Mutyala**] [Tutor: D. Eisenhardt]

Hammer, M. (1993) An identified neuron mediates the unconditioned stimulus in associative olfactory learning in honeybees. Nature 366:59-63

Hammer, M. and R. Menzel (1994) Neuromodulation, instruction and behavioral plasticity. In R. Greenspan and B. Kyriacou (eds): Flexibility and constraint in behavioral systems. Chichester, UK: J. Wiley & Sons, pp. 109-118

[4 **Anna Galicka**] [Tutor: D Eisenhardt]

Stollhoff, N., Eisenhardt, D. (2009) Consolidation of an extinction memory depends on the unconditioned stimulus magnitude previously experienced during training. J Neurosci, 29 (30): 9644-9650

2 Decision making: Behavior & Neurophysiology

Working memory – a prerequisite for perceptual decisions

[5 **Christoph Standfuß**] [Tutor: D Eisenhardt]

Zhang S, Bock F, Si A, Tautz J, Srinivasan MV (2005) Visual working memory in decision making by honey bees. Proc Natl Acad Sci USA 102(14):5250-5 (*behavior*)

[6 **Adriana Schatton**] [Tutor: Ch Häusler]

Romo R, Brody CD, Hernández A, Lemus L (1999) Neuronal correlates of parametric working memory in the prefrontal cortex. Nature 399(6735):470-3

Romo

Additional reading:

Curtis CE, Lee D. (2010) Beyond working memory: the role of persistent activity in decision making. Trends Cogn Sci. 14(5):216-22

Perceptual decision making

For background reading and a more general definition of perceptual decision making see:

N. Uchida, A. Kepecs and Z.F. Mainen (2006) Seeing at a glance, smelling in a whiff: rapid forms of perceptual decision making. *Nature Reviews in Neuroscience* 7(6):485-491 (*review article*)

Heekeren HR, Marrett S, Ungerleider LG (2008) The neural systems that mediate human perceptual decision making. Nat Rev Neurosci 9(6):467-79 (*review article*)

[7 **Matthias Kluge**] [Tutor: M. Nawrot]

Uchida N, Mainen ZF (2003) Speed and accuracy of olfactory discrimination in the rat. Nat Neurosci 6(11):1224-9 (*behavior*)

Wesson, D. W.; Carey, R. M.; Verhagen, J. V. & Wachowiak, M. (2008) Rapid encoding and perception of novel odors in the rat. PLoS Biol 6(4), e82 (*behavior*)

Uchida et al. describe fast behavioral discrimination of odorants in rats. Wesson et al. describe an even faster detection of an unknown odor. Combine both papers for presentation with a focus on Uchida et al.2003

[8 ~~**Sophie Schneiderbauer**~~] [Tutor: M. Nawrot]

Stanford TR, Shankar S, Massoglia DP, Costello MG, Salinas E. (2010) Perceptual decision making in less than 30 milliseconds. Nat Neurosci 13(3):379-85 (*behavior, physiology and computational modeling*)

Value-based decision making

For an introduction to value-based decision making see also:

Rangle, A., Camerer, C., Montague, P.R. (2008) A framework for studying the neurobiology of value-based decision-making. Nature Reviews: 9, 545-556 (*review article*)

[9 **Marcus Schröder**] [Tutor: D Eisenhardt]

Heekeren HR, Marrett S, Bandettini PA, Ungerleider LG (2004) A general mechanism for perceptual decision-making in the human brain. Nature 431(7010):859-62

Heekeren HR, Marrett S, Ungerleider LG (2008) The neural systems that mediate human perceptual decision making. Nat Rev Neurosci 9(6):467-79 (*review article*)

[10 **Bastian Kayser**] [Tutor: D Eisenhardt]

Peters J, Büchel C. (2009) Overlapping and distinct neural systems code for subjective value during intertemporal and risky decision making. J Neurosci. 29(50):15727-34. (*human* fMRI)

Social decision making

For an introduction to game theory and social influences on decisions:

Lee D (2008) Game theory and neural basis of social decision making. Nature Neuroscience 11, 404 - 409

Rilling JK, King-Casas B, Sanfey AG.(2008) The neurobiology of social decision-making. Curr Opin Neurobiol. 2008 Apr;18(2):159-65. Epub 2008 Aug 7 (*review article)*

[11 **Maria Kramarek**] [Tutor: D Eisenhardt]

Amé JM, Halloy J, Rivault C, Detrain C, Deneubourg JL (2006) Collegial decision making based on social amplification leads to optimal group formation. Proc Natl Acad Sci U S A. 103(15):5835-40

Halloy J et al. (2007) Social Integration of Robots into Groups of Cockroaches to Control Self-Organized Choices. Science 318 (5853): 1155-1158

[12 **Jia Shen Guo**] [Tutor: F Farkhooi (M Nawrot)]

King-Casas B, Tomlin D, Anen C, Camerer CF, Quartz SR, Montague PR (2005) Getting to know you: reputation and trust in a two-person economic exchange. Science. 308(5718):78-83.

Neural correlates and neuronal circuits of decision making

For background reading on neural correlates and circuit analysis in decision making see:

Kable, JW, Glimcher, PW (2009) The neurobiology of decision: Consensus and controversy, Neuron, 63: 733-745 (*review article*)

Kristan WB.(2008) Neuronal decision-making circuits. Curr Biol. 2008 Oct 14;18(19):R928-32 (*review article*)

Gold J, Shadlen M (2007) The neural basis of decision making. Annu. Rev. Neurosci. 2007. 30:535–74 (*review article*)

[13 **Johanna Stärk**] [Tutor: D. Eisenhardt]

Briggman KL, Abarbanel HD, Kristan WB Jr. (2005) Optical imaging of neuronal populations during decision-making. Science. Feb 11;307(5711):896-901. (*physiology*)

Friesen W.O., Kristan W.B. Jr. (2007) Leech locomotion: Swimming, crawling, and decisions. Curr Opin Neurobiol 17:704-711

The presentation should focus on the first paper, the second paper provides additional background.

[14 **Kersten Döring** [Tutor: Th Rost]

Kim JN, Shadlen MN (1999) Neural correlates of a decision in the dorsolateral prefrontal cortex of the macaque. Nat Neurosci. 2(2):176-85.

See also

Gold J, Shadlen M (2007) The neural basis of decision making. Annu. Rev. Neurosci. 2007. 30:535–74 (*review article*)

[15 **Katharina Grauel**] [Tutor: Jan Sölter]

Romo R, Hernández A, Zainos A (2004) Neuronal correlates of a perceptual decision in ventral premotor cortex. Neuron 41(1):165-73 (*neurophysiology*)

Romo R, Salinas E (2003) Flutter discrimination: neural codes, perception, memory and decision making. Nat Rev Neurosci 4(3):203-18 (*neurophysiology*)

This topic is closely related the next topic where a model is introduced and it is refers to a follow-up study of topic No [6] (Romo et al. 1999)

3 Decision making: computational models and artificial agents

For background reading, see

Chapters 5 'Probabilistic decision-making' + 6 'Confidence and Decision Making' in Rolls ET, Deco G (2010) The Noisy Brain. Stochastic Dynamics as a Principle of Brain Function. Oxford University Press, Oxford (available at the AG Nawrot, Neuroinformatik, Königin-Luisen Str. 1-3) (book chapter)

Wang XJ (2008) Decision making in recurrent neuronal circuits. Neuron 60(2):215-34 (*review article*)

Gold J, Shadlen M (2007) The neural basis of decision making. Annu. Rev. Neurosci. 2007. 30:535–74 (*review article*)

[16 **Anna Kosenko**] [Tutor: Jan Sölter]

Deco G, Rolls ET (2006) Decision-making and Weber's law: a neurophysiological model.

Eur J Neurosci. 24(3):901-16.

For overview start with: Wang et al. 2008 above; see other review articles cited above

This topic is closely related the previous topic on neural correlates of decision making in the macaque. Please also read Romo et al. 2003 above.

[17 **Hatice Celik**] [Tutor: Gundula Meckenhäuser]

Deco G, Rolls ET, Romo R. (2010) Synaptic dynamics and decision making. Proc Natl Acad Sci USA. 107(16):7545-9. (*modeling*)

This publication improves previous model above. Please also read Romo et al. 2003 cited for [16].

[18 **Nico Güttler**] [Tutor: Gundula Meckenhäuser]

Lo C-C, Wang X-J (2006) Cortico–basal ganglia circuit mechanism for a decision threshold in reaction time tasks. Nature Neuroscience 9, 956 - 963

For an overview read also

Lee, D., and Wang, X.-J. (2008). Mechanisms for stochastic decision making in the primate frontal cortex: Single-neuron recording and circuit modeling. In *Neuroeconomics: Decision Making and the Brain*, E.F.P.W. Glimcher, C.F. Camerer, and R.A. Poldrack, eds. (*book chapter 31, PDF version is included in the online seminar material*).

The Role of Memory in Decision Making

Reward encoding and reward prediction error

Svenja Specovius

SoSe 2010

Introduction to the Experiments

The ability to predict future rewarding events like the presence of food is important for animals. Dopamine neurons have been identified with processing such rewarding stimuli. Further information about the processing of rewarding stimuli have been discovered in studies by Schultz *et al* [3, 4], Mirenowicz *et al* [2] and Ljungberg *et al* [1]. During several experiments the activity of dopaminergic neurons in two male *Macaca fascicularis* monkeys were measured to study neuronal reactions to different conditioned stimuli.
The neuronal activity of dopaminergic neurons was recorded. For this purpose extracellular single unit recording was applied from the ventral tegmental area (VTA) and substantia nigra. They are located in the midbrain. Tungsten microelectrodes that were insulated with glass were used. For acute recording these electrodes were inserted each day into the midbrain of the monkey by a cannula.

The monkeys had to perform different reaction tasks. A trigger signal occurred, when the monkey should perform the task. The trigger signal was a sound or a light. The task the monkeys had to perform was for example pushing a lever. If the monkey reacted correctly, it got a reward, that was a drop of fruit juice or a piece of apple. After the learning phase there were further experiments also with rewarding stimuli. This was called the established phase. In a third phase the monkey received the trigger signal, performs the reaction task, but the reward failed to appear. There were also free liquid experiments where the monkey got liquid outside of a task.

Results and Discussion

Figure 1 shows the Peri-Stimulus-Time-Histograms (PSTH's) and raster plots of one neuron for three different experiments. When the monkey received a reward in the absence of a task (free liquid trials) [2], the dopaminergic (DA) neuron responded to the unpredicted reward with an increased firing rate (Figure 1 top). DA neurons responded in the same way to rewards during the learning phase. In this context *reward* means an appetitive or rewarding stimulus. The same neurons did not respond to aversive stimuli. After the learning phase, the monkey expected the trigger signal to indicate the rewarding stimulus (established phase). The trigger signal acted as the conditioned stimulus (CS), the rewarding stimulus as the unconditioned stimulus (US). In this established phase the dopaminergic neuron did not respond to the rewarding stimulus. However the neuron showed a response to the conditioned stimulus. It reacted by an increased firing rate a few ms after the CS. This shows that the monkey understood the trigger signal as a prediction of the reward. The monkey predicted a reward because of the learned relation between the CS and the rewarding stimulus. This is called reward prediction. The

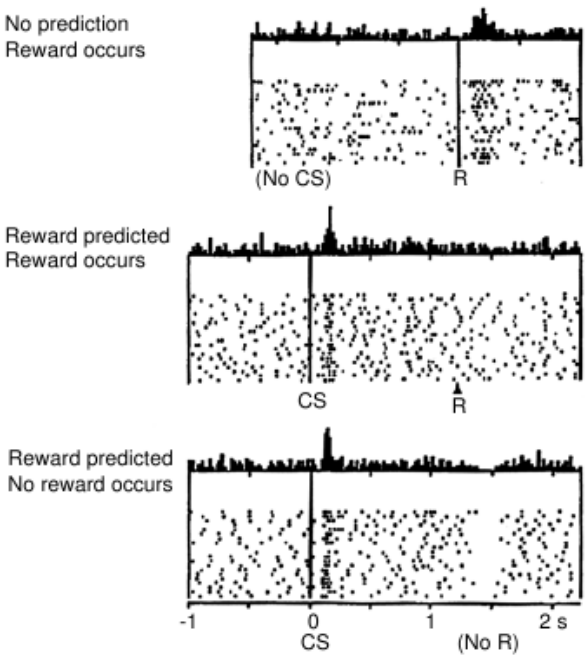


Figure 1: PSTH and raster plots of one DA neuron during 3 experiments, spikes are plotted over time [ms], each row in the raster shows one trial; **top** before learning: no conditioned stimulus (CS), neuron responds to rewarding stimulus by increased activity; **middle** established phase: CS given, neuron does not respond to reward, but to CS; **bottom** third phase: CS given, no reward, neuron respond to CS by increased activity, activity of neuron is depressed by absence of rewarding stimulus

dopaminergic neurons react if the expectation is not fulfilled. Another interesting point is that the DA neuron was depressed by the absence of the rewarding stimulus (Figure 1, bottom). The depression of the DA neuron occurred exactly at the time, when in other experiments the reward was given. This behaviour indicates that the prediction of reward also includes the exact time prediction.

Conclusion

Dopaminergic neurons process reward information due to the expectation of reward. The neurons only respond if the reward differs from the expectation. If the reward is higher than the expectation, the activity of the neurons gets increased which leads to a positive signal in the recording. If the reward is lower than expected, the activity of the neurons is decreased, which leads to a negative signal in the recording. If the reward is absent, the DA neuronal activity is completely depressed. Hence dopaminergic neurons encode the mismatch between reward expectation and reward fulfilment. This is called reward prediction error. Furthermore dopaminergic neurons can precisely encode the time, when a reward is expected.
In summary there are three important functions of the dopaminergic neurons:

- **Reward prediction**
  expectation of a reward (US) due to a conditioned stimulus (CS)
- **Reward error encoding**
  encoding the mismatch between reward prediction and actual reward
- **Temporal prediction**
  encoding exactly the time, when a reward is expected

References

[1] T. Ljungberg, P. Apicella, and W. Schultz. Responses of monkey dopamine neurons during learning of behavioral reactions. *J Neurophysiol*, 67(1):145–163, Jan 1992.

[2] J. Mirenowicz and W. Schultz. Importance of unpredictability for reward responses in primate dopamine neurons. *J Neurophysiol*, 72(2):1024–1027, Aug 1994.

[3] W. Schultz, P. Apicella, and T. Ljungberg. Responses of monkey dopamine neurons to reward and conditioned stimuli during successive steps of learning a delayed response task. *J Neurosci*, 13(3):900–913, Mar 1993.

[4] W. Schultz, P. Dayan, and P. R. Montague. A neural substrate of prediction and reward. *Science*, 275(5306):1593–1599, Mar 1997.

Temporal difference learning as concept of reinforcement learning

Christian Hoppe

Introduction

Temporal difference learning is one algorithm or concept in the field of Reinforcement learning in which an agent ought to make some actions with respect to maximizing some function or cumulative reward. Inspired by behavioral data on how animals actually learn to predict, the temporal difference learning algorithm tries to predict the future reward of an action. Dopamine neurons in the ventral tegmental area (VTA) and substantia nigra have been identified with the processing of reward stimuli and reward prediction. These neurons change their firing rate if a reward stimulus is given (food, fruit juice, etc.). If this stimulus is preceded by another stimulus (light or sound) then the animal begins to associate the first stimulus with the second. The first stimulus is now conditioned (CS). After the learning phase one can observe that the dopamine neurons change the firing rate. An increase of action potentials at the time of the reward in the unconditioned state follows after learning an increase directly after the CS and when the reward is given there is no change in the firing rate. If the reward stimulus is not presented than a decrease in the firing rate occurs at the time of the predicted reward. So the time at which a reward occurs is associated with the CS. The difference of the predicted and experienced reward somehow mimics the prediction error function of TD and researcher found that the brain has implemented some kind of TD for prediction of rewards and the exact occurrence.

Temporal difference

Temporal difference methods were introduced by Richard Sutton and Andrew Barto in the 1980s[1] [2]. The computational goal of learning is to use sensory cues to predict a discounted sum of all future rewards (value function):

$$V(t) = E(\sum_i \gamma^i r(t+i)) = E[\gamma^0 r(t) + \gamma^1 r(t+1) + \gamma^2 r(t+2) + \cdots]$$

with r(t) is the reward at time t, $0 \leq \gamma \leq 1$ is the discount factor and $E[\cdot]$ denotes the expected value of the sum up to the end of the trial. The discount factor affects the view into the future in the way that if it is close to one, the rewards from the far future are taken strong into account and with it being close to zero, nearly all future rewards will not influence the value function. Also the TD has the Markov property, which means that the future rewards depend only on the current time step and not on preceding steps.

[1] R. S. Sutton and A. G. Barto, Psychol. Rev. 88 (no. 2), 135 (1981); R. S. Sutton, Mach. Learn. 3,9 (1988)

[2] R. S. Sutton and A. G. Barto, Proceedings of the Ninth Annual Conference of the Cognitive Science Society (Seattle, WA, 1987); in Learning and Computational Neuroscience, M. Gabriel and J. Moore, Eds. (MIT Press, Cambridge, MA, 1989). For specific application to eyeblink conditioning, see J. W. Moore et al., Behav. Brain Res. 12, 143 (1986)

At each time step there is some information available so that a recursive formula:

$$\hat{V}(t) = E[r(t) + \gamma \hat{V}(t+1)]$$

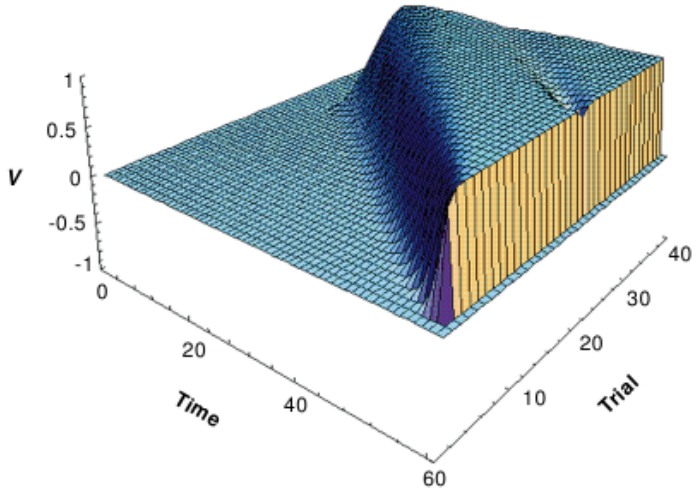
can be obtained. In that way one need not to simulate the whole trial to estimate the possible future reward. Now one can define an error in the estimated predictions with information available at each successive time step:

$$\delta(t) = r(t)\gamma \hat{V}(t+1) - \hat{V}(t)$$

This prediction error can be used too update the current state in which the agent is and change the next possible action to minimize the error and maximize the future reward.

Application

Schultz et al.[3] applied the TD concept to a test case in which a reward is given 50ms preceded by a stimulus. The model predicts the future reward with an increase of the value function (figure below). With each ongoing trial this models adapts to the reward signal and the response of the system shifts to the CS. So that after "learning"(40 trials) the stimulus at 10ms, the model predicts a reward right after the CS.



The value function V(t) as a function of time and trial. In the first trial nothing is predicted as it is the fact that here is the first time where the stimulus is presented. With the next trials an increase can be observed around the time of the reward. And with ongoing trials a shift occurs towards the time of the stimulus. The depression is from one error trial where the reward was withheld.

Figure 1: Response shift in value function while learning

[3]Schultz W. A Neural Substrate of Prediction and Reward. Science. 1997;275(5306):1593-1599

Summary

Dopamine neurons in the VTA and substantia nigra report ongoing prediction of rewards. Evidence for this is reviewed by Schultz et al.[4], Montague et al.[5] and others. Supporting data of these neurons while simple conditioning tasks show that the output is consistent with a prediction error signal which is used in machine learning theory(temporal difference learning is one field) to adjust future actions for maximizing some function or the prediction of reward. TD can be used to estimate the difference between the current state and the associated reward and future rewards. This difference can be used to update the current value of the state and change probably the future action. With this concept it is possible to let computer programs learn along some predefined rules and let robots interact and learn to survive[6].

[4]Schultz W. A Neural Substrate of Prediction and Reward. Science. 1997;275(5306):1593-1599

[5]Montague PR. A Framework for Mesencephalic Predictive Hebbian Learning. Brain. 1996;76(5):1936-1947.

[6]Doya, K, and Uchibe, E (2005). "The Cyber Rodent project: exploration of adaptive mechanisms for self-preservation and self-reproduction." Adaptive Behavior 13, 149–160

Neuromodulation, Instruction and Behavioural Plasticity

Hammer & Menzel (1994). *A write up by Rithwik Mutyala towards the seminar on The Role of Memory on Decison Making. Topic: Reward Encoding and Reward Prediction Error.*

Abstract

Introduction

The success of survival of an organism furthermore that of a species depends greatly on its ability to cope with its environment. The constitution of an organism fixes by genetics and its behaviour determine the thriving or extinction of its species. Although genetics are influenced by environment, it is through behaviour that an organism interacts with, adapts to or modifies its environment. In such a scenario the importance of learning and modifying behavioural responses becomes evident. An organism has to cope with internal states like hunger and external conditions like availability of food and as such needs to respond to the combination of internal and external states. In this chapter some of the mechanisms of the process of Behavioural Plasticity are discussed.

Neural Assemblies

Nervous systems organisation in to circuits and neural networks can be viewed analogically as the hardware of the system which defines the capabilities of the system. Then the observed flexibility of the system is explained by the software which is the neural assemblies. Authors suggest that "Neural assemblies can be thought of as actual interpretations of possible states of a given net, and are equivalent to functional meaningful states of activity." The questions that arise then are

- How are neural assemblies generated?
- What are the mechanisms that help switch between them?

Adaptation and Neural Assemblies

Two mechanisms have been hypothesised for the behavioural adaptation

1. Selective activation and modulation of already existing assemblies
2. Experience dependent reorganisation and generation of functional assemblies. These then lead to addition of new and meaningful states of networks.

Neuromodulatory neurons play a major role in former whereas the later utilizes or depends on the mechanisms of Neuromodulation. And hence it should be noted that these two are not mutually exclusive but in many cases work in concert.

1. Selective activation and modulation of already existing assemblies

In this case the already existing relationships between external/internal cues to pre-defined behavioural patterns are modulated or previously inactive systems are activated in response to the cues. These could be achieved by

1. Action at Synapses: modifying the synaptic gain through chemical neuromodulators like Serotonin. These compounds modify the transmission at synapses.
2. Action on Neurons: modifying the properties of neurons themselves in as assembly through chemical neuromodulators. As was shown in rhythm generator circuits (in the chapter examples), this can essentially change the output of the network. Thereby giving rise to new functional modalities.
3. Direct action of Modulatory Neurons: modifying the tonic (the continuous stable activity of the neruon) activity of the particular neurons themselves. These in turn might activate different assemblies based on the activity level.

The references in the chapter provide examples for the above mechanisms which would be discussed in the presentation. Also since the effect of a neuromodulator is determined by the receptor of the target neuron, it is evident that the neuromodulator activity is target specific. This in turn implies that the same neuromodulator can have opposing effects on the target assembly.

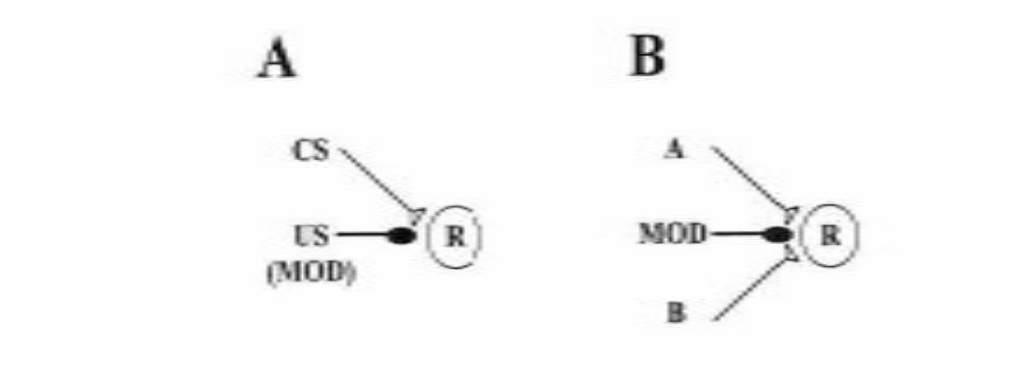
2. Re-organisation and Generation of New Assemblies

In this case the existing behavioural patterns (or neuronal assemblies) are learned to associate with new cues. This further raises the question about

1. Which stimulus combinations should be given new meaning (in terms of behaviour in the simplest case)
2. Which meaning should the stimulus get. (eg. Defensive, appetitive, aggression, withdrawal etc)

A solution to these seems to come from the *instructive* influence of other neurons. Classical conditioning has been shown as a good example where the

role of these instructors becomes clear. Here a genetically determined, biologically relevant response to a stimulus (referred to as US: unconditioned stimulus) is associated with a earlier biologically meaningless new stimulus (referred to as CS: conditioned stimulus). The chapter shows examples of *Aplysia* and *Honey –Bee* as model systems for illustration. The following figure shows two plausible mechanisms for reorganisation and generation of new assemblies.



In case A: the US activates a behavioural response (motor in Aplysia and Honeybee) and an arousal response. The US generally activates a modulatory pathway which overlaps with the CS pathway. When temporally contiguous (CS -> US), the activities of the system associates the target US assemblies with that of CS. This implies that the CS now can generate the behavioural as well as arousal properties of US and therby act as an instructor.

In case B: here the activity of two neurons is either potentiated or depressed depending on the correlated or anti-correlated activity respectively (related to hebbian learning). Thus two different inputs can be associated by either increasing or decreasing the synaptic strengths. In this case the modulatory systems act as either permissive or gain-setting systems. In many hebbian systems attention has been shown to act as the modulatory system by affecting the sub-threshold firing of the target.

Conclusion

Neuromodulation appears to be involved at all organisational levels of nervous systems and mediate mechanisms of behavioural adaptivity. Studies of these systems have proven to be powerful tools for further analysis in bridging the gap between cellular (functional assemblies) mechanisms and observed meaningful behaviour.

A case study of investigating neuromodulatory systems can be seen from the publication by **Martin Hammer, 1993, 'An identified neuron mediates the unconditioned stimulus in associative olfactory learning in honeybees'**

In this study an interneuron is identified as a plausible agent in associative learning of feeding behaviour (Proboscis Extension Reflex: PER) and specific odours (CS) by classical conditioning. In determining so, the author looks at the physiology as well as the functional properties of the neuron.

Physiologically the identified neuron **VUMmx1** is associated with primary olfactory system (which has been shown to mediate arousal), Mushroom bodies (essential sites for induction of a stable olfactory associative memory) and the output region of the brain (Lateral Procerebrum). Thus the neuron provides a good convergence between different pathways. Functionally the neuron is associated (with Sucrose as US) with long-lasting firing ~30s and also the arousal of the olfactory system.

To test the hypothesis that the identified neuron is indeed the modulatory agent in association, the US was replaced by depolarisation of the VUMmx1. The subjects were clearly shown to exhibit associative learning in this scenario between odours (as CS) and behaviour (observed as PER).

This investigation also shed light on some of the properties of the learning. For example,

- Learning was achieved only when CS is presented before VUMmx1 stimulated firing by current injection and not after. The requirement of **temporal contiguity** to classical conditioning is clearly implicated in this example.
- **Parallel processing** of modulatory and reflexive behaviour is also shown as VUMmx1 evokes little or no motor activity (PER) when CS is presented after US. This uncoupling has been hypothesised to allow for more complex forms of learning.
- Also the **Plasticity** of the VUMmx1 to respond differently to learned versus not-learned odour stimuli was shown.

In conclusion, among the above results, this investigation showed for the first that a single neuron could affect associative learning. This study clearly demonstrates the usefulness of studying Neuromodulation pathways in further understanding and unravelling the underlying principles of behavioural learning and specifically associative learning.

Anna Galicka

Summary will be handed out during the seminar.

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Visual working memory in decision making by honey bees
Zhang et. al.

Christoph Standfuß

Seminar: The Role of Memory in Decision Making
Summer semester 10

1 Introduction

In the past decades it was shown that bees have perceptual and "cognitive" capacities and are able to abstract general features of a stimulus. Like monkeys, pidgeons and other vertebrates, bees can be trained to use symbolic rules, e.g. for navigating. The simple nervous system of bees is an attractive model system, displaying essential elements of many many complex behaviors.

2 Methods and Materials

For the experiment 15 bees were marked individually. They were trained to fly through a tunnel and then into a decision chamber at the end of the tunnel (see figure 1 a). In the initially training phase the feeder was placed at the entrance of the tunnel and then moved step-by-step through the tunnel. Depending on the experimental series a sample pattern was presented at a point in the tunnel. Reinforcement learning was used in the training phase: Bees that made the correct choice in the decision chamber were rewarded by sugar solution. In the training phase bees were trained to match a sample pattern with one of the two pattern presented in the decision chamber. The sample pattern was presented alternatively in 20 min blocks during the testing and training phase. The positions of the comparison pattern in the decision chamber were swapped every 10 minutes.
Altogether there were 3 series of experiments. In the first one it was tested how long the sample could be retained in working memory, in a second series two sample pattern were placed in the tunnel (one representing the correct one). In the third experimental series bees were trained using a two sample pattern placed one behind the other in the tunnel.

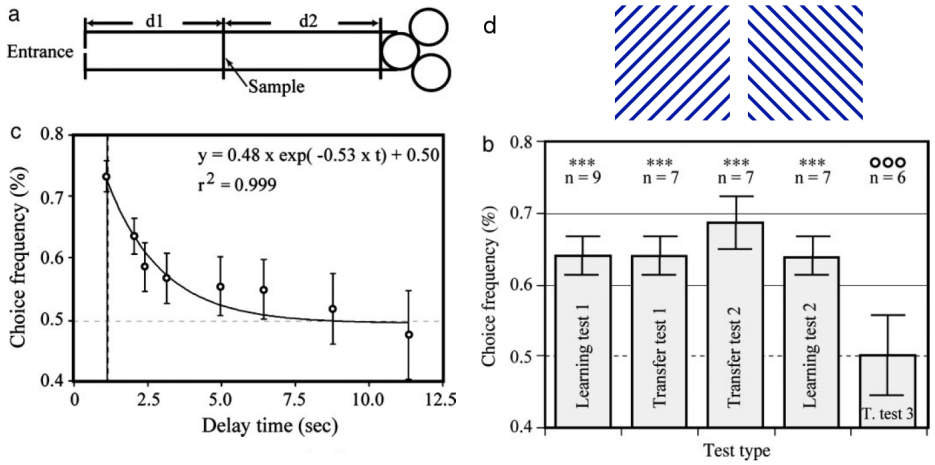

Figure 1: (A) Illustration of the apparatus used, consisting of a tunnel and a decision chamber attached to the end. (b) Results of series II showing the choice frequency in different learning and transfer tests. The results show that bees are not able to decide on untrained sample patterns (Transfer test 3). Moreover the choice frequency for two sample pattern (one of them beeing the correct one) at different distances to the entrance is better than random choice. (c) Results of experimental series I indicate an exponential decay of matching accuracy with increase of flight time. (d) Sample pattern used for training and testing.

2.1 Series I.

In this series the tunnel was 4.8 m long, except of the last two trials where the length was increased to 7.2 m. The sampple pattern was positioned 25 cm from the decision chamber. In the decision chamber the bees had to choose the pattern that matched the sample pattern presented in the tunnel to get a reward. To measure an estimate of the retention time, the delay time was defined as the duration between the bees passing the pattern and entering the decision chamber.
During the test phase, the position of the sample stimulus was varied systematically.

2.2 Series II.

In a training phase, bees were trained with a single pattern. This sample pattern was positioned 120 cm from the entrance of the decision chamber. After that the bees were tested with two pattern, one representing the "correct" one. The position of the sample pattern was 120 cm from the entrance of the decision chamber, whereas the incorrect pattern was presented at a distance of either 50 cm or 170 cm from the entrance of the decision chamber.

2.3 Series III.

In the training phase of the 3rd series, bees were trained with 2 sample pattern 50 cm apart. During the training the positions of the two samples were changed regularly, but the distance was always kept and the sequential order of the correct and incorrect sampled was always preserved. In one training experiment the correct sample pattern was always the first one, in a second training experiment the second pattern was the correct one. To test whether bees could generalize the rule they learned, they were also trained with with novel patterns.
In the test phase the pattern positions were randomly varied.

2.4 Data collection

In 20 min training blocks, sample pattern were presented alternatively during training and testing phase. The position of the comparison patterns were swapped every 10 min. For the data analysis all choices for each visit of the bees were taken and the performance of each bee was evaluated separately. To ensure statistical independence of the samples the sample size (n) was taken to be the number of bees. To determine whether the performance of the choices was better than random t-test was used.

3 Results

The performance of the experiments was measured over all 286 visits by the 16 bees.

3.1 Series I.

With an average frequency of choice of 75 ± 3 percent in favor of the matching pattern, bees showed a strong significant preference. The average delay time measured was 1.24 ± 0.1 sec. The experiments with different tunnel length revealed, that the accuracy with with the bees matched the sample pattern in the decision chamber decreased with as the distance increased (Fig. 1 c). At a tunnel length of 375 cm the average delay time was 6.52 ± 0.86 sec, with a performance significantly better than random choice. At a tunnel length of 475 cm the average delay time was 8.86 ± 1.23 sec, with a performance at randome choice level.

3.2 Series II.

In the training tests, the bees choosed the correct pattern with a rate of 64 ± 3 percent (see figure 1 b). The bees continued choosing the right matching pattern in the decision chamber at a rate of 64 ± 4 percent, when the incorrect sample pattern was presented behind the correct pattern. In the third set of tests, the correct sample pattern was placed 50 cm and the incorrect at a distance of 170 cm before the entrance of the decision chamber. Having a training distance of 120 cm before the entrance of the decision chamber, the bees were confused and choice frequency of 50 ± 6 percent was at random choice level.

3.3 Series III.

The results of the first experiments show, that bees are able to learn to choose the first sample pattern presented. With a choice frequency of 73 ± 3 percent the rate was significantly better than random choice. Confronting the bees with unfamiliar sample sets the choice frequency was 66 ± 4 percent.

4 Discussion

The results of series I revealed that sample pattern can be held in memory for period of 5 sec. It was also shown, that the information retained in the working memory decays exponentially as a function of time. The experimental results of series II demonstrate, that not only sample pattern are learned, but also acquire information about the distance to the dicision chamber are taken into account. The experimental results of series III indicate, that bees

can learn which of presented patterns is the pattern to be matched. The learned rules can also be applied to novel sample patterns. In contrast the bees were not able to make decisions by learning the position of the relevant sample.

5 Supporting material

The supporting material contains a video, showing the apparatus and the flight of the bees. This video can be found on:
http://www.pnas.org/content/suppl/2005/03/21/0501440102.DC1/01440Movie1.mpg

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Adriana Schatton

Neuronal correlates of parametric working memory in the prefrontal cortex.

L. Romo | C.D. Brody | A. Hernández | L. Lemus

1999 Nature 399(6735):470-3

Summary

In this study the authors first present electrophysiological evidence for PFC (prefrontal cortex) neurons which presumably encode information about one-dimensional sensory stimulus quantities in working memory. In order to test their hypothesis, Romo et al. applied the 'vibrotactile discrimination task'. The subject's (human or monkey) finger tip touches a mechanical stimulator which delivers a certain vibration. After a delay of three seconds a second stimulus in a different frequency is applied (Fig. 1a). The subject now has to compare these two stimuli and pushes one out of two response buttons depending on whether the frequency of the second stimulus was higher or lower than the first one. As the different frequencies lie on a continuous scale between 6 and 42 Hz, this task is parametric. Two different stimuli sets were used (Fig. 1b, c).

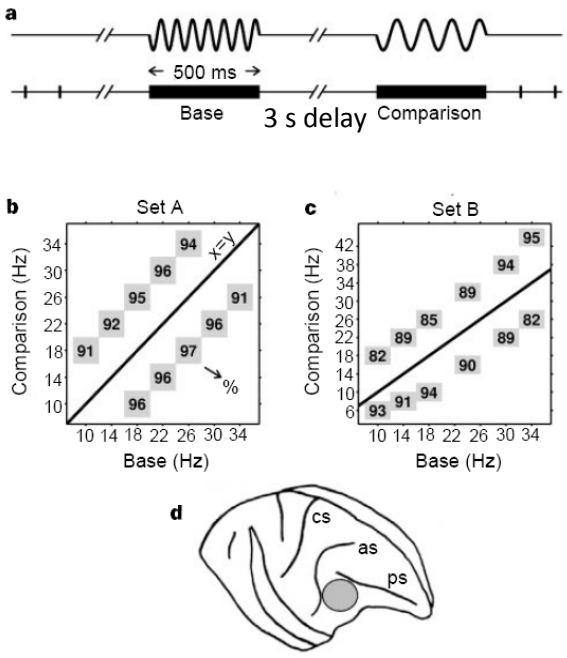


Fig. 1 vibrotactile discrimination task. a, sequence of delivered stimuli. b, pairs of frequencies, numbers in grey boxes give the percentage of correct trials. Set A: Probability (p) to experience a lower comparison stimulus varies between 0 and 1. c, Set B: p=0,5. d, insertion site in the PFC next to the principle sulcus (ps)

After training, neurophysiological recordings were made during task performance. Therefore, four monkeys (*Macaca mulatta*) were trained to accomplish the task. During test performance, seven independently movable microelectrodes (500µm apart, in parallel) recorded from the prefrontal cortex. In a pilot study conducted earlier, the authors found neurons only in the inferior convexity of the PFC (Fig. 1d) responded during the whole task. In this study they were exclusively interested in the neuronal activity during the **delay period**. From the first 3 macaques (stimulus set A) they successfully recorded 318 neurons that discharged during the delay and categorized them according to their discharge features. Two main groups could be distinguished: 'positive monotonic neurons', which increase their discharge rate with increasing base frequency and 'negative monotonic neurons' whose firing rate decreases with higher base frequencies (Fig. 2a, b, e, f).

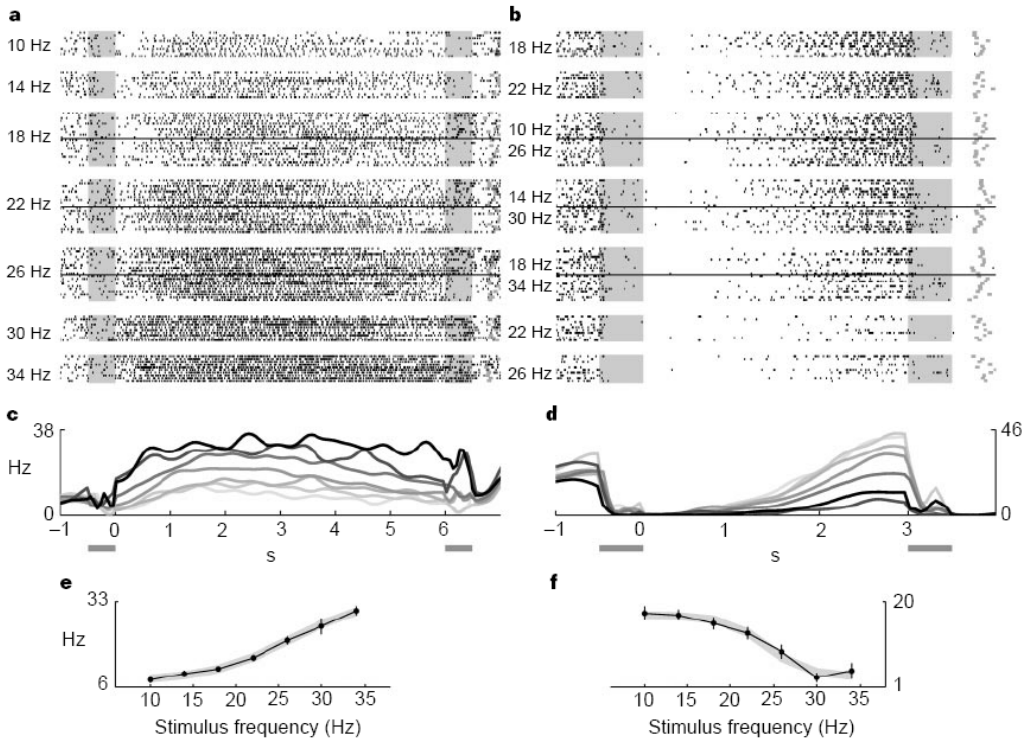


Fig. 2 discharge of recorded neurons. a, c, e positive monotonic. b, d, f negative monotonic. a, numbers on the left indicate base frequency, numbers in the center comparison frequency, every line of dots comprises a trial, each dot is an action potential, grey boxes in a, b, c, d: delivered stimuli. e, f, mean firing rates averaged across delay period plotted against the base frequency. b, grey dots at the end indicate motor movement (to push the button)

In both groups most of the recorded neurons could be further subclassified into **a) 'early neurons'**, responding quickly after the base stimulus, **b) 'persistent neurons'**, carrying a signal about the base stimulus during the whole delay period (Fig. 2c) and **c) 'late neurons'**, responding during the last second of the delay period (Fig.2d).

These amazing results led to the question **'Which information do PFC neurons of the inferior convexity encode actually – the base frequency or the anticipated motor act?'** With the help of a very clever idea Romo et al. could find the answer: Instead of delivering stimuli set A (Fig. 1b) where the probability for the comparison stimulus to be lower than the base frequency varies between 0 and 1, they applied stimuli set B (Fig. 1c). Here, the base frequency doesn't carry any information about the anticipated motor act (to push the right button) because there is always a 50:50 chance for each button to be the right one. As the proportion between the different neuron classes ('early', 'persistent' and 'late'), which were recorded in the fourth macaque, was the same as in the set A trials, the recorded PFC neurons shouldn't encode any information about the base frequency. The authors conclude that monotonic neurons were encoding the memorized base stimulus frequency itself.

Summarized they had two findings: **1)** working memory responses for tasks that do not include a spatial component are preferentially found in the ventral region of the lateral PFC, **2)** PFC neurons can retain working memory information also induced by non-visual modalities.

Speed and accuracy of olfactory discrimination in the rat

Matthias Kluge

1 Introduction

Odorant receptors are located in the olfactory bulb and compose the glomeruli. An odor activates such in a unique pattern, some even with highly overlapping glomerular representation, which can be discriminated by rats. The conventional paradigm is that olfaction is a slow sense, implying a trade-off between speed and accuracy of discrimination over the time scale of the temporal evolution of the representation. Several studies suggest that the identification of distinct odors can be achieved in $<= 0.5s$[1]. In contrast, humans performing difficult binary mixture discriminations are quite slow with 1 - 2 s.

The results of the presented study was obtained by operant conditioning using a two-alternative choice odor discrimination. A dissimilar odor pair was discriminated with a median odor sampling time(between odor onset and withdrawal from the odor port) of 223ms[229ms] and an accuracy of 97.4%[95.6%] and a median movement time(between withdrawal from the odor port and entry into the choice port) of 274ms[272ms]. Similar results were obtained for highly overlapping glomerular activation patterns shown in the brackets before.

2 Discrimination speed

The relationship between similarity in glomerular representations and the accuracy and timing of the discrimination is examined by intrinsic optical imaging, which maps the responses of the olfactory bulb to different odors. Glomerular activity patterns were more similar within a odor class[2]. Odor similarity was quantified using a vector distance metric[3].

Based on these results pairs of similar and dissimilar odor pairs were chosen and four rats were trained for each set. $>$ 90% accuracy was achieved, with a significant correlation between odor similarity and accuracy, as shown in figure 6. Despite

[1] for example, see original paper refs.
[2] three aliphatic acids and four alcohols
[3] cosine measure and euclidian distance

our paradigm the odor sampling time was not significantly correlated with odor similarity, as well as with movement time and odor similarity. Therefore no additional time is needed for accurately discriminating odors which activate largely overlapping glomerular representations.

Since the mono molecular odor trial may not be sufficient enough of a challenge to the olfactory system, mixtures containing different proportions are introduced to increase difficulty. These results are described by a sigmoidal psychometric performance function, with discrimination accuracy dropping sharply for mixture ratios near 50/50, as shown in figure 6.

To see if this rapid odor discrimination behavior holds to differing experimental manipulations the following were tested.

- delivering the single difficult mixture pairs throughout a session
- lowering the odor concentration 100-fold
- increasing the variance of the random foreperiod(latency between nose poke and odor onset)

None of these differing conditions increased the absolute odor sampling time. Therefore a rapid odor sampling strategy for discrimination which is independent of the difficulty and further experiment parameters is implied.

3 Discrimination accuracy

Using a conditional accuracy analysis[4], the discrimination accuracy increased only over the first $200ms$. Also, performance could not be positively correlated with the sampling time beyond $250ms$. Therefore, beyond a relatively short time, longer odor sampling times tended to be associated with degraded rather than improved accuracy.

4 Maximum discrimination

Temperature sensors were implemented to measure the nasal flow, thus, recording the odor sampling sniffing pattern. Linear relationship can be approximated between the number of sniffs and the odor sampling span. At odor onset, the sniffing frequency was highest with a following decline. Usually, one till two sniffs were sufficient to discriminate and there was no change with difficulty. Repetitive sampling could not improve odor discrimination.

Novel odors increase the respiration cycle significantly and is termed 'exploratory sniffing'. Distinct behavioral responses to novel and learned odorants can emerge in under 200 ms. Given that the respiration frequency at the time of odor sampling is 1 till 2 Hz, this result implies that novel odors are identified as as such after only one inhalation.

[4] makes use of the natural variability in reaction tune within a single condition

5 Discussion

Only a small trade-off between the difficulty of discrimination and the required odor sampling was found during the rat-trials. Independent of the odor mixture, one or two sniffs were used to perform the discrimination. That less than 200 ms were sufficient to achieve the maximum accuracy could be deducted by the natural variability in the odor sampling period. When more sniffs were taken, no improvement of the discrimination accuracy was measured. Deciding between two odors with largely overlapping glomerular representations, can be carried out as fast as the limits imposed by the olfactory sampling process.

Performance of fine odor discriminations by the rat does not depend on slow temporal processing, as this would have introduced an obligatory increase in accuracy during the refinement of the representation. The data suggests that repeated samples did not improve the representation of odor identity. This suggest that olfactory information may be temporally chunked or quantized by the respiration cycle, such that each sniff constitutes a discrete olfactory sensory image, also referred to as a snapshot. Crucial for the encoding of olfactory sensory information may be the respiration cycle. The firing of olfactory neurons is strongly patterned by the respiratory rhythm, and information about odor identity and concentration can be encoded in the phase of spiking relative to respiration-driven oscillations.

6 Methods

- Odor discrimination task: The correlation between odor sampling time and performance was calculated on the conditional accuracy function.
- Odor delivery: A custom olfactometer was constructed of Teflon tubing, fittings and solenoid valves.
- Intrinsic signal imaging: Long Evans rats (200 – 250 g) were used for imaging experiments. Animals were deeply anesthetized with medetomidine, fentanyl and diazepam and the bone and dura covering the dorsal surface of one olfactory bulb were removed. A well of dental cement was constructed, filled with agarose gel, and sealed with a glass cover slip to reduce brain movement. Anesthesia was maintained by periodic dosage with medetomidine. Light reflectance from the olfactory bulb (630 nm wavelength illumination from light emitting diodes) was captured using an analog CCD camera, frame grabber and custom acquisition software written using MATLAB.

7 Sources

Speed and accuracy of olfactory discrimination in the rat | Naoshige Uchida & Zachary F Mainen Nature Reviews Neuroscience
Rapid Encoding and Perception of Novel Odors in the Rat Daniel W. Wesson, Rayn M. Carey, Justus V. Verhagen, Matt Wachowiak PLoS Biology

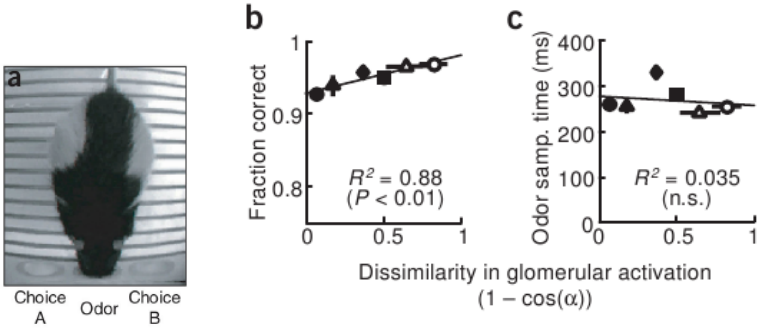


Figure 1: (a) Still frame of a rat performing a two-alternative forced-choice odor discrimination task. The rat is shown making a nose poke at the central odor port to trigger the delivery of an odor. Subsequently, the rat is rewarded for making a nose poke at the correct choice port (A or B), depending on the identity of the odor.(b–c) Performance accuracy (b), odor sampling time

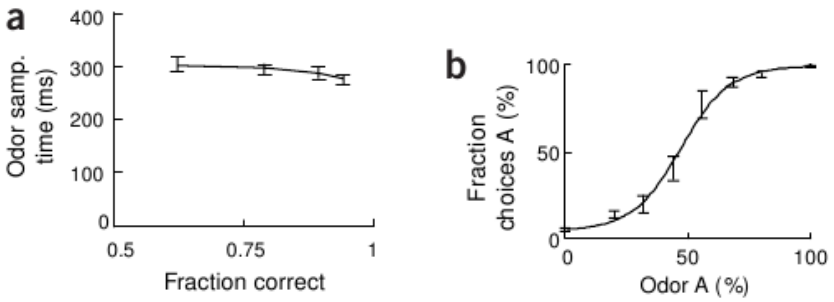
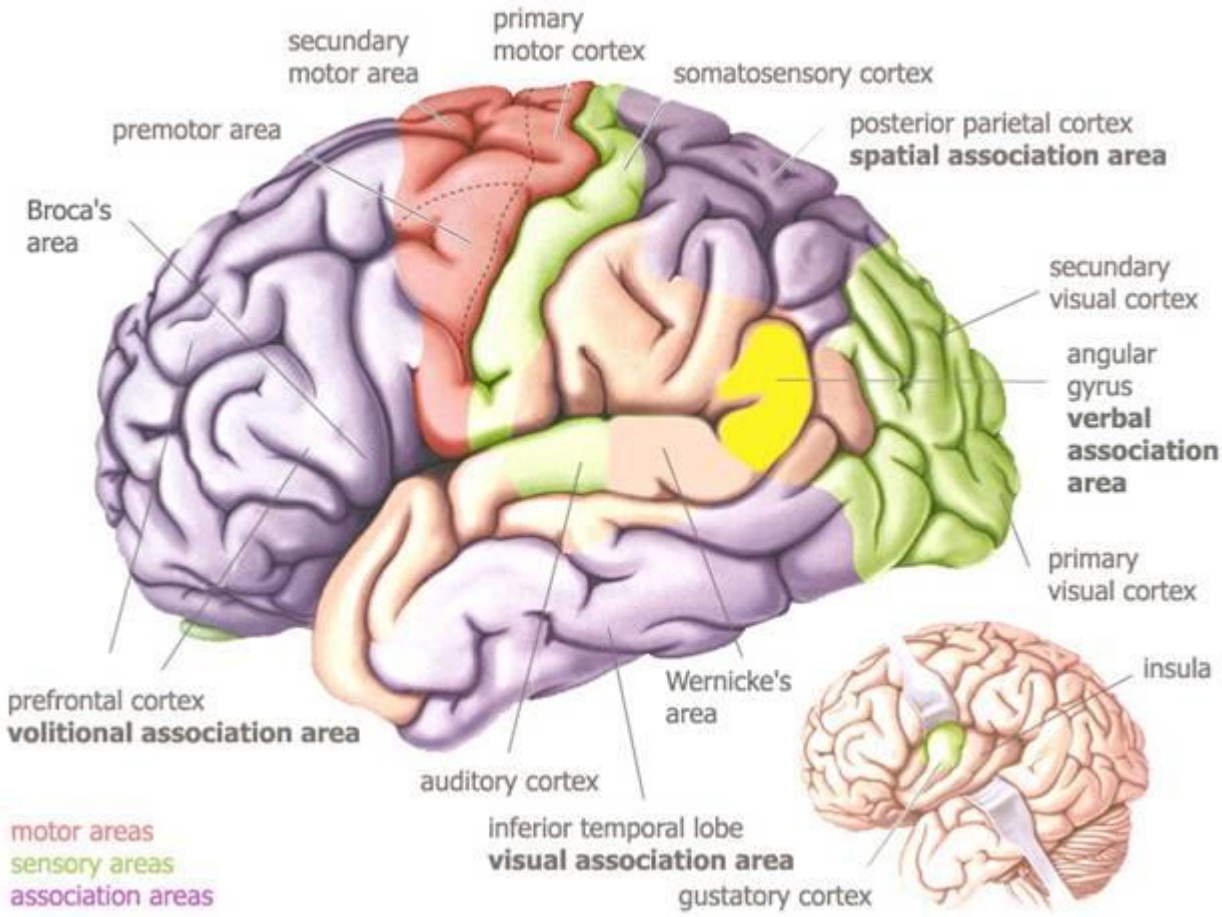


Figure 2: Odor sampling times are fast and largely independent of discrimination difficulty. (a) Median odor sampling time. (b) Performance of one rat in discriminating valeric acid and hexanol



Perceptual Decision Making In The Human Brain

A summary by Marcus Schroeder, September 2010

Each and every day your brain has to process hundreds of impressions you either see, feel, touch or smell. More important some of those impressions play a major role in what you are going to do next. For example you are in a grocery store and you want to make a nice fruit salad for dinner. You have to kinds of strawberries to choose from. One is really red, feels firm and smells like strawberries from your croft next door. The other is very soft with pressure marks and even worse you can also spot some mould. Depending on your sensory information and your experience of life you would probably go and take the first one to the cashier. In this summary I describe the process that is going on in the human brain if you have to make a decision depending on sensory information. This implies the location of important regions in the brain and the methods to obtain knowledge about decision making.

What is perceptual decision making?

The process of choosing one option from a set of alternatives based on sensory information is called perceptual decision making. Sensory information is gathered from lower-level sensory systems in the brain and will be combined and later on used by higher-level decision areas to compute the decision variable and to make a statement which course of action seems to be the best one.

Perceptual decision making is also influenced by some other factors like attention, task difficulty, prior probability of occurrence of an event and the outcome of the decision. If and how perceptual decision making influences the valuation of our decisions is not yet clear (Rangel, et al., 2008).

(Heekeren, et al., 2008) provide a model to sketch the neural architecture for the process of decision making. This model consists of the following four complementary modules that are in parts overlapping (see Figure 1):

(1) Accumulate and compare sensory evidence
(2) Detects perceptual uncertainty and signals if more attentional resources are required
(3) Represents decision variables and includes motor and premotor systems
(4) Monitors performance (detecting errors and signalling to adjust decision strategies)

The process from perception to action is non-linear which means that the modules mentioned above can be active in parallel. For example while you are reading this text you are processing the information that is written but for that you don't have to stop reading e.g. this means you continue getting visual information to process.

Although humans have a more abstract decision making network than monkeys, which allows us to establish a better link between decision and action, it is very likely that the neuronal architecture for decision making has its roots in the brain in a common ancestor of humans and monkeys.

Based on the assumption that decisions are formed by continuously accumulation of sensory information the process of perceptual decision making can be modelled as a stochastic diffusion process. Depending on the strength of the sensory signal and the accumulation rate a quantification of evidence (e.g. the decision variable) will increase faster or slower until one of two criteria is reached (See Box 1). With a model like this it is also possible to predict the decision of an individual with neuroimaging techniques (Heekeren, et al., 2008).

Where is perceptual decision making located in our brain?

Humans usually are able to smell scents, hear sounds, see landscapes etc. For each kind of stimulus there exists a specific region in the brain that is important for decision making (also for something like recognition of faces we have the fusiform-face area (see Box 1)). The primary and secondary somatosensory cortex can be activated by tactile stimuli. Visual stimulation can result in activity in the ventral temporal cortex and sounds can stimulate the primary auditory cortex. Olfaction can activate for example the posterior piriform cortex (Uchida, et al., 2006). Depending on the kind of stimulus different regions in the brain are activated which accumulate and compare the input of specific sensory neurons. For example for tactile stimuli it is the dorsolateral prefrontal cortex (DLPFC). For visual stimuli it is the lateral intraparietal area. The neural activity increases faster on easier tasks than on difficult. Easier tasks are processed by lower-level decision areas and harder

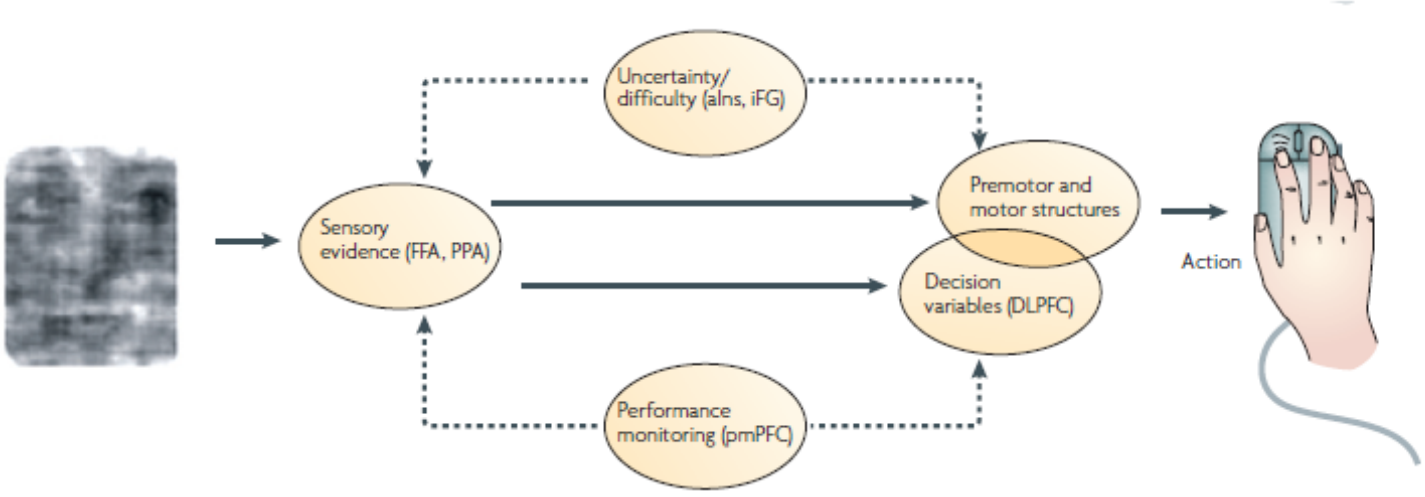


Figure 1| A model for the neuronal architecture of perceptual decision making.
Sensory information like a picture of a face stimulates the corresponding sensory evidence area in the brain (for example the fusiform-face-area (FFA)). The information is accumulated and compared to compute a decision variable (for example in the dorsolateral prefrontal cortex). The whole time the module *performance monitoring* checks for errors in perception and signals if adjustment of action or decision has to be made. Another module (uncertainty/difficulty) checks for the task difficulty and if the amount of sensory evidence is not sufficient. (Heekeren, et al., 2008)

tasks by higher-level decision areas, like the posterior portion of the left DLPFC. Comparison of the outputs of selectively tuned lower-level sensory neurons may serve as a basis for the computation of decisions in higher-level regions. Higher-level regions also show a specific behaviour. They have the highest activity in tasks that have a large amount of perceptual conditions of a specific category and their activity is correlated with the difference between the output signal of the two brain regions containing pools of selectively tuned lower-level sensory neurons (Heekeren, et al., 2004). Regions that are important for selecting and planning play an important role in deciding which action to execute. Those regions do not just accumulate sensory evidence they also translate the evidence into an action independently of response modality. Performance monitoring (like checking for errors in the perception), and signalling the need for adjustment of actions are important tools of our behaviour. To date it is not so clear if the monitoring systems selectively adjust sensitivity of the sensory regions or if they adjust the decision criteria.

How to measure decision making?

The first steps in analyzing the process of decision making were done in neuroimaging experiments with monkeys. The monkeys had to solve easy problems like which of the buttons has a higher vibratory frequency. Therefore the monkeys had to

Box 1| Face-house categorization task

Participants have to decide whether an image presented on a computer screen is a face or a house, while in the meantime their brains are observed with fMRI. The two regions fusiform-face area for faces and the parahippocampal place area, both lying in the ventral temporal cortex, showed a greater response to faces than to houses and vice versa, while the response was greater on images without noise (see Figure 2a). Only correct answers were used to calculate the mean fMRI response. When the pictures got more and more degraded two areas – the Frontal Eye Field and parietal regions – answered with a higher neural activity. Higher-level decision making areas – like the left posterior DLPFC, the posterior cingulated cortex and the superior frontal gyrus – showed a greater response (BOLD-activity) for more fuzzy pictures. It is assumed that higher-level regions take the output from lower-level regions. The overall response-time gets also slower, if more noise is added to the pictures (see Figure 2b). (Heekeren, et al., 2004)

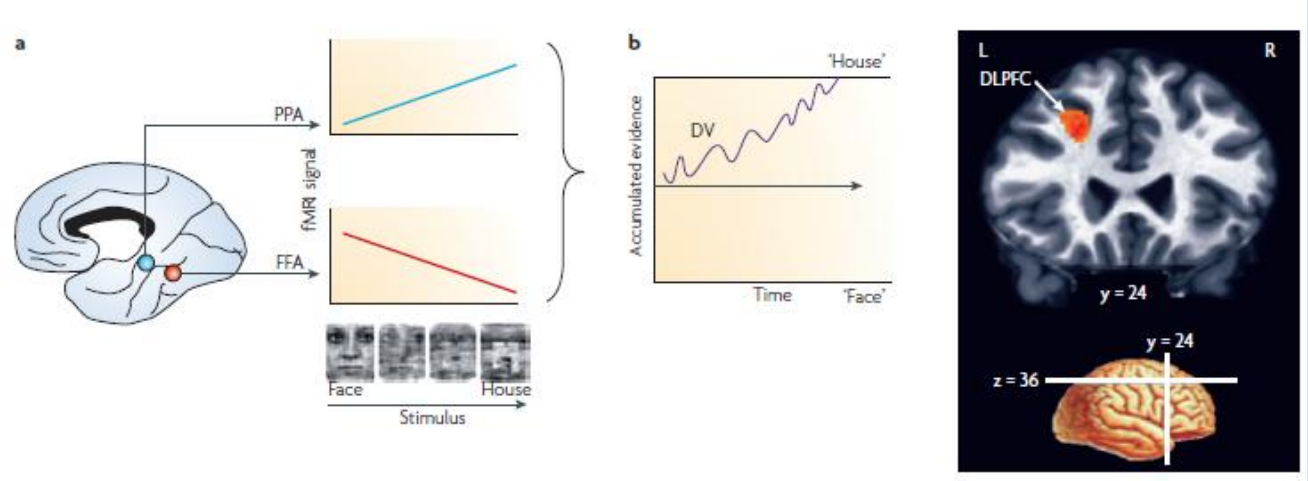


Figure 2| Representation of sensory evidence in lower-level regions and perceptual decision making in the posterior DLPFC
a) If the test person saw a clear picture of a house the fMRI signal in the corresponding region (parahippocampal place area, fusiform-face area) was larger and decreased with increasing noise. b) A decision variable (DV) is computed by comparison and accumulation of the output of lower-level sensory regions. The DV drifts between two boundaries until it reaches a certain threshold and a decision is made (“House!”). The DV is computed in downstream cortical regions like the dorsolateral prefrontal cortex (red area). (Heekeren, et al., 2008)

touch the buttons to feel the difference and then to decide - based on their perception - which button they should press. During the performance single neurons were observed for example with micro-electrodes. This procedure is called *single-unit-recording study*.

To research decision making other technical methods *like functional magnetic resonance imaging* (fMRI) and *electroencephalography* (EEG) were used. FMRI measures the change in blood flow related to neural activity in the brain or spinal cord. FMRI has a high spatial resolution but relatively poor temporal resolution. It can also be used to measure the *blood-oxygen-level-dependent* (BOLD) signal. Increases in the bold signal are proportional to changes in the neuronal activity in given regions. EEG monitors the electrical signals from the brain that reach a threshold and measures the neural activity this way. It has a good temporal resolution and a poor spatial resolution. EEG and fMRI are complementary techniques and should be used simultaneously.

Other methods to obtain neuroimages are the *transcranial magnetic simulation* (TMS), *magnetoencephalography* (MET) and the *positron emission tomography* (PET).

Tasks like the one just mentioned can be made up for humans as well. For different kinds of stimuli different types of tasks had to be performed. Vibrotactile tasks were used to identify those regions that are important for decision making based on tactile information. The main area therefore is the primary somatosensory cortex. For the visual information the test person had to decide if they see a face or a house on a given picture. In this face/house-task a fusiform-face-area (recognizes faces) and a parahippocampal place area (recognizes houses) were identified in the ventral temporal cortex. The clearer the image was the greater was the response in one of the regions. An auditory task revealed information about the processing of auditory stimulus. Therefore the test person had to identify speech sounds which were more or less degraded with noise. What we know today as the primary auditory cortex seems to represent the sensory evidence that is relevant for making decisions based on auditory evidence.

What are the benefits?

A better understanding in how humans make decision and where the process of perceptual decision making takes place will provide a deeper insight about clinical brain disorders like indecisiveness, inflexibility, hallucinations, misperceptions and schizophrenia. But it helps us also to gain knowledge in the complex decision making processes of everyday life. Another field of interest is how the brain values different choices and how the perceptual decision making system interacts then with valuation.

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Summary: "Overlapping and Distinct Neural Systems Code for Subjective Value during Intertemporal and Risky Decision Making" by Jan Peters and Christian Bchel

Bastian Kayser

September 6, 2010

1 Introduction

One of the most challenging fields in decision neuroscience is to identify and understand the neural mechanisms of human decision-making. One aspect of this research area is the study of value-based decisions which are involved in all areas of human behavior from watching tv to stock market trading. In most decision theories it is assumed that subjects condense the various parts of an option and its outcome (reward) into one subjective value and than choose the option with the highest value [7].
In their paper "Overlapping and Distinct Neural Systems Code for Subjective Value during Intertemporal and Risky Decision Making" the authors Jan Peters and Christian Büchel used functional magnetic resonance imaging (fMRI) to investigate the neural systems that are involved in probabilistic and intertemporal decision making. The main goal was to find neural systems that code for subjective value during delayed and probabilistic decision processes involving monetary rewards.

2 Methods

Two experiments were conducted. The first (Experiment 1) consisted of two behavioral tests, one behavioral test under fMRI and one behavioral session to determine long-term stability of discounting.
The second experiment (Experiment 2) consisted of one behavioral test and was designed to examine if delayed rewards had a higher preference than probabilistic rewards or vice versa.

2.1 Risky(probabilisitic) and delayed(temporal) decisions

Temporal decisions Delayed decsisions have a temporal delay between the decision and the outcome. In the experiments presented in the work of Peters and Büchel the reward was an amount of money which actual payment was delayed.

Probabilistic decisions Probabilistic decisions have a certain probability assigned to the outcome of an option, e.g. a subject can choose between €20 with a probability of 1 or €26 with a probability of 0.8.

2.2 Experiment 1

First two behavioral tests In the first behavioral session volunteers made repeated choices between a immediate monetary reward of €20 and greater amounts available at different delays (delay discounting (DD)) or probabilities (probability discounting (PD)). The algorithm used to generate the choices increased the amount of the delayed/probabilistic option after two successive choices of the immediate reward. After two successive choices of the delayed/probabilistic option, the algorithm decreased the amount of these options. Decrease and increase where done in a stepwise manner. The algorithm terminated, as soon as the difference between the accepted/rejected amount reached a delay/probabilistic-specific threshold. From these results the authors calculated the "indifference amounts" by averaging the amounts of the delayed/probabilistic option at which the participant's preference of choice between the delayed/probabilistic and immediate reward was reversed. These indifference amounts were converted into proportions of he fixed reward (€20) and the following function were fit against them to obtain the discount-rates k for each participant:

$$SV_{DD} = \frac{1}{1 + k \cdot D}$$

$$SV_{PD} = \frac{1}{1 + k \cdot \theta}$$

where SV is subjective value, D is delay in days and θ is the odds-against-winning transformation of reward probability P

$$\theta = \frac{1 - P}{P}$$

. In other words: θ is the odds that the reward is not paid.

For one participant, the best-fitting discount-rate k describes that individual's choice behavior. These values were compared between the different behavioral sessions to test for long-term and short-term stability in the choice behavior.

This behavioral session was repeated after a median time span of 9 days to test stability of participants choices and to compute adequate delayed/probabilistic offers for the fMRI test session.

fMRI test During the fMRI test session, the participants made choices between the immediate reward of € 20 and a delayed or probabilistic reward. The offered rewards were chosen individually according to the behavioral pretests. The offers were calculated in such a way that the participants chose the delayed/probabilistic offer in ∼50% of trial. The fMRI scan was conducted 4 days after the second behavioral test.

Behavioral test for long-term stability A third behavioral session was conducted 4 month after the fMRI session to test for long-term stability in choice preferences. The test itself was similar two the first behavioral tests.

2.3 Experiment 2

To verify the assumption that delayed and probabilistic rewards were equally valuable, the authors conducted a second behavioral experiment. Here the participants had to chose between a reward of € 20 with a given probability and € 20 with a given delay. The probabilities and delays were calculated such that in half the trials the delayed option had a greater subjective value, in the other half of the trials the probabilistic option had a greater subjective value. The calculations were based on behavioral prestests.

2.4 functional magnetic resonance imaging (fMRI)

Functional magnetic resonance imaging is a noninvasive medical imaging technique and belongs to he class of nuclear magnetic resonance imaging (NMRI) procedure. These techniques use the fact that hydrogen atoms in the human body, i.e. the hydrogen nuclei, can be influenced through electromagnetic fields. In NMRI, electromagnetic signals emitted by the hydrogen nuclei in a strong magnetic field are detected and used to construct an image. This is possible because the behavior of the nuclei depend on their molecular embedding which varies between different tissues. This and the different concentration of water in the body shows up in the constructed images and is used to differentiate between anatomical structures.

In functional magnetic resonance imaging, the change between oxyhemoglobin and deoxyhemoglobin is detected through their different behavior in the magnetic field that is applied in fMRI. While the deoxyhemoglobin locally decreases the field intensities, oxyhemoglobin does not have this effect. Different levels of capillary oxygenation therefore show in the detected magnetic field intensities. The underlying assumption is that different levels of neural activity are reflected by metabolic changes (oxygenation/deoxygenation).

In the fMRI test session the authors recorded the blood oxygenation level depend (BOLD) signal while varying the subjective value of the probabilistic and delayed monetary reward. This allowed the analyses of overlapping and distinct neural systems involved in subjective valuation during probabilistic and delayed decision making. The analysis of the fMRI results was done with the General Linear Model (GML) approach. For details see [3] and [4].

3 Results

3.1 Experiment 1

Long-term and short-term stability of decisions The subset of 13 subjects who participated in the long-term behavioral experiment showed a high long-term stability in their choice preferences. A linear regression of the discount rates k from test and retest gave a p-value of 0.009 (DD) and 0.0026 (PD). See figure 2(a,c) for details.

The participants showed also stability in their choice preferences between behavioral test sessions and the fMRI session. See figure 2 (b,d) for details. The results also showed that the participants discarded delayed/probabilistic

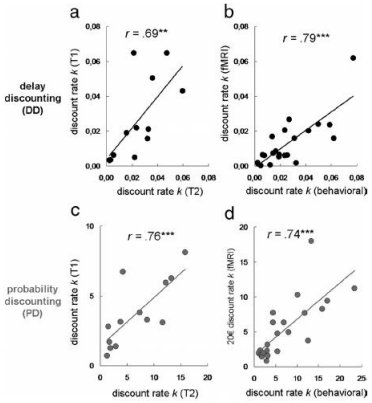

Figure 2. Discount rates (k parameters) showed long-term stability across 4 months ($n = 13$ subjects; ***a***, delay discounting, $p = 0.009$; ***c***, probability discounting, $p = 0.0026$) and between behavioral and fMRI sessions ($n = 22$ subjects; ***b***, delay discounting, $p = 0.00001$; ***d***, probability discounting, $p = 0.00008$).

rewards in a hyperbolic manner over time/probability (not shown).

fMRI data The fMRI images were searched for areas of high activity which correlated with subjective values of delayed or probabilistic rewards. These subjective values were calculated by multiplying the objective amount of a reward by a subject-specific discount fraction for that delay/probability. This discount fraction was determined in the behavioral pretests.
Along the regions that showed a high correlation with subjective values of delayed rewards were the **posterior cingulate cortex**, **the medial prefrontal cortex (PFC)**,**bilateral parietal cortex** and **the left ventral striatum**.

Along the regions that showed a high correlation with subjective values of probabilistic rewards were the **right superior/inferior parietal lobule**, **the left middle occipital gyrus** and **the left ventral striatum**. The authors looked also for regions that showed a high activity during probabilistic and delayed discounting. The **left ventral striatum** and the **right central orbifrontal cortex (OFC)** showed a a positive correlation with subjective values during delayed and probabilistic discounting. For details and a complete list of all regions involved see [2] and [5].

3.2 Experiment 2

This behavioral experiment showed that there was no general preference to delayed or probabilistic rewards. For further details see [2] and [5].

4 Conclusion

The behavioral experiments showed short-term and long-term stability in the subjects choice preferences. Furthermore the participants discounted monetary rewards in a hyperbolic manner. It was also shown that there was no general preference towards delayed or probabilistic rewards. Therefore both discount options seem to have the same intrinsic value.
The fMRI scans showed that the neural systems involved in temporal and probabilistic value-based decisions differ for most regions. This suggests that there exist distinct neural systems for valuation of risky and temporal decisions.
The fact that the ventral striatum and the right OFC were involved in both decision types suggests that these code for subjective values in a domain-general manner. Overall the experiments confirm and extend the current results in decision neuroscience.

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Social Decision Making

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Prof. Dorothea Eisenhardt

9th - 11th September 2010

1 Introduction

Decisions must be made in everyday life. It can be especially hard if the individuals live in the group, as it is the case in many insects. In order to achieve their goals such as finding resources they must cooperate to increase individual success. One example of such social animals are cockroaches. In case of german cockraoaches (*Blatella germanica*) it is the common preference to look for the dark places and to live together which increases their reproductive opportunities, sharing of resources like shelter or food, etc.

The interesting questions are: *(i)* how do they make the decision and *(ii)* how do they cope with the crowding effect.

Halloy et al. (2007) studied these questions in a group of custom-designed robots which by imitating the insects were able to join the group and change their decision of preferable shelter. Another approach was used by Ame et al. (2006) who designed the behavioral model describing how cockroaches optimize group size and then tested it experimentally. Both contributions try to explain how cockroaches or other social animals make decisions that do not involve leadership. Both studies will be briefly reviewed here.

2 Collegial decision making based on social amplification leads to optimal group formation

Ame et al. (2006) who performed experiments looking at how a group of cockroaches would split into seperate shelters. Experimenters varied

the number of shelters, their sizes and darkness. After cockroaches were placed inside the plate, they first scattered randomly around, arbitrary choosing one of the shelters. At some point, enough of them were under one patch so that critical mass was reached and this hiding place became more attractive to the others. If there was any shelter able to house all the insects, all of them chose to hide under it. If, however, there was no such a shelter present, but still all were of equal quality (the same amount of light passed through) the cockraoaches divided themselves up perfectly within the shelters. For example, if there were 50 insects and 3 shelters, each able to house 40 animals, the group divided itself to two equal (25 cockroaches each) subgroups, while the third shelter was left empty.

The above findings were used to design a simple model of cockroach social behaviour. The model assumed that the cockroaches use only two pieces of information in deciding where to go: darkness of the place and the number of individuals occupying it. The more insects are under the shelter, the greater probability that none of them leaves, but also the lower probability for any other insect to enter it. The system stays dynamic at all times. Any cockroach can change the decision at random of leaving the group and explore again.

3 Social Integration of Robots into Groups of Cockroaches to Control Self-Organized Choices

Cockroaches recognize each other using antennas (which are very sensitive olfactory organs). They are not very discriminative, therefore, the experimental group of cockroaches accepted the robots which had the same smell and roughly the same size. To ensure that the robots are truly accepted, they were programmed to act similarly to their natural brothers that is to prefer the crowds and darkness (in experimental conditions cockroaches chosen darker shelter in 73% of the trials; Figure 1) [2]. Since the gathering behaviour did not change after the robots were introduced to a group of cockroaches it was concluded that the robots were treated as equals. Then, to check if cockroaches' decisions can be altered, researchers preprogrammed the robots so they preferred the lighter shelters but they still preserved their strong need for being with others. The results showed (Figure 1) that even if there were less robots, in many cases, the machines were still able to encourage the others to come under the lighter patch which was not observed in their absence (in 61% in comparison to 27 % when robots were not present). Because of their social behavior, however, in 39% robots were driven by the insects under the darker shelter.

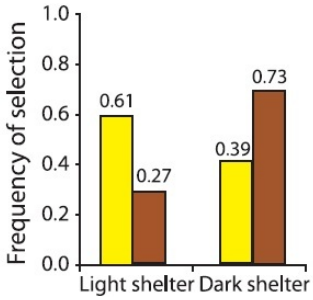

Figure 1: Experimental collective choice between dark and light shelters. Groups of cockroaches without robots (brown bars) selected the dark shelter in 73% and the light shelter in 27% of the trials. Mixed groups with robots programmed to prefer the light shelter (yellow bars) selected it in 62% of the trials. Figure adapted from Halloy et al. (2007)

.

4 Conclusions

Results of both studies allowed the researchers to develop a mathematical model of cockroach group behaviour. Additionally, it was shown that there is no leader in the group of insects. However, an introduction of artificial agents can make the group follow them to arbitrary shelters. An open question remains if also other animals, such as goats, could be led by artificial agents to some predefined places.

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Getting to know you: Reputation and trust in a two-person exchange game

Brooks King-Casas, Damon Tomlin, Cedric Anen, Colin F. Camerer, Steven R. Quartz, P. Read Montague

Summary by Jia Shen Guo

Introduction

Reputation and trust are two fundamental elements in human society which are believed to have influenced the cognitive evolution of *Homo sapiens* (Tomasello et al. 2005) as well as given rise to complex cultural institutions such as trade. In everyday life they alter our behaviour towards fellow beings, for example in competitive or cooperative situations, by means of evaluation and prediction. From a neurobiological point of view the question arises how these decision are achieved by our brain respectively how and where they are encoded. The given article tries to shed some light on this issue by providing a series of results obtained in an economical game.

Decision making is a highly complex process involving many variables which have to be taken into account so in order to assess it scientifically experiments are commonly carried out in an artificial situation with set conditions incorporating elaborate social circumstances into more or less sophisticated games derived from game theory (Neumann & Morgenstern, 1994). These games may serve as a model for a wide variety of competitive or cooperative social interactions between the players when they are faced with the decision how to maximise their payoffs. Consequently, game strategies and leaning processes can be examined for example at the neural level via neuroimaging.

Methods

In the given study investigators were specifically interested in the effects of trust and reputation on social behaviour and the corresponding neural responses. Therefore they instructed two persons to play an economic exchange game. Each round of the game started with the first player (investor) investing any amount of his credits (starting with 20$) with the other player (trustee). The invested amount was then tripled and the trustee could decide which fraction he wanted to return. Concerning validity the game was played for ten consecutive rounds so that players could adapt to each ohers behaviour. Player identities were not revealed in order to minimise unwanted influences on trust. As for the neural analysis event-related hyperscan-fMRI was used to monitor brain activity which was converted into a blood oxygenation dependant (BOLD) signal. Scanning was done simultaneously allowing a direct comparison of the trust and reputation model and their corellations between both participants.

Results

48 pairs of subjects were analysed. Data revealed that reciprocity provided the best results for future predictions concerning trust changes which was mirrored in decreased or increased payments. These deviations were the reaction of one player to his partners behaviour in previous rounds. It turned out that the deviations from the investor's point of view were the most accurate predicting future changes in payment by the trustee so this was put into the center of attention. Three variations of reciprocity were identified. Benevolent reciprocity meant that the investor reacted to a previous decline in trustee payments by increasing the amount sent whereas malevolent reciprocity led to a decreased amount invested because the trustee returned more. In a neutral condition payments from both parties stayed the same.

Using the BOLD signal four regions (inferior frontal sulcus, superior frontal sulcus, thalamus and inferior/superior colliculli) were identified in the trustee's brain to be highly responsive to benevolent or malevolent changes in the investor's behaviour. Especially the head of the

caudate nucleus (located aside the thalamus) turned out to be highly sensitive to benevolent reciprocity expressed by the investor.

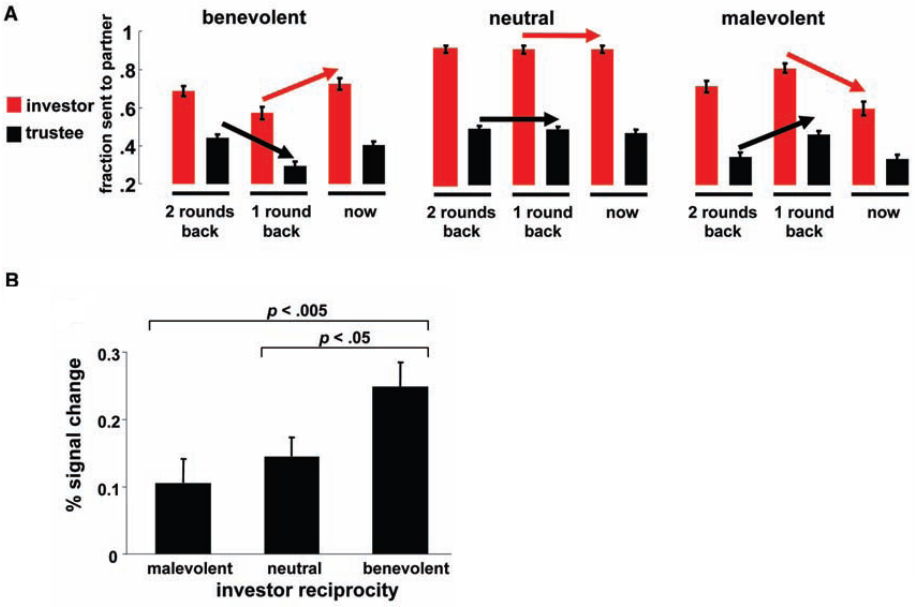

Figure 1:

A: Depicting the three different types of investor reciprocity

B: Depicting the response level of the trustee's head of caudate to different investor reciprocity. Signal is highest for benevolent reciprocity.

The head of the caudate was then subjected to a region-of-interest analysis (ROI) and the signal was termed the "intention to trust" signal. The expectation was that the caudate encoded future trust changes in the trustee's brain and that these trust signals should be represented in the investor's brain as well since he must be aware of the consequences of his behaviour. Correlations could be observed between the investor's MCC (middle cingulate cortex), the trustee's ACC (anterior cingulate cortex) and the trustee's caudate. Interestingly, the designated "intention to trust" signal in the caudate received a time shift of approximately 14 seconds forward during later rounds of the game.

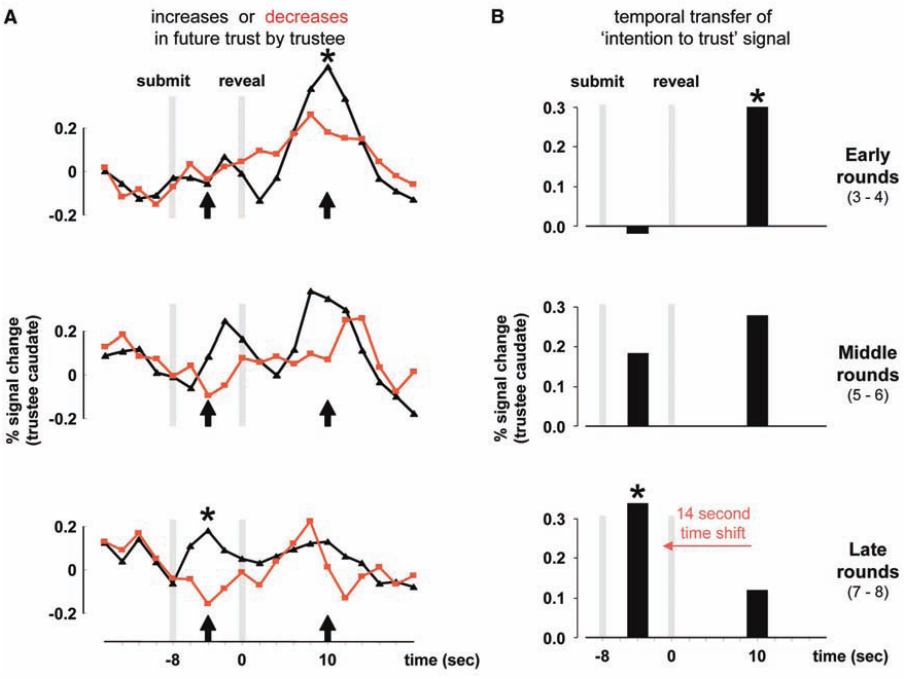

Figure 2:

A/B: Depicting the temporal shift of the caudate signal as a function of reputation building and learning. During later rounds the trustee seems to have evolved a model on the basis of the previous exchanges which enables him to anticipate the next investment.

This seemingly supports the idea that the player is building a model of his partner based on the previous rounds reflecting the investor's reputation, thus enabling the trustee to anticipate the next moves before the investment has been revealed. It is noteworthy that the caudate response only shifted in the case of benevolent reciprocity by the investor. To further evaluate this assumption a variation of the game was played where the trustee was instructed to guess the next investment. Guesses were most accurate during middle and late rounds of the game.

Discussion

On a whole the results suggest that reputation and trust during social decision making are taken into account and computed in different regions of the brain with the caudate involved in assessing the fairness of the situation and affecting the future decisions based on this evaluation through the "intention to trust" signal which is mainly connected to positive trust changes. The role of the caudate is reminiscent of observations found in reinforcement learning processes which involve dopaminergic neurons. In these kind of experiments a neutral stimulus is combined with a delayed sudden reward which evokes a strong reaction in dopaminergic neurons. Through repetition the burst reaction from the reward diminishes but instead the earlier neutral stimulus now triggers the response. The authors suggest that in this case the revelation of the increased investment would serve as the sudden reward evoking the "intention to trust" signal because it is not predicted early on in the game. Later on the increased investment is not surprising anymore shifting the signal forth in time. However it is unclear why based on this explanation the signal would alway occur just before the revealing of the investment.

Considering the accuracy of the study it should be remarked that the spatial and temporal resolution of the fMRI-(BOLD)-signal is only moderate, better serving as a means to highlight input to specific areas than their output (Logothetis & Wandall, 2004). Therefore it could be questioned whether the head of the caudate is indeed involved in the encoding of the "intention to trust" signal or if it simply functions as some sort of relay receiving information from different regions of the brain, maybe even as some kind of motor information since the striatum is also engaged in motor behaviour. As the authors pointed out there are at least four different regions active during decision making (their focus being the head of the caudate). Furthermore, the players had to press a button in order to confirm their decision, so consequently the question arises if the "intention to trust" signal could be substituted by "intention to act (press)" with the computed information coming from somewhere else and converging in the caudate/striatum region.

Finally, it is worth mentioning that the complexity of social decision making modelled into an artificial game automatically alters the neural basis. Previous studies have shown that moral instances modulate trust significantly impairing the neural responses (Delgado et al. 2005). Moral among others is likely to factor into many decisions made in real social interactions. Further influences would include cultural or genetic differences which on their hand affect personality (Penke et al. 2009). This said, investigators should consider the validity of results obtained under idealised conditions in regard to reality.

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Optical Imaging of Neuronal Populations During Decision-Making

K. L. Briggman, H. D. I. Abarbanel, W. B. Kristan
Science, 2004

Summary by Johanna Stärk

1. Introduction

In their publication Briggman et al. investigate the question whether a decision is triggered by single neurons alone or if rather the dynamic interactions of many neurons are responsible for the decision-making process. To resolve this question they used the isolated nervous system of the medicinical leech (*Hirudo medicinalis*), which consists of 21 segmental ganglia, a head and a tail brain. By applying identical stimuli to peripheral nerves of the nervous system, two characteristic motor patterns, generated by central pattern generators can be evoked at about the same probability. These patterns are consistent with swimming and crawling behaviour in the intact animal. The stimulation of the nerves in the isolated nervous system mimics touching the leeches skin, so that swimming and crawling are two possible ways for the leech to escape from this stimulus.

2. Methods

For electrical stimulation and recording of the peripheral nerves (located dorsally between ganglia G13 and G16) two suction electrodes were used. The nerves were stimulated with electrical train pulses for 60s with an intertrial interval of three minutes. Simultaneously about 130-150 ventral neurons of a midbody ganglion (located between ganglia G7 and G10) were imaged using FRET (fluorescence resonance energy transfer)-based voltage sensitive dye imaging during the first 10s of each trial. FRET- imaging enables to record from many neurons at the same time and is based on a physical process by which energy is transfered nonradiatively, thus without the emission of photons. This can only occur in between small distances like the neuronal cell membrane.Using FRET- imaging Briggman et al. stained their neurons of interest with the membrane-bound dyes oxonol and coumarin. Energy can be transfered from the donor molecule (coumarin) to the acceptor molecule (oxonol) through dipole-dipole interactions. When the cell is in a resting state the two molecules are associated. When the cell is depolarized they dissociate, which leads to a change in fluorescence which can then be measured. FRET- imaging has a very high resolution so that changes of less than 5mV are still detectable.
The characteristic crawling or swimming motor patterns usually started at about 4 s after the electrical stimulus, so the decision-making process is expected to happen in between this time.

3. Results

"Discrimination by single cells"
Due to differences in their membrane potential, single neurons that were able to discriminate swimming from crawling trials could be observed before either motor pattern was accomplished. As a result of the optical data from the FRET- imaging neurons that showed a response towards the stimulus could be classified as nondiscriminating cells, early, late and transiently discriminating cells. The earliest discrimination time of each single cell (t_{SC}) was determined by a sliding window analysis (ANOVA). The discrimination time based on motor neuron activity (t_{NERVE}) was also determined by performing an ANOVA. 17 cells that discriminated before t_{NERVE} could be observed. These cells are possible decision making neurons.

"Discrimination by populations of neurons"
To check whether populations of neurons still can discriminate before early discriminating single cells Briggman et al. performed a principal component analysis (PCA). The PCA transforms a number of

possibly correlated variables into a smaller number of principal components that account for most of the overall variance and resemble linear combinations of neurons in this experiment. The goal was to find a linear combination of neurons that discriminates earlier than any single cell. They performed the analysis on 143 neurons and considered the first three components. The data was plotted three-dimensionally, using the principal components as axes in the coordinate plane (Fig. 1). Each line in this system resembles one trial (blue = swimming, red = crawling). The decision making process must occur before or at the time when the curves of the trials significantly separate and neurons that are most responsible for this separation are possible decision-making candidates.

To find out the time at which these two paths come apart and to find out what neurons are most responsible for this divergence a linear discriminant analysis (LDA) was performed. LDA is a classification method that projects grouped data points onto a line (the linear discriminant), so that they are maximally separated. Using this method t_{LDA} (the time at which the curves of swimming and crawling significantly diverge) could be determined. Neurons contributing most to the linear discriminant, are the ones that are most important for the discrimination between swimming and crawling. Therefore these neurons were visualised by projecting a color-coded map of their contribution to the linear discriminant onto a spatial map of the ganglion cells (Fig. 2). Early single-cell discrimination times (t_{ESC}) were then compared to t_{LDA}. Interestingly, t_{LDA} always occured before t_{ESC}. Remarkably the single cells that discriminated early were not the same cells that highly contributed to the linear discriminant.

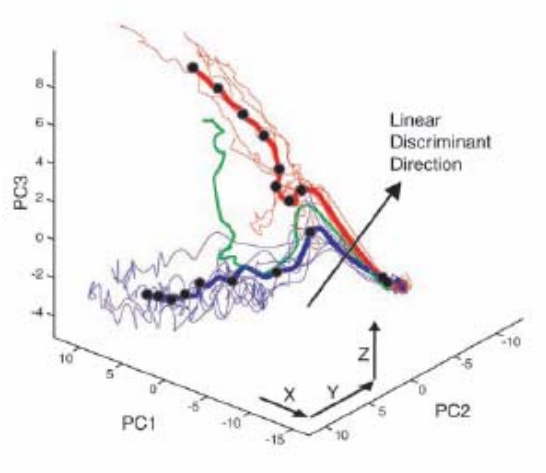

Figure 1: The contribution to the three principal components of each cell projected into a 3-dimensional space. Each curve resembles one trial (red = crawling, blue = swimming). The average of all swimming and crawling trials are shown in bold. Dots show 1s intervals. The arrow shows the linear discriminat for one time bin.

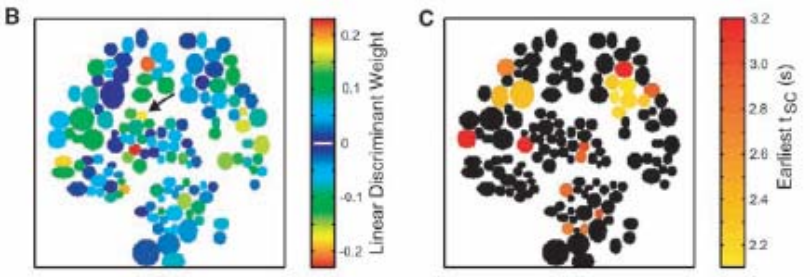

Figure 2: Color-coded map of the mid-body ganglion from a single experiment. (B) The contributions to the linear discriminant are color-coded (whereas red means high contribution and blue low contribution) and is mapped on the cells of the midbody ganglion. The arrow marks cell 208.(C) Color-coded earliest discrimination times [s] of the single cells (whereas yellow is very early and red is less early)

"Cell 208 biases decision"

To check whether single cells can influence decision-making, possible candidates were then depolarized and hyperpolarized before, during and after the electrical stimulus.

Only one cell, cell 208 (Fig. 2A) that highly contributed to the linear discriminant was able to bias the decision but only when it was stimulated during the nerve shock. A depolarization lead to a crawling motor pattern, whereas hyperpolarization led to a swimming motor pattern in most cases.

4. Discussion

The co-varying activity of a population of neurons can discriminate between crawling and swimming earlier than discriminating single cells. The individual discriminating cells are not consistent with the group discriminating cells thereby. One cell belonging to the discriminating population of neurons is cell 208, which can bias the decision when depolarized or hyperpolarized during the stimulus.
To test whether populations of neurons really bias the decision the result needs to be verified by manipulating these neurons during decision making. Therefore hundreds of neurons would have to be stimulated at the same time, which is technically not possible yet.
Even though the leech nervous system is relatively simple and the decision whether to crawl or to swim seems to be of equal value to the animal it is not possible to predict the choice. This might be due to two reasons: 1.) The choice depends on the resting state before the choice or 2.) The system is reset each time and the two behaviours have equal probability and diverge statistically due to noise. Further investigations may provide the answer.

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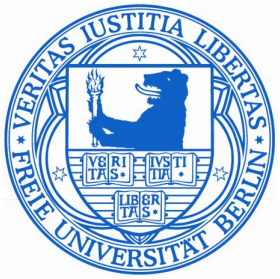

The Role of Memory in Decision Making

Summary:

"Neural correlates of a decision in the dorsolateral prefrontal cortex of the macaque"
Jong-Nam Kim and Michael N. Shadlen [February 1999]

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Berlin, 6th September 2010

Outline of concept

The investigation of how sensory information is integrated in the brain to guide behavior is in recent progress. Kim *et al.* have tried to elucidate the elements of decision making during a visual motion-discrimination task by recording neurons in the brain of rhesus monkeys. The hypothesis is that sensory information from direction-selective neurons in the extrastriate visual cortex (areas MT and MST) is integrated over time by neurons in the dorsolateral prefrontal cortex (PFC). The neural correlates of these neurons can be used to predict into which direction the monkey will move its eyes.

First of all, the theoretical terms of “evidence” and “decision variable” have to be introduced referring to the signal detection theory (STD).
Evidence can be a spike count of a neuron or the difference of spike counts between pools of neurons. It represents a variable that contains relevant information dependent on the stimulus which is given by the experimenter. Evidence is momentary and its integration over time can be described by a decision variable. The behavioral outcome depends on the accumulation of information within this variable until a certain threshold is exceeded, which, in this case, leads to a categorical choice of eye movement.

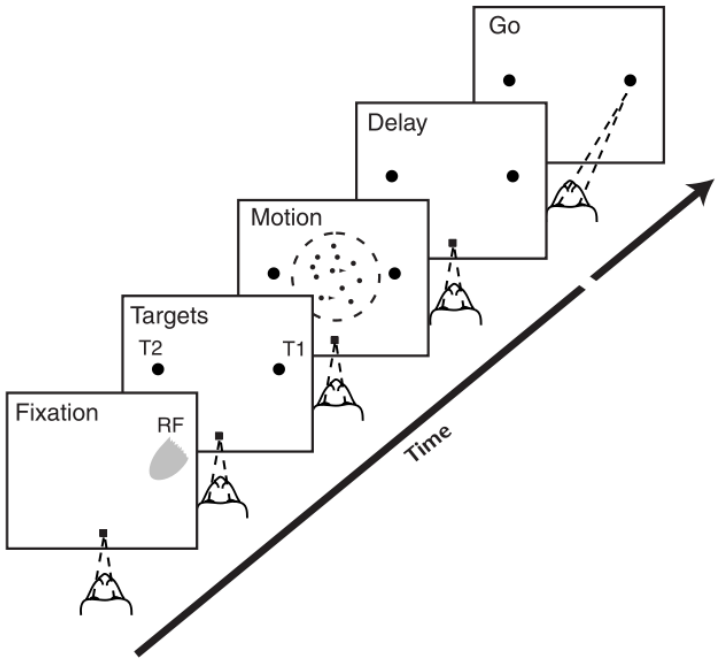

Figure 1: Sketch of the direction-discrimination task [1, p.178]

The sequence of experimental steps, the monkey had to perform to get a reward, is given in figure 1. The macaque was trained to gaze at a certain fixation point for around 2.5 s. After the first 350 ms, two target points were presented for about 200-300 ms, one of which lying in the neural response field (RF, shaded). After that, a random dot kinematogram appeared between the targets for 1 s, consisting of a certain percentage of coherently moving dots either to the RF side or the other direction. Finally, the dots disappeared and the monkey had to wait until the fixation point was turned off. That was the moment, the monkey should shift its eyes to the target point that was indicated by the motion of dots. The delay until this saccade was initiated took 0.5-1.5 s. The animal was rewarded for choosing the right direction, independent of the degree of difficulty.

For the selection of neurons in the PFC, that do respond to the presentation of the target point in the RF, a shortly flashed target was presented to the monkey. After a delay of 0.5-1.5 s, the animal had to remember this target by shifting its eyes to that region. Thereby, 88 neurons were screened for the experiment shown in figure 1.

Results

The neuron's response in the prefrontal cortex predicted the monkey's decision. In general, its response was modulated larger for a saccade towards the RF and attenuated for the opposite direction.
One important thing, referring to figure 1, is that evidence must be interpreted to reach a decision. Therefore the delay in turning off the fixation point, after the kinematogram disappeared, is important to distinguish between sensory evidence and integration to decide for motor action.
For the whole time of dot motion, the responding direction-selective MT neurons fired at a nearly constand rate, directly initiated by a short rise in discharge. This recording represents the evidence for the model.
While the direction-selective neurons stop responding when the motion stimulus is absent, the PFC neurons maintain there activity until the saccade is done.
That means, the evidence of the MT neurons is accumulated in the decision variable of the PFC neurons until a certain threshold is reached. Thereby, the starting point of integration began 200-300 ms after turning on the dot motion. The time, until the macaque shifted its eyes towards the target point, varied with the percentage of moving dots. For a strong stimulus with 51.2% coherently moving dots (orange curve), the reaction-time was about 400 ms, for 0% it took up to 900 ms (blue curve), shown in figure 2. The onset of the kinematogram is represented by the different starting points of the curves, clearly showing the short delay of evidence integration by the

rising firing rate of the recorded neuron.

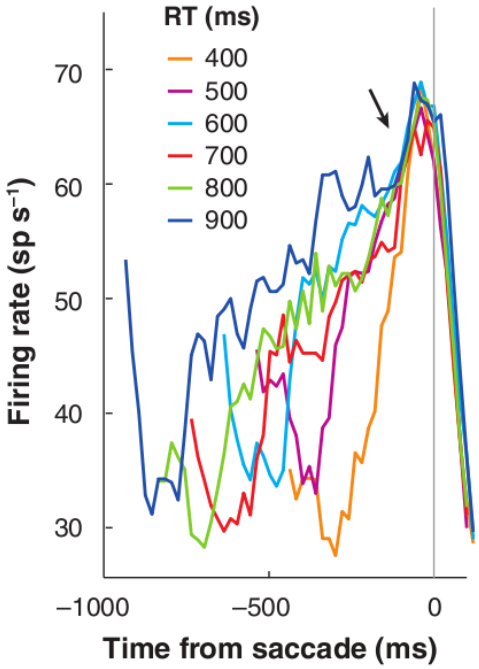

Figure 2: Choice-reaction time for different levels of stimuli, orange curve - 51.2% coherently moving dots, blue curve - 0% [2, p.548]

These responding curves indicate another finding - for any stimulus strength, there is an equal starting point of accumulation. In contrast, the recorded firing rate is strongly dependent on how many dots are coherently moving, meaning for strong stimuli, the monkey's decision is generated really fast. That means that even noise is integrated somehow over time such that the saccade to the target is initiated. In figure 2, it is shown, that this threshold is a spike rate of 60-70 Hz stereotyped for about 70 ms (indicated by an arrow) before saccade initiation (t = 0).
Therefore it is negligible how much time is needed for reaching this threshold - if it is reached, it takes always the same duration to initiate the saccade independent of the stimulus strength.
The psychophysical threshold was about 12.9% coherently moving dots, declaring the minimum amount of dot motion for a statistically significant correct saccade initiation.

Conclusion

By analyzing the error trials, in which the monkey chose the wrong direction, Kim *et al.* infers that the response was dominated by the judgment of direction, meaning what the monkey planned to do, rather than what it saw. The argumentation is that within the erroneous trials towards the RF, the firing rate was always higher than within the ones choosing the target opposing the RF. Those erroneous trials towards the RF were slightly attenuated, saying the response cannot be described completely by the behavioral outcome.
The model suggests that a PFC neuron, which responds with a high spike rate to dot motion towards the RF, compares the rightward *cumulant* to the leftward *cumulant* of the sensory MT neurons. If the difference of "right" and "left" is positive, the monkey will choose the right target, otherwise it will shift its eyes towards the left target.
Thereby, the recordings of the MT neurons show quite differing spike rates, depending on the stimulus strength. Finally, the computation of the spike rate in the PFC remains unclear, as the only indication for rightward choice is a higher firing rate.
The model shows quite good theoretical approaches from decision theory, consisting of evidence, a decision variable and a resulting categorical binary choice, but the moment the monkey decides the direction of motion cannot be described exactly, if there is such a discrete moment. Because of the delay, the sustaining response of the PFC neurons can be interpreted as a neural correlate of short-term memory for spatial location.
As a consequence, there are still a lot of experiments that have to be done for the whole region of sensory integrating neurons that prepare motor action to elucidate further complexity of decision making processes.

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Katharina Grauel

The flutter discrimination pathway

Recently, a combination of neurophysiological and psychophysical methods has led to major progress in elucidating the neural dynamics underlying decision making in the somatosensory system. In these studies monkeys are trained to perform a vibrotactile discrimination task while the activities of single neurons are recorded in different cortical areas thought to be implicated in the cognitive process. Relating neural activity to the psychophysical performance of the animal then allows for a better understanding of the function of those areas.

A very commonly used task is the so-called flutter discrimination task in which successively two stimuli with different frequencies are presented (Figure 1). The monkeys then have to indicate whether the frequency of the second (comparison) stimulus (f2) is higher or lower than the frequency of the first (base) stimulus (f1). This task can be subdivided into several cognitive steps: the base frequency f1 needs to be encoded and maintained in the short-term or working memory during the delay period, the comparison frequency f2 needs to be encoded, f2 has to be compared to the memory trace of f1 and finally the comparison result has to be transmitted to the motor system.

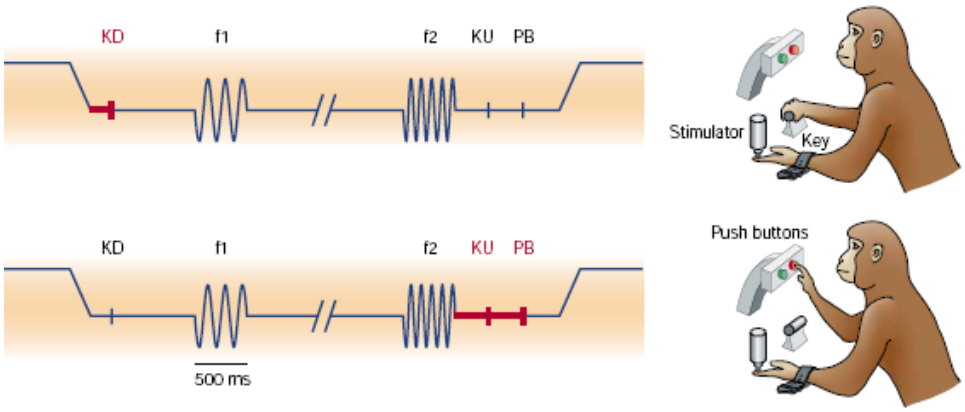

Figure 1 Flutter discrimination task - sequence of events: KD: monkey places hand on an immovable key; f1: base simulus presentation via a mechanical stimulator; f2: after a delay period, presentation of a second mechanical vibration; KU: mokney releases key; PB: monkey presses one of two buttons indicating its decision. From Romo and Salinas, 2003

Experimental results indicate that several areas, including the primary and secondary somatosensory cortices (S1 and S2), the prefrontal cortex (PFC) as well as the medial and ventral premotor cortices (MPC and VPC), are involved in the flutter discrimination pathway. No single area can be assigned to one of the above mentioned steps of the decision process. Instead encoding, working memory and comparison tasks seem to be spread over several cortical areas with different temporal patterns.

Even though primary afferents and S1 neurons show a certain periodicity in their activity that is dependent on flutter frequencies, evidence suggests that it is not this periodicity that carries the frequency information. Instead, the firing rate seems to be the important parameter. As the firing rates of the primary afferents do not depend on the flutter frequency, the S1 neurons must extract this information from the time intervals between afferent spikes.

As they are only active during stimulus presentation, S1 neurons seem to be involved only in the encoding of flutter frequencies. With few exceptions, their firing rates depend on the stimulus frequency in such a manner, that higher frequencies result in higher rates. However, there is contradictory evidence for some mnemonic activity as well.

S2 neurons do not show periodic activity. Their firing rates during f1 presentation increase or decrease as a function of f1. It is not clear whether S1 and S2 are organized in parallel or serially. About one third of the S2 neurons are also active during the delay period indicating their participation in the mnemonic process.

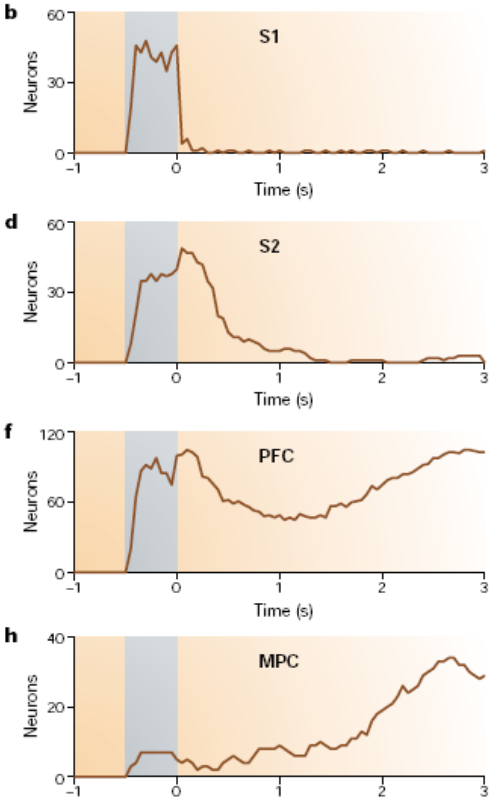

Figure 2 Number of neurons active about the base stimulus in different cortical areas as a function of time. grey area: base stimulus presentation; time point 0: beginning of delay period; S1: primary somatosensory cortex; S2: secondary somatosensory cortex, PFC: prefrontal cortex; MPC: medial premotor cortex. From: Romo and Salinas, 2003

The main structure involved in the short-term storage of information about f1, though, appears to be the prefrontal cortex (PFC) which has been implicated in working memory before. A neuronal cluster in the inferior convexity has been found to show significant f1 dependent activity not only during the stimulus presentation but also during the entire delay period. This activity resembles the activity in S2 during stimulation. The PFC neurons display a preference for high or low frequencies and can be further subdivided into subpopulations active mainly during the stimulus presentation and the beginning of the delay period (early neurons), activated only towards the end of the delay period (late neurons) or firing throughout the entire delay period (persistent neurons).

Since other neuron populations in the VPC and MPC are also active during the delay period, these probably also participate in the working memory.

The actual comparison is the core of the flutter discrimination task. It can be viewed as the computation of the sign of the frequency difference and takes place upon f2 presentation. As for the working memory, results indicate that the comparison takes place in a distributed fashion. It can be observed in all implicated areas apart from S1. For example, upon f2 presentation S2 neuron firing rates are largely dependent on f2 frequency. With time, this dependency changes and a few hundred milliseconds after stimulus onset the firing rates become a function of the difference between f2 and f1 (f2-f1). This comparison signal can then further evolve into a signal that is consistent with motor choice.

The premotor cortex is another area majorly implicated in the flutter discrimination task.

In the ventral premotor cortex (VPC) different neuron subpopulations exist whose activities reflect the whole sequence of processing steps. For example, one group of VPC neurons only responds during stimulus presentation as for S1 neurons and their firing rates only depend on the frequency of the current stimulus. Another group shows significant activity only during the delay period and the comparison stimulus presentation. While the firing rates during the delay are a function of f1, they

transform into a function of f2-f1 during the second stimulus presentation. This also resembles the activity of a subpopulation of neurons in the medial premotor cortex (MPC). The shift in firing rates might reflect the actual comparison process.

There are also other neuron populations in the MPC as well as in the VPC involved in the flutter discrimination task but not active during the delay period. They also develop differential activity and are most active during the comparison or reaction time. It is speculated that their activity might either reflect the results of the frequency comparison or the actual motor plan.

Literature:

Romo R, Hernández A, Zainos A (2004) Neuronal correlates of a perceptual decision in ventral premotor cortex. Neuron 41(1):165-73

Romo R, Salinas E (2003) Flutter discrimination: neural codes, perception, memory and decision making. Nat Rev Neurosci 4(3):203-18

Decision-making and Weber's law: a neurophysiological model

Gustavo Deco and Edmund T. Rolls, European Journal of Neuroscience, Vol. 24, pp. 901–916, 2006

In this paper, authors describe an integrate-and-fire attractor model of the decision related activity of neurons in the ventral premotor cortex (VPC) during a vibrotactile frequency comparison task. This model is based on the neurodynamical model first introduced by Brunel & Wang (2001). One of the important findings the authors made was the understanding that the Weber's Law is implemented not through the firing rate of the decision units presented in the network, but through shunting effects acting on pyramidal cells that are produced by inhibitory neuron inputs. The structure of the model and these findings are described later in this abstract.

Structure of the underlying experiment

The experiment of the vibrotactile frequency comparison task was performed and investigated by Romo and colleagues. In this experiment a trained monkey (*Macaca mulatta*) has to decide and report (through pushing one of two buttons), which of two mechanical vibrations applied sequentially to their fingertips has the higher frequency of vibration. It was shown (Romo *et al*., 2004), that the behavior of VPC neurons reflects the remembering of the first applied mechanical vibration frequency (*f1*), the encoding of the second applied mechanical frequency (*f2*) and of the comparison step of two frequencies as well as the encoding of the motor response. That describes the actual process of decision making and this is the reason, why the dynamic behavior of the VPC neurons was of particular interest for the authors and was used for creating this model.

Model

The probabilistic decision-making is modeled by a network of interacting neurons organized into a set of populations. Population of neurons is a group of excitatory (pyramidal cells) or inhibitory (interneurons) neurons sharing the same inputs and connectivity. Specific populations in the model encode the categorical result of the comparison between the two sequentially applied vibrotactile simulations *f1* and *f2*. These populations are *(f1>f2)* and *(f1<f2)*. There is also a non-specific population named *"Non-Specific"*, which includes all the other excitatory neurons in the modeled brain area not involved in the current task. The inhibitory neurons of the local brain area are grouped into the *"Inhibitory"* population. The conductance values for the synapses between pairs of neurons are modeled with weights, which can be 1, W_+ (e.g. between the neurons of one population) or W_- (e.g. between neurons of populations which are likely to have anti-correlated activity). The weight W_I denotes for inhibitory-to-excitatory connection. The values λ_1 and λ_2 encode the two vibrotactile stimuli to be compared and thus increase the rate of Poisson train to the neurons of the specific populations *(f1>f2)* and *(f1<f2)*, respectively. The presented model is a single attractor network with the two populations *(f1>f2)* and *(f1<f2)* which represent the decision states. One of these populations becomes active when a decision is made. The design of the model is shown in the Figure 1.

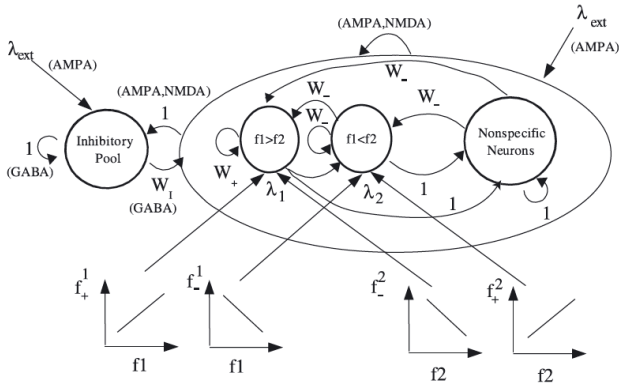

Figure 1: The architecture of the neurodynamical model for a probabilistic decision-making network

Results and conclusions

After the model was implemented, a series of experiment simulation was performed on the model. Applying mean-field analysis to the stationary phase of the model led to the conclusion, that the network behavior is quite robust.

In another experiment the probability of correct discrimination was linked to the difference between the two presented vibrotactile frequencies to be compared. The threshold of correct classification of the difference between f_1 and f_2 was set on 85%. The results showed that with increasing frequency f_2 the difference between the two frequencies had to increase as well in order to reach the threshold of 85%. So the difference threshold increases linearly as a function of the base frequency (f_2). This corresponds to the Weber's law, which states that the ratio of the difference threshold to the background intensity is a constant.

In the further experiment the difference in frequencies was linked to the firing rate of a specific population and it was observed, that the firing rate of the population encoding the result of the comparison does not encode Weber's law. Thus the conclusion was made, that the dynamics of which state (attractor) is reached probabilistically represent the origin of Weber's law.

It was also shown, that the average firing rate of the population *(f1<f2)* is only dependant on the sign of f_2 - f_1 and is not dependant on the f_1, f_2 or on the absolute value of the difference between the two frequencies. This observation confirms again, that Weber's law cannot be encoded in the firing rate, but only in the probability with which that firing rate can be reached.

Further simulation experiments showed the fact, that the larger the probability of correct classification, the faster is the decision making. By investigating the probability of incorrect classification, a converse behavior was observed: a low probability of incorrect discrimination implies also shorted reaction times.

Another important conclusion was made by observing the behavior of inhibitory interneurons as the base frequency increases. As the base frequency increases, more excitation will be provided to the specific populations *(f1>f2)* and *(f1<f2)* by λ_1 and λ_2, respectively. This in turn will increase the firing rate of pyramidal cells, which will provide larger excitatory input to the inhibitory interneurons. Thus the inhibitory neurons will fire faster and the inhibitory connection to the specific states will be more active. The inhibitory input to the specific states acts divisively upon the excitatory inputs from λ_1 and λ_2. To compensate for this effect, f_1 and f_2 will need to increase in proportion to the base frequency. In the simulation was shown, that the firing rate of inhibitory neurons increases linearly with the base frequency, as can be seen in the Figure 2. Therefore the authors proposed that Weber's law is implemented by shunting effects on the specific states produced by inhibitory neuron inputs, which increases linearly as the base frequency increases.

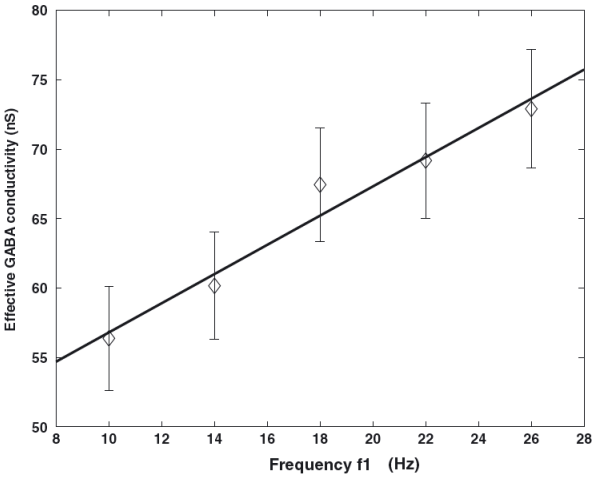

Figure 2: The conductance produced by GABA inputs to specific states as a function of the base frequency

Summary of "Synaptic dynamics and decision making (Deco et al.)"

To make a decision we have to remember and compare stimuli that occur at slightly different times. As it is well known the comparison of 2 vibrotactile stimuli applied sequentially are qualified for such studies for decision making. The next step for the study would be to use an attractor network that has 2 inputs for the 2 evidences which would be applied as bias λ_1 and λ_2. The 2 population would encode decision through interconnected neurons. After that there would be a competition between these 2 populations of neurons via inhibitory interneurons. The final decision between these 2 evidences depends on the population which is enhanced nonlinearly by the positive feedback which is the winning one. This common model is not usable for the ventral premotor cortex (VPC), because in the VPC the inputs λ_1 and λ_2 are encoded by the same type of neurons (the partial differential neurons) according to experimental data. The task in the experiments that the network based on is to decide which of the 2 mechanical vibrations applied sequentially to the fingertips of the subjects is the higher one. The experiments have the following process: (i) perception of the first stimulus f_1 a vibration for 500 ms; (ii) a delay of 3s to store of a trace of f_1; (iii) perception of the second stimulus f_2 for 500 ms; (iv) report the decision between the 2 stimuli. Deco et al. model the partial differential neurons with a network using integrate and fire neurons that are able to memory the first stimulus under some conditions. In this model a single population of neurons receives inputs from the vibrotactile stimuli. These neurons have excitatory interconnections that use short term synaptic facilitation. To implement the short term synaptic facilitation is more suitable. On the one hand the short term memorize f_1 during the delay period and on the other hand the comparison in the decision period can be done. Some characteristics which are in that network modeled are following: (i) spiking dynamics; (ii) facilitating synapses; (iii) synaptic utilization.

For a better understanding of the behavior of the firing rate of f_1 and f_2 during decision making are simulations for two different set of pairs of stimulus combinations f_1 and f_2 performed. The one type is $f_2>f_1$ ($f_2=f_1+8Hz$) and the other type is $f_2<f_1$ ($f_2=f_1-8Hz$). These differences are based on experimentally measurements. The neuronal responses in the simulations are analyzed as functions of f_1 and f_2. The results of the simulations reproduce the 4 phases that are in the experiments described before. For each of the phases the firing rate is calculated. The easiest way to qualify the dependence of the selective neurons and f_1 respectively the firing rate is to describe the population rate r(t) by an arbitrary linear function of f_1 and f_2 ($r(t)=a_1(t)f_1+a_2(t)f_2+a_3(t)$; in which $a_1(t)$ and $a_2(t)$ serve as direct measurements of the firing rate dependence on f_1 and f_2). But in this arbitrary linear equation does not reflect the memory behavior of f_1 really and does not show clearly the sensitivity of the differences between f_1 and f_2 for a given frequency f_2. To achieve this the linear correlation method can be used for the analysis of the neurophysiological experiments and simulations. Therefore the function of the firing rate can be rewritten as $r(t)= a'(f_1-f_2)+b'f_2+c'$. The simulations and calculations for the new equation are in Deco et al. also done. The comparison between these two equations shows that the

results of the simulations of the second equation reflect clearly the behavior of memorizing f_1. The simulation of synaptic utilization from the second equation supports the experimental data too. That improvement in the equation of the firing rate enables the comparison between the memorized frequency f_1 with the second frequency f_2 during the comparison phase. This accurate comparison enables the correct decision. This is a further step for a realistic biological model.

Computational models in decision making:

"Cortico–basal ganglia circuit mechanism for a decision threshold in reaction time tasks"

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September 2010

Introduction

Analog to the superordinate title, this part deals with models for decision making simulated by computers. If one breaks down the subordinate heading, the basic principle and goals are there: For real neural networks in decision making, computational models should be developed. In general, most approaches exhibit a similar structure: Real data is gained from biological experiments and artifical networks are tried to be created accordingly. Thereby models serve in two ways. Either one has an idea of the neural network setup and designs adequately, or development is done until the network output fits with real data. In the end, both ways try to establish a reasonable image of reality, with which one can work with.

In particular, the study mentioned in the second title deals with neural networks responsible for processing visual information and sending movement signals back to the eyes themselves. Studies were conducted on non-human primates (monkeys) but the results should represent primates in general; if not not other biological orders too.

More specific primates are instructed to register a certain visual stimulus and react with eye movement, according to their decision. By recording single neuronal firing at the same time, one can make quantitative and qualitative predictions about the decision making process. After that, real work is done by building a model in the computer. When the network is at hand, one is able to run diverse simulations without doing the actual experiments.

Experiment setup

The experiments for this work can be splitted in two parts. First real tests on monkeys. Monkeys were trained to sit in a straight position and fixate a computer screen. Next a yellow square in the middle of the screen was presented to them. After fixation the experiment started and dots showed up on the screen as well as to identical green dots at left and right side. The dots on the screen started to move in either direction, towards the green dots or moved randomly without destination. This is were one imporant word comes into play, namley the coherence level in percent: The fraction of dots moving into the same direction, taken from all moving dots, is called the coherence level, since they move a certain direction.

Anatomy

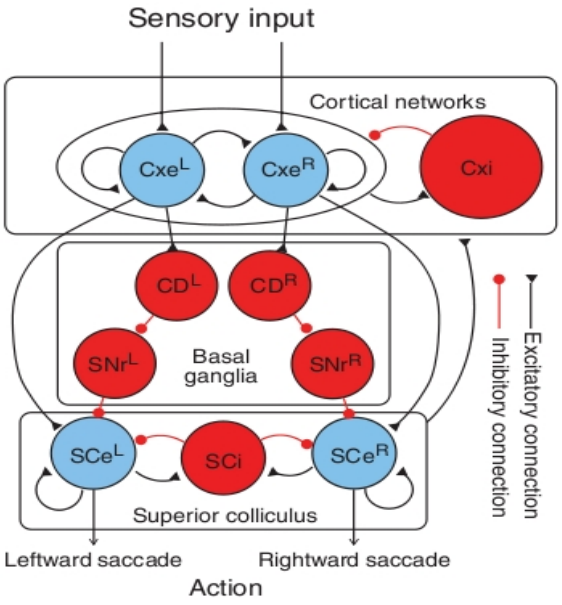

Figure 1: Neural network setup with visual information input going into the cortex. Information processing happening in the cortex. Information forwarding through the basal ganglia which is serving as a filter until the firing from cortex reaches a certain threshold. And the superior colliculus as information receiver. The network consist of an excitatory and inhibitory balance of neurons. Simultaneously in every compartment neurons for left and right eye motion compete against each other.

The network analysed and reconstructed in the computer is shown in figure 1. The network is responsible for receiving visual input, processing information by taking knowledge into account, and deciding by sending motor information back to eyes. Sensory input from the eyes goes into diverse cortical structures. As in every follwing compartment, neural pools for left and right eye movement compete against each other throught inhibition. Depending on the neural pool that first inhibits the other, information is sent forth areas in the striatum (CD). Striatum regions are the "executor" of cortical decisions. Since the structure after CD, the substania nigra (SNr) continuously inhibits burst firing neurons in the superior colliculus, SNr neurons are inhibit by CD firing. Through this action, burst firing neurons in the superior colliculus are free to fire. Those neurons are sending movement signals eye motor neurons according to the direction that dominates.

Methods

The actual work was conducted in the computer by modeling the neural network. The network's outline is descibed in the "Anatomy" section. Similar to the real network outlook, the artifical system consisted of three independent parts: Cortex, basal ganglia and superior colliculus. Neurons in the computational model used the "Integrate-and-Fire" model as basis. This model takes membrane time constants into account and works with an input-output function, depending on an excitatory or inhibitory nature. Furthermore the information integration in the cortex was modeled with a so called "Attractor-Network-Model". This model consists of excitatory neural pools that stimulate each other, whereas pools of different interest (left, right) inhibit each other. Communication among each other was simulated by synpases that can be tuned with a weight factor. More weight means the strength on the neural signal across this synpase is increased.

Results

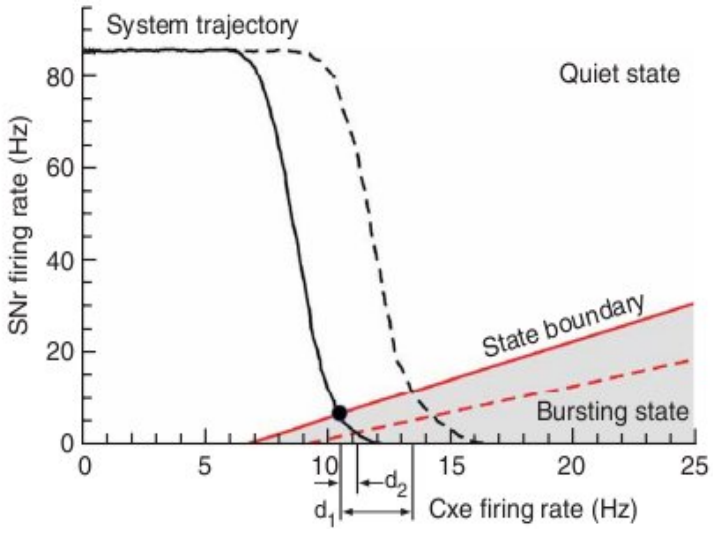

Figure 2: Artifical network tuning with increasing the synpase efficiency of the cortex-striatum pathway (black dashed line) and cortex-superior colliculus pathway. Cortex-striatum tuning shows to be the reasonable one, since the point of information forwarding (black dot) is improved.

In general the results of the network simulation showed, that the real network could be tuned by improving the work of cortico-striatal synpases. One good representation is pictured in figure 2: The point of neural firing in the superior colliculus, the network's output structure, is increased, when the Cortex-Striatum pathway is improved. This is because the faster neurons in the striatum reach a certain threshold of incoming firing form the cortex, the faster they inhibit areas in the substantia nigra, so that output neurons in the superior colliculus are able to fire.

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List of Participants

	Name	First Name	Topic	Email	Program
1	Celik	Hatice	**5** / 4 / 2		
2	Doering	Kersten	**4** /3 /5		
3	Galicka	Anna	**1**		
4	Grauel	Katharina	**4** / 3 / 1		Diplom Biochchemie
5	Güttler	Nico	**5** / 2 / 4		
6	Guo	Jia Shen	**4** / 3 / 2		MSc Neuro & Behavior
7	Hoppe	Christian	**1** / 5 / 2		
8	Kayser	Bastian	**4** / 3 / 1		
9	Kluge	Matthias	**3** / 2 / 5		
10	Kosenko	Anna	**5** / 4 / 3		
11	Kramarek	Maria	**4**		MSc Comp Neurosci
12	Mutyala	Rithwik	**1** / 4 / 5		MSc Comp Neurosci
13	Schatton	Adriana	4 / **2** / 1		MSc Neuro & Behavior
14	Schröder	Marcus	**4** / 3 / 5		
15	Specovius	Svenja	**1** / 3 / 4		
16	Stärk	Johanna	**4** / 3 / 2		MSc Neuro & Behavior
17	Standfuss	Christoph	4 / **2** / 3		

Canceled participation: Klock (12.8.) Kuchenbecker (12.8.) Mendt (13.8.) Haufe (13.8.) Schultze-Kraft (19.8) Ranft () Topcu-Alici (20.8.), Schneiderbauer (6.9.)