Aus dem Institut für Pathophysiologie der Universitätsmedizin
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Cognitive and neural mechanisms of adaptive behavior in a psychophysical decision task with asymmetric reinforcement

Kognitive und neuronale Mechanismen adaptiven perzeptuellen Entscheidungsverhaltens

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c	Criterion
CRR	Controlled reinforcer ratio
EC	Error-correction
HTT	High Threshold Theory
IFC	Interval-forced-choice task
LEM	Lower envelope model
LIP	Lateral intraparietal Cortex
LPFC	Lateral prefrontal cortex
LTT	Low Threshold Theory
ms	Milliseconds
min	Minute/s
N	Noise-stimulus
ORF	Objective reward function
PFC	Prefrontal cortex
mPFC	Medial prefrontal cortex
R	Response
s	seconds
S	Signal
sd	Standard deviation
SDT	Signal Detection Theory
SN	Signal-and-noise-stimulus
TT	Threshold Theory/threshold theories
URR	Uncontrolled reinforcer ratio
YN	Yes/No (task)

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1. INTRODUCTION

All living organisms are constantly in the position to make decisions. Depending on the number and character of different alternatives, some situations are easier, some are harder to manage. Furthermore, amongst others, the final decision is a complex result of current external and internal stimuli, environment, and earlier experiences in life. In the end, all of these multiple factors lead to adaptive reaction patterns that finally form individual behavior.

The following work will therefore focus on the fundamental question, firstly, how well a vertebrate's brain produces goal-directed, adaptive behavior in adaptive choice tasks, and in a second step, what cortical areas and neural processes are involved in making perceptual decisions with and without dynamically changing reinforcement contingencies.

First, the Literary Debate will lead into the scientific matter of signal detectability and introduce scientific theories to the over-arching question of this work. The main focus will be placed on the Signal Detection Theory (SDT) to examine whether its principles best fit to explain adaptive behavior in contrast to other models, especially to the competing threshold theories (TT).
Further, the methods of the training and testing procedures will be shown as well as the materials used for brain surgery and the experimental set-up.
Finally, the results of the behavioral and neural experiments will be presented, before these outcomes will be contextualized with important scientific findings of that research field.
Finally, conclusions about adaptive behavior in signal detection tasks will be summarized.

2. LITERARY DEBATE

This chapter is divided into five sections: firstly, the general research project will be introduced through a practical example of a security officer's everyday life problem leading over to the theoretical background of the conducted task procedure. Secondly, the TT will be explained as important competing model to SDT. Thirdly, the latter will be discussed thoroughly as being the main theoretic fundament for the conducted experiments; and fourthly, former and current research in the field of signal detectability will be presented. The last and fifth section will deal with scientific insights of the prefrontal cortex (PFC) concerning its role for signal detection and discrimination.

2.1. The fundamental decision problem

At the beginning, to give a better understanding about the theoretic background, a security officers working experience figuratively represents what stands for the fundamental question of this work (cf.(Wolfe et al., 2005, Domjan, 2010). A security officer's daily job is to detect weapons (e.g. knives) in the luggage of thousands of flight passengers. In order to do so, an apparatus of a digital screening program helps him to discriminate between harmless tools and weapons. Nonetheless, the filtered selection of possibly dangerous items still requires a critical and watchful scanning by the officer himself. Also, the consequences of one or the other decision must be kept in mind: a strict performance through a time-consuming opening of the bags may lead to a higher detection rate but is not practical at crowded airports; however, not detecting the knife surely leads to even worse outcomes. So the enormous quantity of different items that can be mixed up with the knife still asks for a certain strategy to increase the chances of success. So how will he encounter that responsible task? Besides a good training, he could adopt a certain search pattern like distinguishing between different forms or sizes, paying attention to special locations of the bag, or considering certain colors on the computer screen. In the end, the officer needs to detect a rarely existing knife within thousands of distractive items (in scientific terms, to separate "signal" from "noise"[2]). Yet, from the officer's perspective there are two mutually exclusive states[1]: the existence or absence of a knife. But in order to evaluate his success rate, four possible outcomes need to be considered: 1. The luggage contains a knife and the inspector correctly detects the knife (="hit", Table 1). 2. The luggage again contains a knife, but the officer falsely misses it (="miss", Table 1). 3. The bag does not carry a knife and the inspector correctly classifies the bag being harmless (="correct rejection", Table 1). 4. The bag does not contain a knife, but the officer falsely presumes the existence of a knife and instructs the bag to be opened (="false alarm", Table 1). Thus, in relation to this example the question is what parameters lead to one or the other decision. Or in different words, what parameters are the result of a yes- (=knife present) or no- (=knife absent) choice, and further, what theoretical principles give the most adequate answers to those fundamental decision problems?

-Table 1-

	Knife present	Knife absent
Officer claims knife is present	Hit	False alarm
Officer claims knife is absent	Miss	Correct rejection

Four possible outcomes exist in a decision task. Referring to the example given (see text) the scanning of a weapon can lead to four different states:
The bag contains a knife: 1. Correct detection (=hit); 2. Missing out on the knife (=miss)
The bag does not carry a knife: 3. Correct classification of a harmless bag (=correct rejection); 4. Falsely presuming the existence of a knife (=false alarm).

Now transferring the given example to a laboratory task, the experimental set-up was reduced to essential components in order to scientifically analyze decision making. As mentioned before, Yes/No (YN) tasks are a simple way to better understand detection problems. In the current study a modified YN task was established with signals and noise[2] trials occurring at the

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[1] Comparable with SDT (see chapter 2.3.)

[2] In sensory experiments "noise" subsumes all external and internal factors which affect the evidence variable describing the whole bandwidth of sensory perceptions that is perceived at the same time and distracts from a key stimulus (e.g. in auditory experiments the whole bandwidth of a sound, in visual testing procedures a series of different shades of light/colors).

same frequency. In an auditory decision task the subject had to decide between sound-present and sound-absent trials. Similar to the example of an officer's daily decision problem, also in a YN task four possible outcomes exist. In one condition the sound occurs, so the subject will either detect the sound correctly, or it will miss it. In a second condition, the sound does not occur, and the subject will either correctly reject it, or it will falsely claim it has occurred (Table 2); "On signal trials, yes responses are correct and are termed hits. On noise trials, yes responses are incorrect and are termed false alarms. The hit rate (the probability of responding yes on signal trials) and the false-alarm rate (the probability of responding yes on noise-trials) fully describe performance on a yes/no task." (Stanislaw and Todorov, 1999).

-Table 2-

	Sound present	Sound absent
Subject claims sound present	Hit	False alarm
Subject claims sound absent	Miss	Correct rejection

On the basis of the SDT[1], there are four possible outcomes to a typical single-stimulus decision trial: in scientific terminology:

- first condition: Sound occurs: 1. correct choice (=hit), 2. false choice (=miss)
- second condition: Sound does not occur: 3. correct choice (=correct rejection), 4. false choice (=false alarm)

In a modified version, the study described in this thesis deals with a very similar decision problem. Instead for a YN task like a sound/no-sound task, two signals (S1=sound of low frequency, S2=sound with high frequency) needed to be distinguished. Also in this experimental set-up the four outcomes to the task were possible (cf. Table 1, Table 2), whereby the subject could respond in two ways: Presuming S1 was shown, it responded with R1 (response1), assuming S2 was presented, it responded with R2 (response2).

Regardless whether one looks at the illustrative example of the beginning or rather focuses on the laboratory task, the question of what parameters lead to one or the other decision stays the same: what internal parameters are the result of a yes- (=signal present) or no- (=signal absent) choice, and further, what theoretical principles give the most adequate answers to the fundamental decision problem?

Yet, earlier scientists struggled with similar problems trying to simplify the testing procedure in order to find answers to their questions. They used strictly controlled psychophysical clinical studies with young and trained test persons (Goldstein, 1997) in order to allow a highly qualified and comparable testing procedure. Using Goldstein's reviews of his own and other scientists' studies, also the practical example of the airport officer gives evidence to assume that every subject has a certain sensory threshold enabling him to decide for "signal present" or "signal absent". Thus, the officer says "yes, knife present" when his scanning procedure passed an individual threshold, or he will say "no, knife absent", if the targeting of the knife stays below a certain internal boundary.

Many investigators, however, critically scrutinized the general idea of a threshold at all, or at least, as the only decision parameter in choice tasks (Goldstein, 1997). Critics about the TT as well as SDT will be thoroughly discussed later on.

In order to better understand the structure of the current experimental task procedure, again a YN task in the form of a tone-detection task is introduced to explain some important issues concerning signal detection. In a YN task, the subject can either claim the sound was presented ("yes, sound present"), or the subject feels the tone did not exist ("no, sound absent"). Important for this example is that the existence and absence of the tone happen equally often, and in purpose of comparison, two different subjects (A and B) tackle the task.

From the first sight, the task, or rather the interpretation seems to be clear enough: as the sound passed their internal threshold, both subjects will go for "yes, sound present". Oppositely, they will not react, if the threshold level is not met (=”no, sound absent"). On second sight, however, the sensitivity[3] of both subjects could be very similar, whereby their way to solve the task may vary (Goldstein, 1997). For instance, the lax subject A wants to be very sure not to miss out on the given sound, so it often goes for "yes, sound present" even then when

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[3] Individual ability to detect and discriminate different stimuli

there is just a very slight evidence for the signal. Oppositely, the second rather strict subject B only reacts as it is absolutely positive that the tone was presented.

Thus, although their sensitivity might be equal, subject A approaches the task rather liberally, while the latter follows a stricter reaction pattern (Goldstein, 1997). In psychophysical terms, the former test subject yields a lot of hits for the high frequency of "yes" choices, while at the same time the number of false alarms consequently also increases. Oppositely to observer B that gains a smaller portion of hits along with fewer false alarms (Table 1,2). It is therefore obvious that not only the detectability plays a role in decision tasks, but that many individual factors confronting a subject might influence its choice.

Furthermore, many studies showed that independent from a subject's detectability and also independent from individual factors, reinforcing[4] correct choices and punishing incorrect choices to different extents influence the test subjects' reactions and lead to a changing behavior. So introducing a certain payoff schedule for a yes-response or a no-response in a YN task showed that subjects tend to one or the other alternative. Imagine that both subjects would be additionally rewarded for correctly detecting the stimulus, or oppositely they would be additionally rewarded for correctly claiming the tone was not presented (Table 3, cf. Table 1).

-Table 3-

1. Reward schedule favoring "yes" responses		2. Reward schedule favoring "no" responses	
Hit	+50 Euro	Hit	+5 Euro
Correct rejection	+5 Euro	Correct rejection	+50 Euro
False alarm	-5 Euro	False alarm	-50 Euro
Miss	-50 Euro	Miss	-5 Euro

Two different reward schedules are depicted. The left chart (1. Reward schedule) shows a situation when hits are highly reinforced and misses lead to a great loss of rewards. In the right panel (2. Reward schedule) correct rejections are reinforced to a great extent and false alarms mean loss of rewards. Therefore varying reward schedules influence an individual's behavior depending on the reinforcement schedule (Goldstein, 1997).

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[4] In behavioral science, reinforcement is a technical term for intensifying favorable behavioral patterns, whereby punishing serves to diminish or even eliminate certain behavioral patterns. In scientific experiments, reinforcement can be money for human beings or water for water-restricted animals. Punishment can e.g. be provided through painful electric shocks or air puffs.

In the first schedule, hits provide a significantly higher gain than false alarms cost. Moreover, subjects will lose more money in missed trials than they can gain for correct rejections. Together, the payoff schedule will drive subjects to respond “yes” more often, even when not fully certain. Henceforth, independent from their detectability and individual factors, both officers will relatively more often go for “yes, knife present” in order not to miss out on any knife. The opposite behavior will be observed, if the second schedule is employed. In the latter situation, both officers rather tend to “no, knife not present” since firstly a correct rejection yields a higher gain, and secondly the incorrectly opening of a bag (=false alarm) costs ten times more than hits yield.

On the whole, this simple example stands for any possible experimental condition within behavioral studies demonstrating that multiple environmental factors influence the test object’s behavior; cf. (Busse et al., 2011), (Stüttgen et al., 2011a).

Referring back to the fundamental question, even by now, it is quite clear that studying decision making and behavioral adaptation therefore are complex processes, and only a deeper insight in the neural basis of behavior can sufficiently give answers to the beginning questions of how exactly a decision problem is solved and what interior parameters lead to certain reaction patterns.

To address these and other important factors, first the TT will be introduced and later on it will be compared with SDT as main fundament to all modern theories coping with behavior and decision making.

2.2. The Threshold Theory

In the mid 19th century, Theodor Gustav Fechner, one of the earliest students of psychophysics, published his work “Elements of Psychophysics” (FECHNER, 1860) offering first ideas how signal detection could possibly function. For that he developed multiple experiments that he mainly conducted by himself using the human visual and auditory faculty, the human sense of sensibility (he often cited EH Weber`s studies (Weber, 1996) concerning two-point discrimination) or just different weights. With that he was eager to find out what it needed that two stimuli could be detected apart from each other. For instance, over months he followed a schedule in which he lifted weights that minimally differed in heaviness, just to find out how many grams of weight and seconds of lifting were necessary to make a difference. Finally, he defined that “the boundary point, exactly when a stimuli [was] just recognizable or [faded] away, [was] called threshold including any sensation and sensation differences…that [could] be perceived from that boundary point onward” (FECHNER, 1860).

About 100 years after Fechner’s experiments, and although being a harsh critic of non-continuous theories (cf. “Is There a Sensory Threshold?”(Swets, 1961)), John A. Swets still gave credits to Fechner’s detailed approach of what ”…energy [was] required for a stimulus to be just detectable, or the difference between two stimuli necessary for the two to be just noticeably different” and Swets simply described the threshold “…as a barrier that must be overcome” (Swets, 1961). Another recent definition came from a current group of European and American scientists stating that “…[threshold models] postulated two distinct mental states – ‘‘detection’’ and ‘‘no detection’’ – which were separated by a fixed sensory threshold…”(David Kellen, 2016).

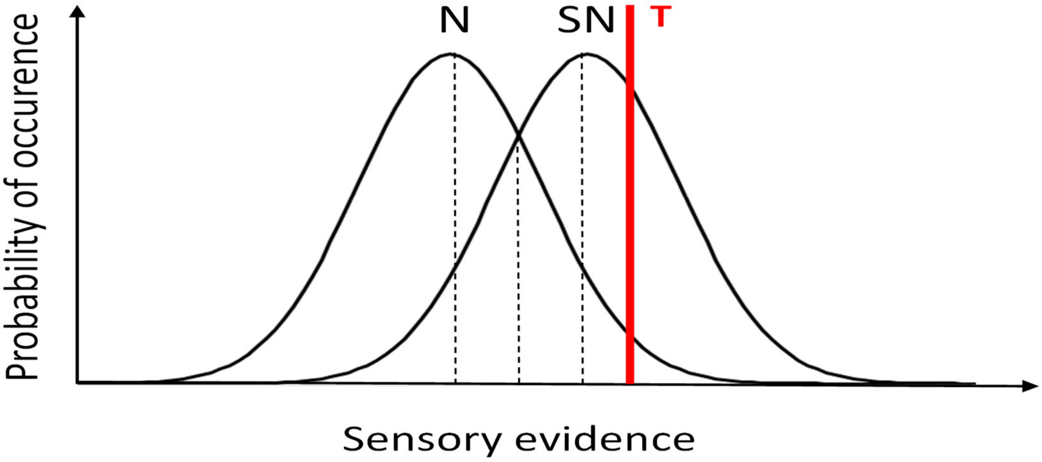
Remarkably, Fechner already understood that perception itself was hard to be measured as he stated that generally applicable methods to measure differences of stimuli sensations did not exist since they were influenced by the experimental set-up and the individual performance (FECHNER, 1860). To be more precise, he realized that the individual outcomes, even for trials of the same subject, resulted from interior (subject-related) and exterior (related to the experimental set-up) factors that could not be completely eliminated. Over 150 years later Stüttgen et al. therefore concluded that while being successful at making outer psychophysics the cornerstone of the evolving science of psychology, physiological methods at this time were not developed enough to allow direct investigation of inner psychophysics, and Fechner was well aware of this limitation (Stüttgen et al., 2011a).

On top of that, Fechner was quite sure that no experiment could determine the "true" threshold, but described it as the current best estimate of a certain experiment. He concluded that by then the best outcome must be seen as upper boundary, whereas the true threshold was located below that value, which was of main concern and could only be reached through optimal interior and exterior circumstances (FECHNER, 1860). Interesting was that he described perceivable stimuli as those that became conscious, whilst others that could not be perceived lay beyond human consciousness and meant to be "negative sensations"; the latter term being heavily debated from that time onwards (cf. (Cheesman and Merikle, 1986, Barry H. Kantowitz, 2015).

From Fechner's first model onwards, many scientists within the psychophysical field tried to develop the idea of a certain sensory threshold shaping the human being's decision making process. In the following, three of the multiple scientific developments will shortly be introduced:

Almost 100 years after Fechner's influential work, 1953 H.R. Blackwell further developed the idea of sensory limits and with his studies the term was coined for a "High Threshold Theory" (HTT) in his originally unpublished work "Threshold psychophysical measurements" (Blackwell and Institute, 1953). Even in our days, Kingdom et al. felt that this term was perfectly appropriate, since "this threshold [was] assumed to be sufficiently high that it [was] only very rarely surpassed by the system's internal noise on its own" (Kingdom et al., 2015). In terms of signal detection the threshold was set high enough that the observer was very sure about the existence of the signal, so that false alarms (2.1. Table 1) did hardly play a role. However, the observer did not recognize signals with less evidence. Looking at Gaussian distribution functions, this meant that for the observer a great perception of stimulus intensity was necessary that the signal was detected among white noise. Henceforth, in standard HTT, the threshold was not variable but fixed. So when subjects are given incentives to respond "yes" more often, they cannot lower their decision threshold but will simply say "yes" randomly on some fraction of trials when no stimulus is perceived. Swets later reflected Blackwell's intention saying "…that, whereas the observer [might] be lead to say "yes" when noise alone [was] presented, only very infrequently [was] his threshold exceeded by the sensory excitation arising from noise – so frequently, in fact, that these instances [could] be ignored"(Swets, 1961).

Figure 1 shows graphically what the assumption of the HTT in a YN-task really means. Again, giving a task where to detect a sound (of a certain sound pressure) within white noise (the latter will be thoroughly explained in the next chapter) four conditions are possible: the signal is presented and the subject says “yes, sound present” or it goes for “no, sound absent”. The same options occur for a trial when the sound was not presented. The sensory evidence can therefore be depicted as Gaussian distribution for N- and SN-stimuli (Fig. 1). In HTT the threshold (T) lies at the very end of the N-distribution, so that this internal noise rarely surpasses the threshold and becomes conscious. However, weaker stimuli of less sensory evidence (left part of the SN-distribution) neither pass the threshold, which means that the subject will not detect sounds with a low sound pressure. .

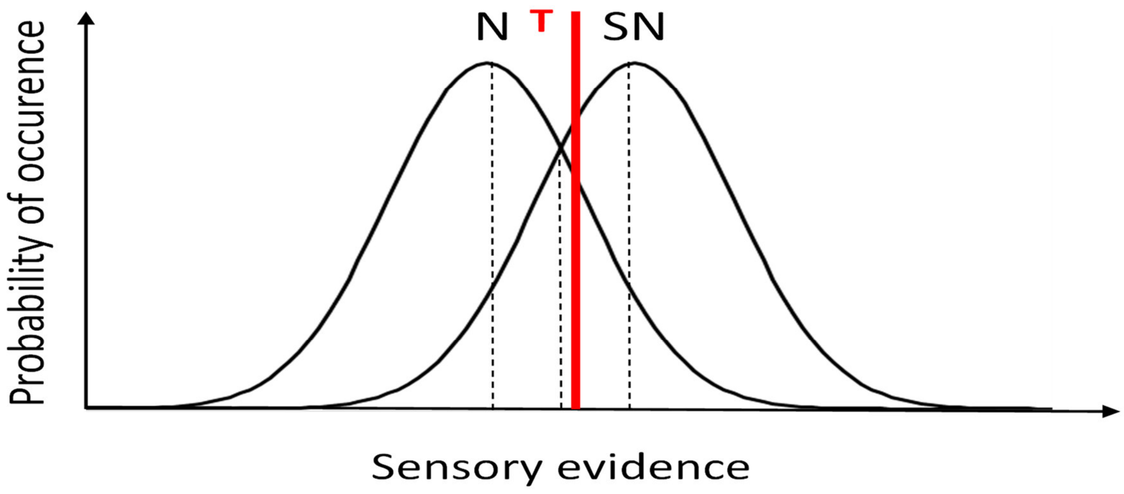


-Figure 1-

In a YN task, two responses are possible: “yes” for an existing signal and “no” for an absent signal. The x-axis shows the sensory evidence of a certain stimulus and the ordinate the probability for a sound to occur. Two Gaussian distribution curves of N- and SN-functions are depicted (in detail explained in 2.3.2.) and, the red straight line (T) shows the location of the “high” threshold. According to HTT, the threshold is located at the upper end of the noise distribution, such that internal noise (e.g., stemming from spontaneous neural activity fluctuations) only rarely surpass the threshold and become conscious. A weak stimulus may for the same reason (noisy neural processing) yield different perceptions of intensity from one trial to the next, which is described by a Gaussian distribution). Only when the internal (neural) response surpasses the threshold, the subject is believed to consciously perceive the stimulus.
Modified from (Birdsall, 1955).

Meanwhile, R.D. Luce presented an alternative model of signal detection cf.(David Kellen, 2016, Atkinson and Juola, 1974). He postulated a certain “lower” barrier that lead to a “yes” or “no” response after a given stimulus. In contrast to the HTT, however, his “low” threshold was not set at a point when only signals of high evidence could be detected by the sensory system, a lower threshold allowed the observer to respond “yes” even then when a signal with a very low evidence was presented (Fig. 2). With that, Luce incorporated other non-sensory states like reactions favorable concerning the task’s pay-off or memory-associated behavioral patterns (cf. chapter 5) (David Kellen, 2016). Since Luce’s theory allowed to say “yes” for less evidential signals and to say “no” for highly evidential stimuli that were not only dependent on the stimuli intensity but subjective and objective influences, so that “individuals [could] express a “liberal” or “conservative” response strategy…” (David Kellen, 2016). But although Luce’s theory tried to incorporate non-sensory states, like certain internal and external factors that influence decision making, later investigations showed that also Luce’s idea was not complex enough. Further explanations to that will be discussed in following chapters. Nonetheless, Luce’s experiments lead the way to a deeper scientific research of the human and non-human complex sensory system.

Figure 2 illustrates what has been said before: comparing the location of the threshold in both theories, in the LTT the threshold is shifted to less evidential signals. Whilst in the HTT, noise stimuli hardly overcame the threshold and mostly stayed unconscious, in the LTT more signals with low evidence are detected.

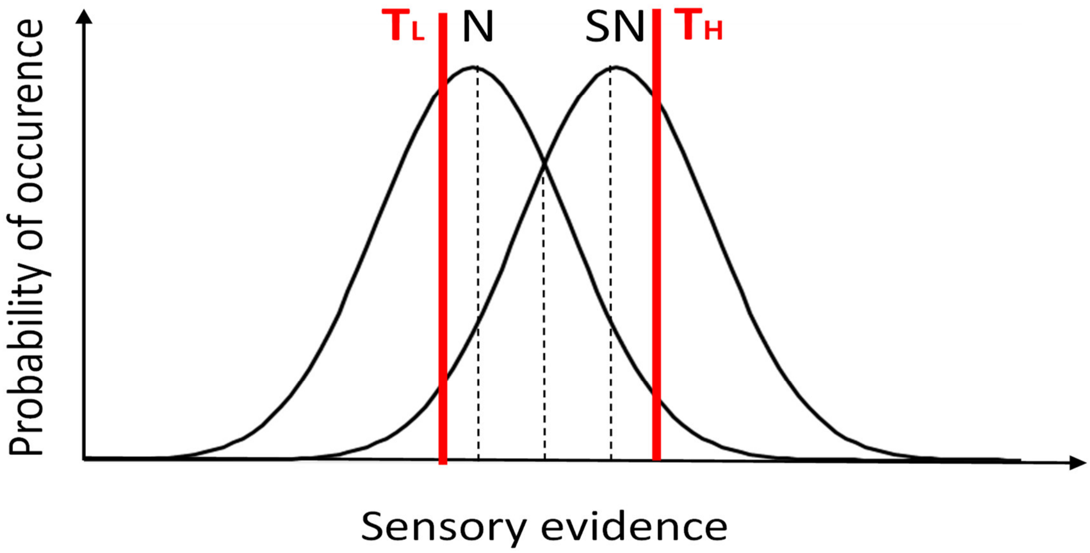


-Figure 2-

Again, a YN is employed comparable with Fig. 1 (cf. panel description). In comparison to the high threshold model, the red bold line shows a possible location of the “low” threshold (T) within Gaussian distribution curves. Comparing with the HTT, the low threshold is located to rather neutral parameters leading to a greater decision corridor which leaves room for more subjective and objective influences. Modified from (Swets, 1961)

In the late 1950s a third idea was brought up by D.M. Green. At first sight his “Two-threshold Theory” seemed to be only an advancement to the LTT and the HTT, but Green accomplished to further point out the complexity of decision making. He thought of two thresholds, ”… a lower threshold, below which lies true rejection, and an upper threshold, above which lies true detection” (Swets, 1961). Henceforth, he developed a three-category model along with a more detailed gradation in sensory excitation. That meant for the task procedure that the subject could give answers to the different categories depending on the strength of each stimulus and, what was undoubtedly clear back then, other subjective and objective influences. Speaking in terms of any threshold-category model, each new category lead to a more accurate description of the subject’s stimulus perception. It was obvious, that the more categories a task offered, the more detailed was the analyzation of the test subject decision behavior. Without forestalling what will be discussed later, it was quite clear that the more categories and the more thresholds existed, the more the fitted threshold would approach the best fitting curve to the subject’s individual task response (see section 2.3.5.).

Again, Figure 3 graphically reflects what has been described before: The two Gaussian distribution curves depict where both thresholds (T) are located in accordance to the S and SN distribution curves. So instead of just one threshold, the subject can categorize a stimulus in three different gradings of “true rejection”, “true detection”(Swets, 1961), and an indifferent state depending on its perceived sensory evidence.



-Figure 3-

Comparing this figure with the two upper graphs (Fig.1,2, see panel description), the red bold lines show possible locations for the two thresholds (TL, TH) within Gaussian distribution curves in a general forced choice task. Modified from (Swets, 1961)

Finally, having provided the key principles of a basic threshold model by Fechner as well as the developed advancements, the following chapter will explain SDT as a fundamentally different model trying to give answers of how signal detection functions in human and non-human animals. Later on, former and current research about signal detection will give word to critical opinions about SDT and the main competing TT.

2.3. Signal Detection Theory

2.3.1. Historic background

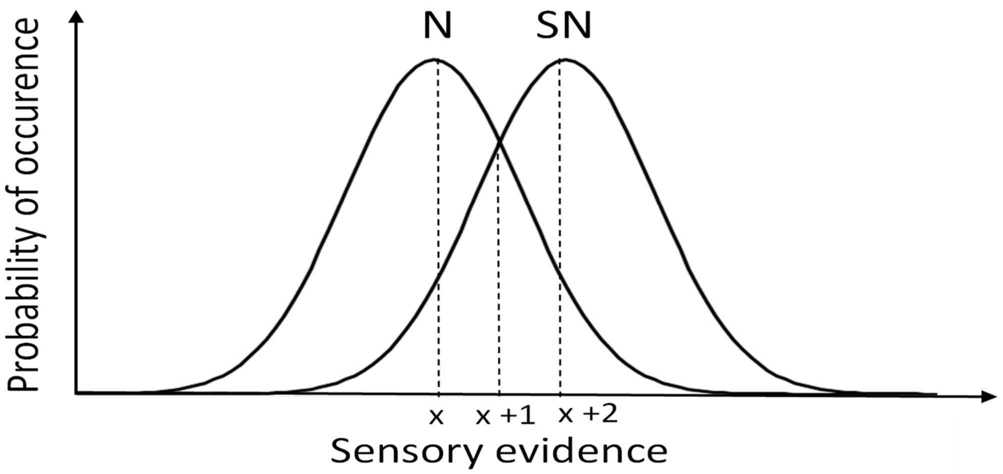
Firstly mentioned in World War II, signal detectability became necessary when one single officer at the southern coast of Great Britain was in charge of the whole radar operating system, obliged to identify hostile fighter aircrafts. It is thoroughly investigated that the radar technique was developed poorly at that time, so radar points on the computer screen were not always caused by the presence of hostile aircrafts, but also other environmental factors (e.g. weather conditions). So how would the officer know whether a specific dot on the screen ("signal") was caused by weather changes ("noise[2]", cf. 2.3.2.), or actually indicated the presence of an enemy plane? (Reading, 2003, Johnson et al., 2017).

"As a statistical model, SDT rests on a set of assumptions. These include the premises that (1) events to be detected (signals) are always embedded in a background of irrelevant sensory information (noise); (2) the distributions of noise and signal-plus-noise are of normal form and equal variance; (3) observers are both sensors and decision makers, and they adopt a criterion of sensory magnitude for deciding whether a given event is a signal or a non signal; and (4) measures of perceptual sensitivity [e.g., *d′*] can be treated as if they were independent of measures of response bias…." (Bohil et al., 2015).

These four assumptions give a concise overview about the theoretical fundament of SDT. In the following, these basic principles will be explained in order to understand SDT that became "…one of the most prominent scientific developments in psychology of the past 60 years" (Bohil et al., 2015, Estes, 2002).

2.3.2. Signal and noise

It was mentioned before that SDT is based on experiments with a subject participating in a decision task of many trials on which a signal is either present or not (cf. a YN task explained in section 2.1.), whereby noise-alone (N) and signal-plus-noise (SN) trials are equiprobable. As the observer tries to detect the specific signal, it perceives a sequence of other distracting background stimuli. Again, this distraction from the real signal is called “noise” (i.e. dots on the radar screen could not only be caused by foreign marines, but also by certain weather conditions). Consequently, two states exist that need to be distinguished: signal-plus-noise (SN)[5] or noise-alone (N)(Fig. 4), whereby the occurrence of N and SN on a specific trial is determined by the experimenter.



-Figure 4-
In an auditory decision task the subject has to decide whether a signal is presented on any given trial or not. The x-axis describes the sensory evidence of a certain stimulus, and the y-axis the probability of a signal to occur. Subjectively, two stimuli (e.g. x and x+2) differ in their perception of stimulus intensity. Consequently, a tone x+2 on the ordinate has a stronger subjective sensory evidence than a sound of x., which enables the subject to distinguish between different stimuli (see further text and 2.3.3.).

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[5] Stimulus-plus noise (SN): a receiver does not only perceive the key stimulus, but all surrounding sensory inputs presented at the same time.

In SDT, N- and SN-probability density functions are assumed to follow Gaussian distributions along an axis of perceivable stimuli with different sensory evidence. It is important to know that in a signal detection task the tone of interest, speaking of auditory stimuli, has the same physical intensity throughout the experiment, while the subjective impression of its intensity is different from trial to trial. SDT does not specify the source of this variability, but it is conceivable that fluctuations in attention of noisy transmission in the auditory pathway are crucial contributors (Goldstein, 1997).

So how is signal detection possible? Correct detection of SN is only possible because the sensory evidence differs between N and SN. If the subject perceives a certain stimulus having a stronger sensory evidence (e.g. x+2, Fig. 4), this perception is more likely to occur in SN trials than in N trials. Vice versa, a low perceived intensity (such as x in Fig. 4) has a higher likelihood to occur on N trials. For a YN task, SDT therefore postulates that a single value drawn from either the SN or the N distribution is the only data point the observer can base his decision on, and it does so by comparing the magnitude of that value to an internal decision criterion; "If the decision variable is sufficiently high during a given trial, the subject responds yes (a signal was presented); otherwise, the subject responds no (no signal was presented). The value that defines sufficiently high is called the criterion[6]" (Stanislaw and Todorov, 1999).

To cut it short, the ability of a subject to distinguish between two stimuli of N and SN Gaussian distribution functions participating in a decision task of many trials on which a signal of a certain sensory evidence (e.g. x, x+1, x+2,… Fig.4), is either present or not, depends on the relative distance of these two distribution functions (more to this in section 2.3.4.).

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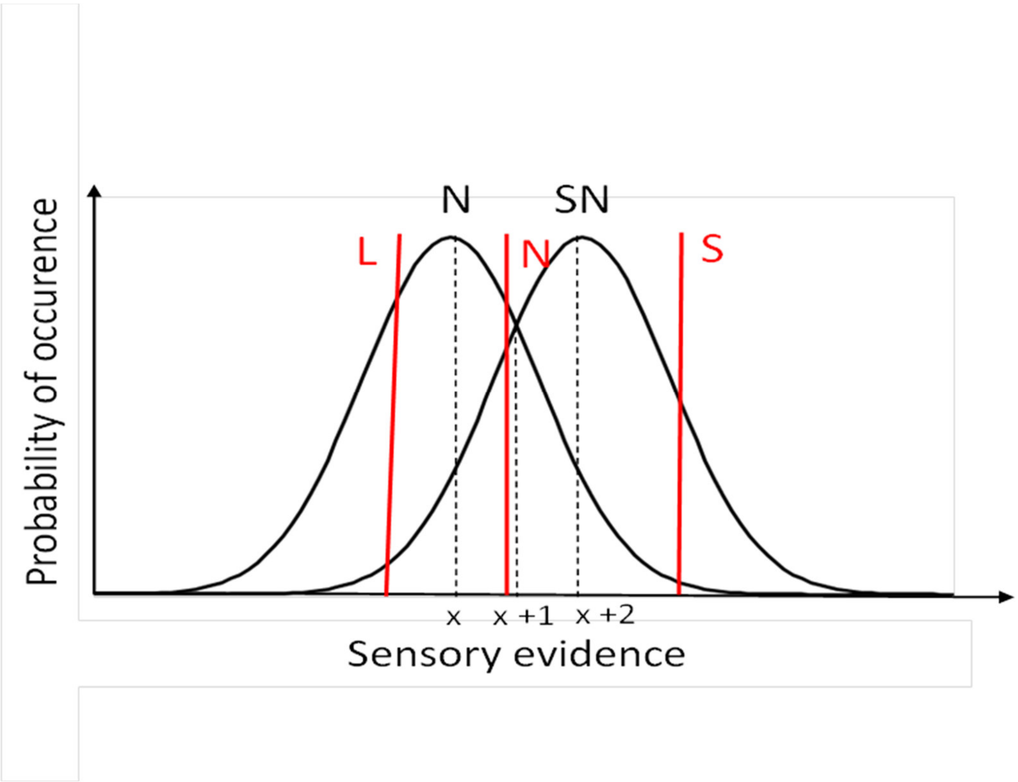
[6] The role of the decision criterion for SDT will be explained separately in section 2.3.3



-Figure 5-
This figure illustrates SDT's conception of signal detection for three different positions of the decision criterion. Again, the x-axis contains the subjective sensory evidence of a stimulus. The y-axis depicts the probability for the occurrence of a signal. The red lines show different criterion settings: a lax criterion (L), a neutral criterion (N), and a conservative criterion setting (S). All stimuli with a perceived sensory evidence stronger than the criterion are accepted as SN-stimuli, whereas stimuli with an evidence falling below the criterion are seen as N-stimuli.

2.3.3. The criterion

The previous subsection made clear that signal detection depends on stimuli with subjective sensory evidences drawn from the N or SN distribution functions. Speaking in terms of SDT, the observer relies on a certain decision-making tool, called "criterion" (c). There are two possible conditions: in the first condition, the sensory evidence is stronger than c, comparable with a "yes, signal is present" trial in a YN task, so the subject decides for SN (correctly or not). In the second condition, a stimulus of lower intensity than the internal criterion is presented (cf. YN task with "no, stimulus is not present", 2.1), and the observer chooses N. Hence, in SDT a subject to solve a signal detection task develops an interior boundary called "criterion" that helps the test object to decide between N and SN.

Additionally, it is necessary to understand that criterion setting depends on different factors, i.e. the observer's individual characteristics (like fluctuations in attention) or special surrounding conditions (Stanislaw and Todorov, 1999, McNicol, 2005).

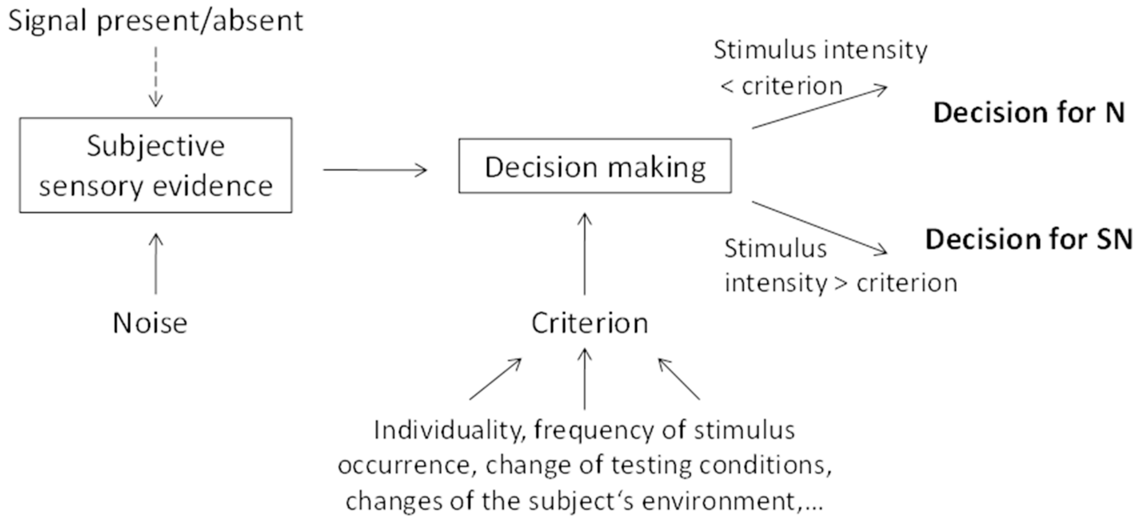
Being more precise, the very beginning example (section 2.1.) demonstrated that in certain situations the security officer showed different response behaviors independent of his sensitivity.

In Figure 5, the red straight lines show three conceivable criterion placements: L stands for liberal criterion setting (resulting in a large fraction of hits but also false alarms), N shows a neutral criterion (equating the fractions of false alarms and misses), and S stands for a conservative criterion setting (yielding few hits but even fewer false alarms). Transferring the subjects' behavior onto the N- and SN- distribution in Figure 5, and employing the reward schedule 1 (Table 3), the officer would rather "liberally" respond (gaining more rewards by finding the knife) shifting c to the left side of the abscissa (Fig. 5, red straight line L). Under these circumstances, the whole distribution function of SN and also the majority of the N-distribution lie above the decision criterion. Hence, a liberally acting receiver will detect all SN-stimuli correctly (=hits, Table 1), but will also falsely respond "yes" on null trials (N) in >50% of trials (=false alarms, Table 1)(Goldstein, 1997). In contrast, employing reward schedule 2, when correct rejections (correct "no" responses) yield a lot more rewards than correct hits (correct "yes" responses), henceforth shifting c towards higher values of x (criterion S), so no portion of the N-distribution and only a small part of the SN-distribution lies above the criterion, going along with less hits and no false alarms (Fig. 5, red straight line S).

In general, criterion setting can be influenced through experimental manipulations. For instance, if the experimenter manipulates the schedule so that SN trials occur more often, the subject will shift c to lower values of x (thereby increasing the percentage of hit trials as well as false alarms, while increasing overall percentage of correct choices) (Macmillan and C Creelman, 2004).

Referring to the beginning of this chapter, also reinforcement and punishment are sufficient tools to alter behavior in a specific manner (Feng et al., 2009, Stoilova et al., 2019). The experiments described in this thesis will therefore be a way to investigate adaptive behavior under changing reinforcer contingencies and derive a model that sufficiently describes the outcome.

To wrap it up, in SDT c is assigned great importance within the decision making process. In a simple way, Figure 6 reflects how choice allocation proceeds showing that besides stimulus perception the criterion setting has a major impact on the final decision. Nonetheless, c itself is highly variable and dependent on numerous interior and exterior factors.



- Figure 6-
SDT describes how signals are detected in background noise. First, the subject perceives a stimulus, N or SN. Then, depending on the sensory evidence, the subject will eventually decide for either N or SN. As shown in the panel, the decision making process also relies on the decision criterion that is influenced by many different factors (see text).

2.3.4. The d'-value

By now, having discussed important parts of signal detection, it is quite clear that the hypothetical two officers may even have the same sensitivity for the stimuli, but their way to solve the task could individually be different (cf. 2.1., 2.3.3.). The detailed discussion of the last section supports the idea that decision making is influenced by factors asking the subject to shift c in order to choose the correct alternative and to maximize trade-off.

Besides a shifting of c due to changing environmental conditions (as varying payoff matrices and stimulus presentation probabilities) every subject has a different sensitivity to the given stimulus. So before the intensity of adaption process is measured through c, it is of great concern how well the observer solves the given decision task independent of the adaption process and the shifting of c. Henceforth, SDT tries to independently address two main components that are responsible for decision making: first, the analyzation of a subject's sensitivity, and second the analyzation of its reactions to changing environmental conditions measured by c. The separation of sensitivity and response bias, along with the provision of quantitative indices, are considered to be the major contributions of SDT to psychology (cf. (Stanislaw and Todorov, 1999, Luo and Maunsell, 2018, Macmillan and C Creelman, 2004, Bashinski and Bacharach, 1980, Downing, 1988, Wyart et al., 2012)).

Whilst c was explained earlier (see section 2.3.3.), in SDT sensitivity is measured through d' (pronounced: "d-prime")[7]. The d'-value equals the absolute distance between the N-and the SN-Gaussian distribution curve (Fig. 7), or being more accurate in algebraic terms: $(\mu_{SN}–\mu_N)$ / σ, where μ_{SN} and μ_N denote the means of the signal and the noise distributions, respectively, and σ represents the standard deviation. Practically, d' = 0 means that the means of the two distributions are identical. Thus, the subject fails to distinguish the stimuli at all (its performance[8] equals chance level). Yet, for an unbiased observer in a YN task, d'=1 corresponds to 69%, d'=2 to 84%, d'=3 to 93% correct responses. The maximum value of d' is infinity, the minimum value is negative infinity (Stanislaw and Todorov, 1999).

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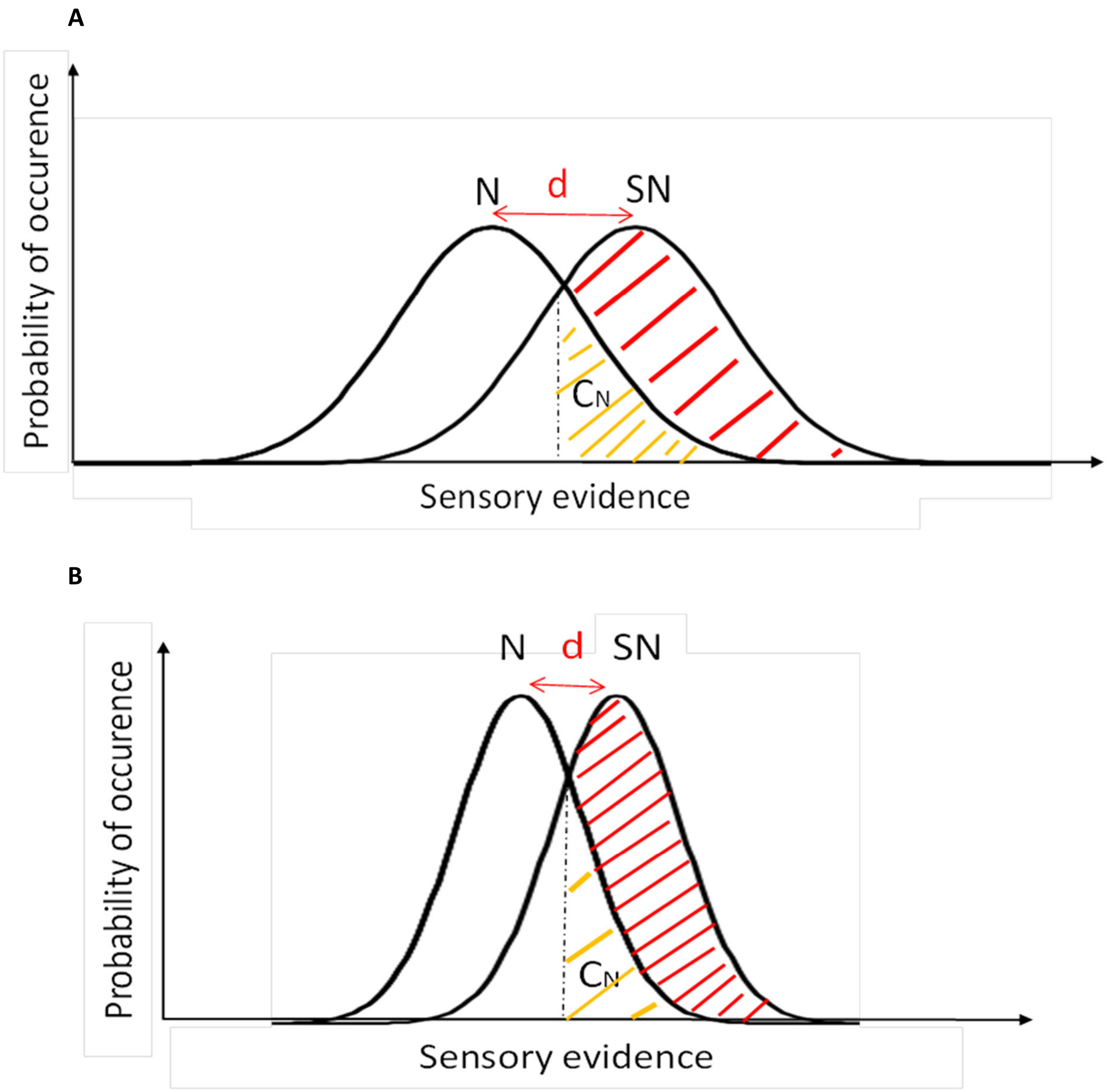
[7] d'-value: the value of d' is expressed in Arabic numerals. d' = 1.0 equals a distance of 1 standard deviation to either side from the center of the two distributions; d'= 2.0 equals a distance of 2 standard deviations to either side from the center of the two distributions; d' = 0 means that both stimuli functions are congruent (s. text for more detail).

[8] performance (hits, misses etc.) depends on a) sensitivity and b) bias (criterion placement)

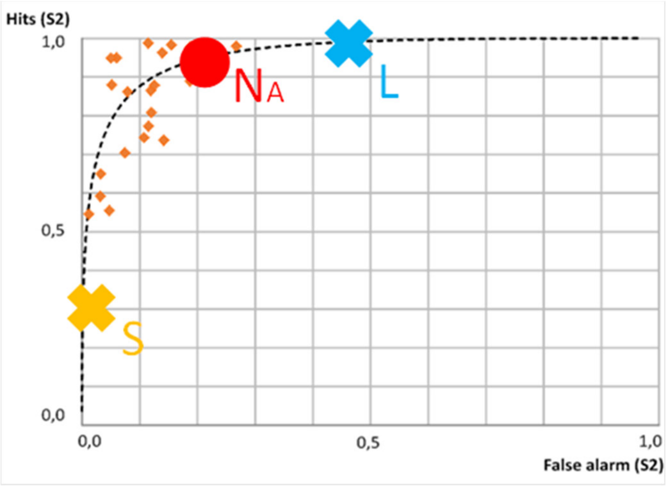
The following paragraph will graphically depict how sensitivity levels between test objects, given by d’, can be distinguished from individual responding behavior represented by individual criterion setting.



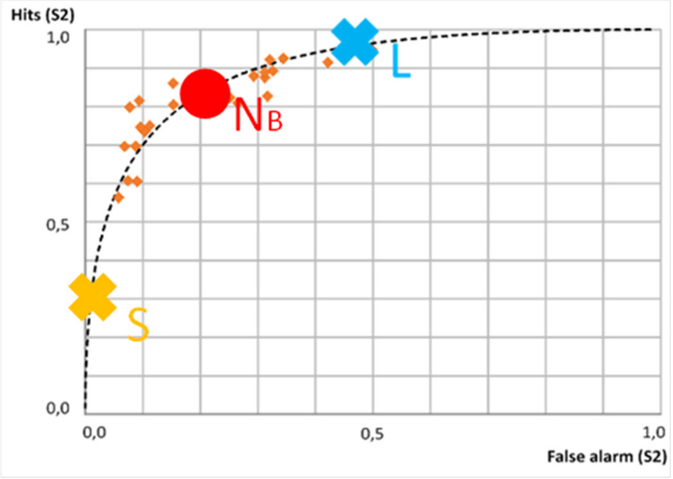
-Figure 7-
For depiction of the ordinate and abscissa see earlier panel descriptions (cf. fig. 4). 7A and B show Gaussian distribution curves for N and SN (s. paragraph 2.3.2). The d'-value equals the distance between the peak of the N- and SN-distribution in units of their common standard deviation. d' is an appropriate measure for the subject's performance, since it illustrates how well it is able to distinguish between N- and SN-trials – the higher d', the higher the subject's sensitivity (compare panels A and B). The outcome is especially meaningful when comparing the test subjects' percentage of hits and false alarms. In 7A the subject often responds correctly (= high probability of hits, red-striped area), but the probability of false alarms is still relevant (orange-striped area) The outcome in 7B results from the same testing procedure, the two curves only differ in the subject's ability to distinguish the stimuli: e.g. this time the subject to Fig. 7B has a probability of almost 100% hits (red-striped) and a very small probability of false alarms (orange-striped area).

2.3.5. The ROC

The receiver operation characteristic (ROC) curve is a graph showing a subject's detection performance (hits and false alarms) as a function of individual criterion setting for a given sensitivity to the stimulus (cf. (Luo and Maunsell, 2018).



Subject A



Subject B

-Figure 8-

The upper and the lower panel both depict ROC curves that originate from different performances of subject A (upper panel) and subject B (lower panel) in a decision task. In both panels the x-axis contains the false alarm rate, the y-axis depicts the hit rate. Comparing two subjects' neutral criteria NA and NB, the former (upper panel) creates more hits and fewer false alarms resulting in a steeper rising ROC curve. If two subjects have an equal sensitivity to N- and SN, but obtain a different responding behavior (=c differs), their coordinates will lie on the same ROC-curve: the outcome by obtaining a strict (criterion S), a lax (criterion L), or rather neutral (criterion N) responding behavior creates the same ROC curve. The data was taken from two of the four experimental subject used for the studies of this paper.

Generally, the ROC-curve plots the hit rate on the ordinate and the false alarm rate on the abscissa. As illustrated above (Fig. 7), both parameters together determine an observer's performance.

Whilst in Figure 7 the subject's performance is depicted by the absolute distance between the peaks of the two Gaussian normal distribution functions (= stimulus sensitivity = d') and by the placement of c on the x-axis, Figure 8 demonstrates another graphical alternative to show a subject's performance in a detection task: subjects with equal sensitivity, but different criterion placement, have the same ROC (the lax subject's outcome corresponds with the blue cross "L" on the bold black line; the stricter test object shows a more conservative responding behavior corresponding with the orange cross "S" (Fig. 8)). Thus, different stimuli sensitivities create different ROCs, while criterion placement is represented along the curve.
Assuming both subjects have a neutral c (Fig. 8, red circles NA and NB), the test subject with cNB is less sensitive than the observer with cNA. Henceforth, the subject with cNB shows a worse distinguishability going along with a smaller d' (s. 2.2.3. and fig. 6).

Finally, having provided the key principles and terms about SDT, the following section will draw the attention to former and current research about signal detection giving word to critical opinions about SDT and the main competing TT.

2.4. Studies about and around The Signal Detection Theory - past research on criterion setting in perceptual choice tasks

In the 19th century when Fechner and Weber introduced the idea of a sensory threshold (cf. 2.2.), only a few years later groups of scientists started their research with human and non-human animals in the field of signal detection (cf. (Killeen, 2015) for a concise modern overview of SDT)). However, many years later in 1954 Peterson, Birdsall, and Fox published "The theory of signal detectability"(Peterson et al., 1954), the groundwork for the classical SDT. Many of these former (and still current) authors' common intention was to primary investigate whether animals were "ideal observers"[9], and if so, which algorithm was underlying the animals' performance in decision tasks.

As mentioned before, they did not believe that decision making exclusively depended on stimuli threshold, but that there were further factors that lead to a person's final choice allocation (s. 2.1. "The fundamental decision problem"). "A key insight by the pioneering researchers was that errors of commission in perception tasks are not necessarily the result of guessing, as assumed by threshold theories (Tanner Jr and Swets, 1954, Bohil et al., 2015).

Generally speaking, early scientists developed a simple behavioral experiment (cf. YN, 2.1.), which is similarly used today and comparable to my outline in 2.3.2. "Signal and Noise", in which the observer was confronted with two different states: stimulus-and-noise, SN, or noise-alone, N (Fig. 4). Then, the observer had to decide which of the two alternatives was presented.

In early research protocols, the experimenters started out listing up the observer's response for each stimulus alternative (Craven, 1992). With this effort, Peterson et al. (1954) intended to find the ideal observer that, belonging to a theoretic model, knew about the given stimuli, their Gaussian distributions, and how many different stimuli were presented. Yet, the observer did not know when each stimulus alternative was presented (McNicol, 2005, Stüttgen et al., 2011b).

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[9] The ideal observer: "is a hypothetical entity [in which an ideal observer has] full knowledge of the stimulus distributions and the values and costs of each possible outcome who places the decision criterion as to maximize a certain decision goal…" STÜTTGEN, M. C., YILDIZ, A. & GUNTURKUN, O. 2011b. Adaptive criterion setting in perceptual decision making. *J Exp Anal Behav,* 96**,** 155-76.

Hence, “the chief conclusion obtained from the general theory of signal detectability…[was] that a receiver that calculates the likelihood[10] ratio[11] for each receiver input is the optimum receiver for detecting signals in noise” (Peterson et al., 1954). Their first assumptions brought forth important parameters within SDT like sensitivity to a stimulus or the shifting of c (cf. 2.3.3., 2.3.4.). Thus, the most relevant parameters to understand and resolve problems of signal detectability were early discovered when scientists started out to become interested about the theoretical backgrounds to proper signal detection. Since then, advancements have been added little by little, and still today scientists conduct experiments to further develop the scientific theory of signal detectability. The primary question whether human and non-human animals yield “optimal” signal detection is not resolved yet, and there also exist theories that encounter the belief of optimality in human and non-human animals at all. The following paragraphs will therefore serve to outline scientific outcomes from the mid-19th century onwards that addressed the field of signal detectability either supporting or condradicting optimal behavior.

In the past, scientists have been interested to understand whether and how animals adjust their behavior to changing reinforcement schedules (remember the different payoff matrices of the beginning example; in fact, the two subjects adjusted their behavior as certain responses were rewarded or punished; s. 2.1. “The fundamental decision problem”). How the programmed decision task influences the bias[12] of the animal will be thoroughly explained later. First, the research project is put into the context of the broad field of signal detection, presenting recent works of scientists that addressed similar questions about adaptive behavior in non-human animals.

Recent scientists studying adaptive behavior of vertebrates were part of M. C. Stüttgen’s laboratory team that conducted experiments that were similar to the basic laboratory YN task (cf. 2.1.). In a visual experiment, pigeons had to differentiate between six different shades of grey (the design of the experiment was comparable with their later conducted experiments in

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[10] Likelihood: shows how likely an outcome is under a certain hypothesis is (e.g. hypothesis H1= SN occurs or hypothesis H0 = N occurs)

[11] Likelihood ratio: shows the relative likelihood of two different hypotheses (e.g. SN over N, see below)

[12] Bias, here: a subject favors one choice over another for whatever reasons (e.g., because one choice yields more rewards)

2013, cf. Fig. 10). The three darker shades constituted category S1; the three lighter grey shades constituted category S2[13]. In short, each stimulus appeared with a probability of 1/6, and there was a chance of 3/6 for either a S1-stimulus (accounting for the three darker shades) or for a S2-stimulus (the three lighter shades of grey), respectively. Before asymmetrical reinforce ratios were established to find out more about adaptive behavior to changing reinforce conditions, many scientists only coped with equal reinforce ratios (cf. (Lea, 1979, Feng et al., 2009). Therefore, Stüttgen et al. questioned whether SDT would also give reasonable answers to signal detection behavior under changes in reinforcement contingencies (Stüttgen et al., 2011b), so instead of equal reward ratios for correct responses (e.g. 0.5 for both, S1 and S2), they employed asymmetrical reward ratios for correct responses ranging from 0.2 to 0.6. After fitting their data to a SDT-based model they could show that the subjects shifted an internal decision criterion in order to maximize payoff, and finally, in terms of SDT, their performance nearly reached optimality (Stüttgen et al., 2011b). Figure 9 illustrates their results: on the y-axis is the proportion of left responses (S2), on the abscissa is the presented stimulus intensity (gray value). Filled rectangles and triangles show the response to S2-stimuli with a higher reinforcement rate, framed rectangles and triangles show the proportion of S2-stimuli with lower reinforcement probability. The psychometric functions of individual birds (the last 5 sessions of each of the six conditions were used) show that overall a larger reinforcer probability for S2 lead to a higher proportion of S2 responses (in Fig. 9 only birds nr.720 was depicted). In terms of SDT, that observation again went along with a subject shifting an internal criterion to maximize payoff what they demonstrated by comparing the task results of an empirical subject (in their case a pigeon) with the results of an ideal observer given by SDT (Fig. 11) (cf. (Stüttgen et al., 2011b)).

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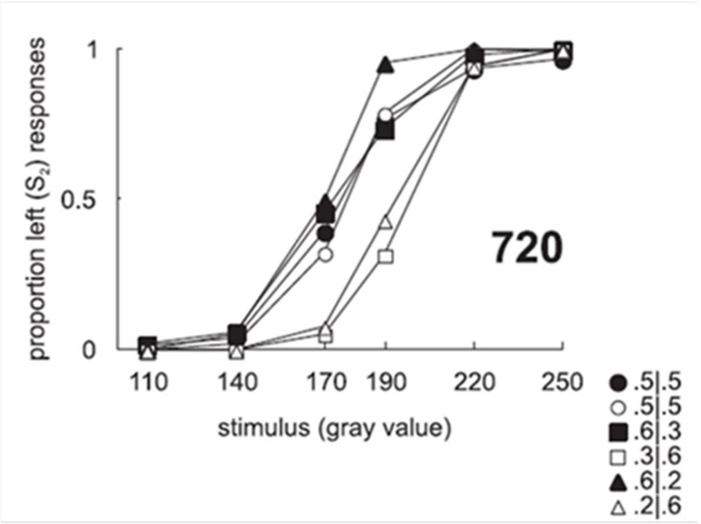
[13] Comparable with a single-interval forced choice task with only-noise(N)- and signal-and-noise(SN)-stimuli



-Figure 9-

In their 2011 conducted experiment, Stüttgen et al. could show the dependence of reward probability and proportion of S2-responses (here: exemplarily bird nr.720). During the task session the subjects were presented 6 different shades of grey color and they had to distinguish between S1 (=3 darker shades of grey) and S2 (=3 lighter grey values). The x-axis depicts the intensity of the grey color value, the y-axis shows the proportion of left (=S2 responses). As the 3 lighter grey values (=S2) were greater reinforced (=bold squares and triangles of the attached table), the birds more often responded with a left choice. (Stüttgen et al., 2011b)

In Figure 10 the abscissa shows the session number, the y-axis plots the pigeon's criterion value. In comparison to the thin horizontal lines that highlight the position of the optimal criterion in each experimental condition, the thick line ("empirical" function) reflects the actual behavior of the animal dependent on the changing reward condition. Additionally, the objective reward function (ORF)[14] (cf. (Maddox, 2002) for each condition is indicated by the shaded background (see right scale). Referring back to the authors' assumption, the shifting of c for reward maximization corresponds with the changing reinforcement rate (Fig. 10). So they concluded that after a certain time of training, the experimental subjects nearly perfectly adapted to the changing conditions, even though this brought about hardly more rewards (Fig. 9 and 10) (Stüttgen et al., 2011b).

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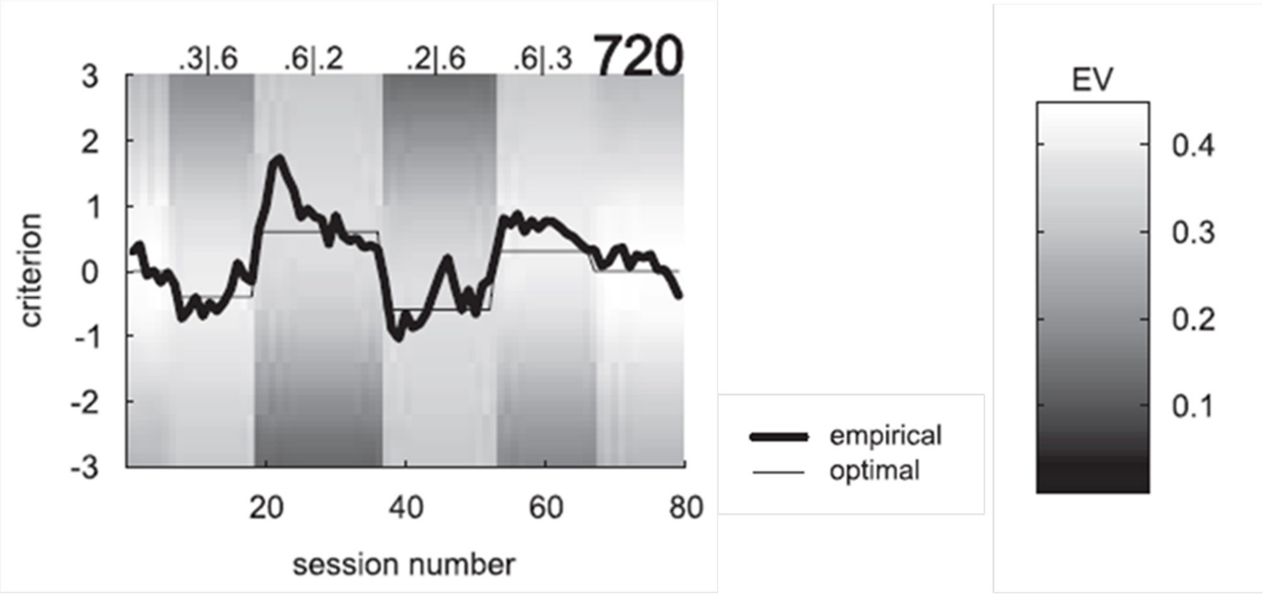
[14] Objective reward function: specifies the expected reward as a function of criterion placement for a subject with a certain d'.



-Figure 10-

Besides the interdependence of reinforcement rate and response rate, Stüttgen et al. also demonstrated with the given figure the dependence of criterion setting from varying reinforcement probabilities. The abscissa shows the session number, the ordinate the criterion placement. The thick bold line depicts the pigeon's real ("empirical") criterion setting depending on the probability ratio (exemplarily of bird nr. 720). The thin straight line gives an orientation for optimal criterion setting as to maximize payoff. The shaded background (see also table on the right) represents the ORF (cf. section 2.3.5.) graded in reward probability for each criterion position. (Stüttgen et al., 2011b)

The results of Stüttgen's 2011 paper gave more evidence for adaptive behavior through changing reinforcer conditions like postulated in SDT. In their following paper "signal detection theoretical model and predictions for criterion placement" (Stuttgen et al., 2013) they therefore tried to understand the mechanisms of criterion placement for an ideal observer maximizing the amount of reward during a certain task session.

In a visual experiment the pigeons had to differentiate between six different shades of grey (cf. experimental design like their previous set-up in 2011; Fig. 11). In Figure 11, the x-axis covers the perceived stimulus intensity, the y-axis contains the reward probability for correct responses ([E(RfS1) + E(RfS2)] = correct S1-stimuli and S2-stimuli (the maximum reward probability was 0.5 and could be achieved only when correct all the time). Figure 11A shows the ORF for the case when each stimulus is reinforced equally (= symmetric reinforcement[15], here

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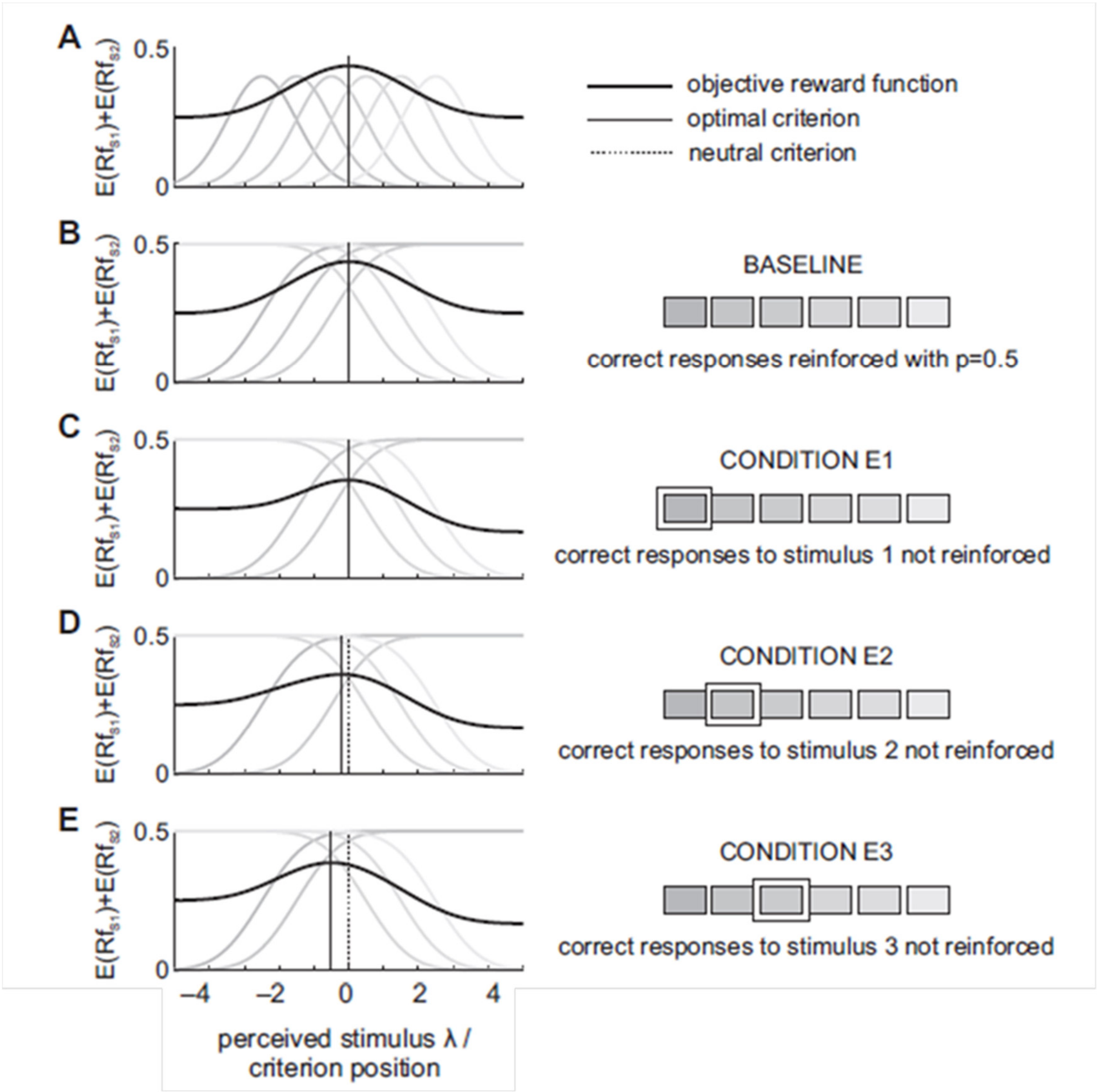
[15] Reinforcement: in a decision task correct choices are either rewarded equally (=symmetric), or correct choices are rewarded unequally (=asymmetric, one choice yields reinforcement more often than the other)

with a reinforcement rate of 0.5), along with Gaussian distributions for all six stimuli. In a symmetrically rewarded choice task, it is quite reasonable that the optimal c (the vertical dark grey line) lies in the middle of S1 and S2, so the animal should not be biased to either side. From the cumulative functions in Fig. 11B follows that the peak of the ORF (thick black line) represents optimal criterion setting as to receive most rewards for the most extreme stimuli (1 and 6), simply because they are easiest to classify (furthest from the arbitrary category boundary between stimuli 3 and 4).

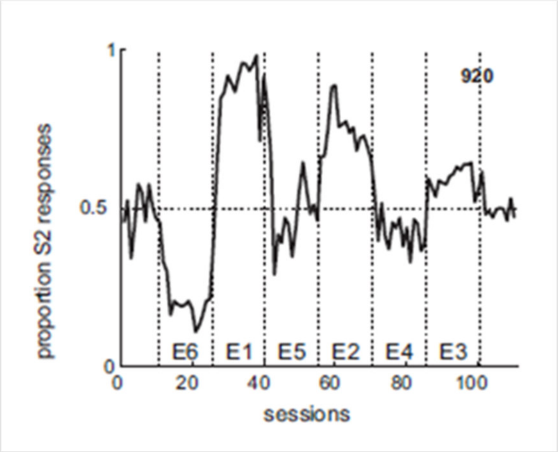
Figure 11B shows the same situation as depicted in panel A, except that the light gray lines represent the expected number of rewards per trial for each stimulus separately, as a function of criterion placement along the x-axis. Stüttgen et al. predicted that a test subject would perform differently with asymmetric reinforcement contingencies, more specifically, when one of the six stimuli (conditions E1-E6, Fig. 11) was not reinforced anymore. Panels C, D, and E show how the position of the optimal criterion and the ORFs change for experimental conditions E1, E2, and E3. If condition E1 was not rewarded anymore, the peak of the ORF would decrease slightly, and its peak (coinciding with the optimal criterion position) would subtly shift (hardly visible in panel C). Because E1 was the darkest condition, the pigeon could easily classify it as an S1-stimulus. Holding back rewards for stimulus 1, however, should only slightly affected the shifting of the criterion and the peak of the ORF for an ideal observer in condition E1 (fig. 11, dashed line). By contrast, omitting reinforcement for stimuli 2 and 3 in conditions E2 and E3, respectively, more substantially influence the position of the optimal criterion. That time, the optimal c moved from the neutral position farther to the left side as the subject received more rewards for E4-E6 conditions in relation to E1-E3 conditions. These observations will be similar for conditions E4, E5, and E6 (ORF and the position of c will alter in the opposite way).



-Figure 11-
Predictions for criterion setting on the basis of SDT. Panel A shows 6 distributions according to 6 different shades of grey the subjects were presented. The 3 left distributions correspond with stimulus S1, the 3 right distributions belong to the stimulus S2. The x-axis therefore depicts the perceived stimulus of grey value (as well as the criterion position), the y-axis represents the expected reinforcement for a given stimulus. The thick bold line is the ORF standing for optimal criterion setting as to maximize reinforcement. Panel B is similar to A, yet the grey lines stand for each condition separately, together with its expected reward. Panels C – E demonstrate, in terms of SDT, optimal shifting of c (black vertical line) when one of the 6 grey values is not reinforced anymore (here only conditions E1-E3 are shown, see right column), compared with an unbiased criterion placement (dashed vertical line). Also, the changing ORF for the different conditions is presented (its peak coincides with the optimal criterion position according with the highest expected reward). (Stüttgen et al., 2013)

Figure 12 shows exemplarily the outcome of bird nr.920. The x-axis contains the session number, the y-axis the proportion of S2-responses. During symmetric reinforcement (on average, every other correct response is rewarded regardless of a given S1- or S2-stimulus) the graph oscillates around a horizontal line at a probability rate of 0.5 for S2-responses. This is expectable as both stimuli, S1 and S2, are reinforced equally. The foregoing predictions about the optimal c in a signal detection task, however, would expect that the deviations from the horizontal line would be most extreme in conditions E3 and E4 right after changing the condition of reinforcement as the optimal c is significantly shifted away from the neutral c, and least extreme for conditions E1 and E6. Therefore, the optimization model postulates that the number of S2 responses would follow the pattern E3 > E2 > E1 > E6 > E5 > E4 (Stuttgen et al., 2013). Though, the results say otherwise: the pigeons number 720 and 920 show a strong deviation from optimality for omitted reinforcement in condition E1 and E6, and a rather small abrupt deviation for E3 and E4 (Fig. 12). Hence, correcting for these observations would lead to the consideration the frequency of S2-responses correlates with E1 > E2 > E3 > E4 > E5 > E6.

To sum up, Stüttgen et al. assumed that SDT was a valid description of choice processes and, through their experiments, they tried to get behind the algorithm underlying criterion setting, which SDT is silent about. Hence, SDT aimed to describe the decision process and allowed one to calculate optimal performance for a given reinforcement contingency and a given d’, and further, it allowed one to compare obtained performance to that theoretical optimal. Nonetheless, since SDT had been debated about, many scientists still questioned optimization as well as SDT as only reasonable theory behind signal detection. Stüttgen’s outcome from his 2013 studies gave every reason to also consider non-optimizing theories as best representation for human and non-human decision making. The following paragraphs will therefore serve to shortly outline possible non-optimization theories that could explain the former presented studies as further imaginable models explaining signal detection (besides SDT’s main competing model, namely the TT).



-Figure 12-
The outcome of Stüttgen’s 2013 experiments showed an overestimated behavior to changing reinforce conditions compared with predictions of optimality in SDT. The abscissa depicts the session numbers, the ordinate represents the quantity of S2 responses. The dashed lines separate the different reinforcer conditions (E1 – E6). Exemplary for all tested subjects, bird nr. 920 showed the most pronounced over-shooting behavior (=most intense reaction bias) for condition E1 and E6 (when the most extreme grey value were not reinforced).
The quasi-optimal behavior seen in Stüttgen’s 2011 conducted decision task did not meet the outcome of 2013. In fact, all birds showed most extreme reactions for conditions E1 and E6, however, SDT would expect the strongest peak for condition E3 and E4; for further information see text (Stuttgen et al., 2013)

Firstly, Stüttgen himself introduced the income-based model as possible non-optimizing theory describing the outcome of their pigeon studies of 2013 (Stüttgen et al., 2013). The income-based model assumes Gaussian distribution functions representing a certain stimulus. Hence, in Stüttgen’s experiments, the six different shades of grey were represented as six equal-variance Gaussian distribution curves, comparable with SDT. Also, decision making is, amongst other factors, dependent on a certain decision criterion that varies from trial to trial within a task session. So, the shifting of c is influenced by the probability of stimulus reinforcement. The more likely a certain stimulus is reinforced, the rather c shifts to either side that makes the reinforced alternative more likely (cf. (Stüttgen et al., 2013)). So in other words, all reinforcements for correct responses are allocated individually determining the shifting of the criterion to one or the other side after every trial (Kac, 1969, Dorfman and Biderman, 1971). Henceforth, the income-based model assumes that a subject learns only from reinforced trials (Stoilova et al., 2019, submitted).

In the income-based model, c therefore complies with a leaky integration of the difference of “incomes” (=reinforcers) gained on either side:

$$c(t+1) = \gamma \times c(t) + \delta \times [RfsS1(t) - RfsS2(t)]^{16}$$

c(t+1) stands for the c of the next trial. γ is a leak factor describing a discount rate that represents the average c-value weighted over the last trials (ranging from 0 to 1). So if the subject is unbiased, γ takes on the value 0, however, the further the integration window goes back the past, γ approaches the value 1. On top of this, δ stands for the learning rate that increases for correct S1 choices and decreases for correct S2 choices. RfsS1 and RfsS2 represent the reinforcement for correct responses of S1 or S2 (1 if reinforced, else 0).

Figure 13 offers a comparison of Stüttgen’s 2013 results when demonstrated through optimal criterion setting vs. income-based criterion order. Relating to the pattern of optimal signal detection and non-optimization, the correlation of missing reinforcements for the conditions E1-E6 (x-axis, Fig. 13) and correct S2-response proportion (y-axis, Fig. 13) favors the income-based model over the theory of optimality. To clarify this, both theories would expect a monotonic decrease of P(S2)[17] on the y-axis with conditions arranged from left to right. One can easily see that this prediction is mostly met in the left column of Figure 13 (income-based model) but not in the right column (optimality-based criterion setting).

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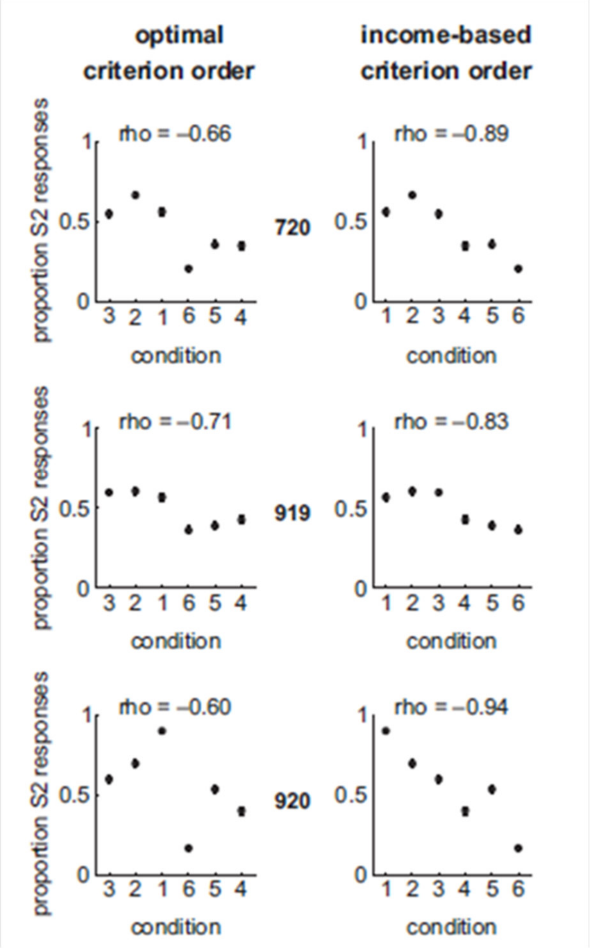
[17] Probability for correct S2 responses



-Figure 13-
In each panel the x-axis shows the testing conditions E1 – E6. The y-axis represents the proportion of S2 responses. Both columns depict the outcome for birds no. 720, 919, and 920, whereby two theories are compared, optimal criterion setting in SDT and a non-optimal income based criterion model. SDT expects that S2 responses would be most extreme for not reinforcing E3 (central grey value of the darker shaded grey signals) and less extreme for condition E4. Therefore, in the left column one would expect a diagonal line from the left side of the panel to the right. Obviously, this is not the case. The income based model (see text) assumes the most S2 responses for condition E1 and the least S2 reactions for E6 forming a diagonal from left to right. Thus, the data pretty well fits to the predictions of the income based learning model. (Stuttgen et al., 2013)

Interesting about these findings is that Stüttgen's team observed different behavioral patterns in experimental analysis two years earlier. While the more recent results of 2013 favored a non-optimizing theory (cf. the income-based model), in 2011 Stüttgen et al. conducted a similar experiment with the same pigeons that rather tended to optimal detection abilities (see above). Yet, in both experiments the animal adjusted its behavior; whilst in the 2011 paper reward probabilities were changed for the entire category of stimuli, in 2013 reward probability was manipulated for one stimulus at a time.

Altogether, the same birds were tested in a similar decision task in 2011 and 2013, but showed slightly different behavior (optimal criterion location in the 2011 study and a non-optimal location in the 2013 study). Interestingly, a reanalysis of the data from 2011 confirmed that the income-based model was able to fit both data sets reasonably well (Stüttgen et al., 2013). Finally, the authors compared the pigeons' behavior also to unbiased reaction: Interesting is that the animals performed nearly optimal, although unbiased behavior would have led to almost the same amount of reinforcement.

As a side-effect, in both studies the birds showed an early overshooting reaction towards the side of higher reward frequency and a following re-approaching towards a steady-state (an observed behavior which will be further discussed later on).

2.5. The prefrontal cortex

As mentioned above, the goal of this study is to get a deeper inside of how well non-human animals perform in adaptive behavior and goal-directed patterns. It is well known that sensory cortices are responsible to filter neural activity of millions of neural inputs to correctly detect, discriminate, localize, and recognize neural stimuli (Stuttgen and Schwarz, 2018). Whilst past studies showed that the prefrontal cortex has a great impact on these executive functions (Chudasama, 2011), this study will mainly examine the medial prefrontal cortex (mPFC) and its role for adaptive behavior (as to maximize reinforcement) in changing environments. The mPFC contains the prelimbic cortex and the anterior cingulate.

The process of decision making in human and non-human animals is constructed of a complex network of neural mechanisms (Kennerley et al., 2006, Rudebeck et al., 2006, de Wit et al., 2009); first within the peripheral and central nervous system that needed to be perfectly co-ordinated, second as inter-hemispheric and inter-cortical functionality, and third on a single-to-single neural level (Carmichael and Price, 1995, Ghashghaei and Barbas, 2002, Chudasama, 2011). Up until today, this continuous stream of millions of neural interconnections has yet not been understood and is part of current intense investigation. Fortunately, from the beginning on, men have always been interested in the human mind and were therefore eager to find out about the cortical functions and their locations. Ultimately, there was sufficient evidence that the prefrontal cortex played a remarkable role for social cognition and a functioning decision process in human behaviors (Ko, 2017, Dolan, 2002, Bicks et al., 2015). Studies with clinical patients showed that the impairment of the ventromedial cortex lead to poor decisions, missing of proper behavioral adaption, and generally meant a loss in maximizing reward (Chudasama, 2011, Bechara et al., 1994). Nonetheless, as mentioned above, many scientist found out that specific decision tasks are not only represented by one cerebral region, but that they need the interaction between many different neural regions (Kennerley et al., 2006). The goal of this paper is therefore to find out more about the importance of the mPFC for its role in adapting to changing reinforcer conditions. Adaption processes, like reversal learning[18], yet asking a subject to adapt to new conditions, seems to be greatly controlled by

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[18] Task procedure in which a subject learns that a correct response (R1) to a certain stimulus (S1) yields reward while another response (R2) to the stimulus (S1) misses reward. Then, the task procedure changes and response R2 leads to reinforcement of S1

the mPFC (Izquierdo and Murray, 2005). The PFC seems to be also involved in updating the internal value for an expected reward, scientifically called reinforcer devaluation, which is the ability to adjust to changes in reward value (Chudasama, 2011). In example, Holland and Rescorla could show that the response to a stimulus of expected food became less attractive for rats when this was paired with illness. (Holland and Rescorla, 1975, Gallagher et al., 1999). On top of this, former groups of scientists examined the specific trait of delay discounting. Overall they found out that human as well as non-human animals prefer sooner smaller rewards before later larger rewards; and they examined, if oppositely to this general observation, which cerebral region was responsible for this adaption process in decision making. Delay discounting must not only been seen as abstract decision trait, but became apparent having a huge impact for drug addiction and other psychiatric disorders like ADHS (Chudasama, 2011, Clark et al., 2004). Additionally, Maroun could show that the plasticity of the mPFC is important for mediating fear regulation and extinction (Maroun, 2013). Ultimately, they showed that the PFC seems to play an enormous role for various fields of decision making. (Bechara and Van Der Linden, 2005, Evenden and Ryan, 1999). Though, likewise with all detailed steps necessary to take a final decision, also delay discounting seems to be represented by many different subregions of the PFC, and scientist can still not exactly identify how many and which exact regions are involved (Berlin et al., 2004). The general consent between different scientists therefore is that decision making is highly dependent on the PFC, though, they are also sure that specific traits within the process of choice taking are represented by different subregions to a higher or lower percentage (Rushworth et al., 2004, Roberts et al., 1998). Obviously, many scientists still continued to find out more about the distinct functions of the PFC's subregions. Some evidence exists that the ventral part of the mPFC is rather responsible for functions that are related with attention, and the dorso-medial PFC is responsible for memorizing motor responses and the processing of received information. The orbitofrontal cortex seems to be greatly involved in reversal learning and delay discounting (Dalley et al., 2004).
Despite this fact, only a few studies examined non-human animals concerning the impact of the prefrontal cortex within the complex process of decision making and its direct role in optimal signal detection (Ko, 2017, Yizhar et al., 2011, Yizhar, 2012). Additionally, only a few research projects really examined the animals' behavior before and after knocking out exactly one cortical region, although animal models and specifically pharmaceutical manipulation of specific cortices have proven to be a proper tool to get a deeper inside in certain behavior

patterns (Chudasama and Robbins, 2006). So the focus of this study was to go down to the neural level by blocking the neural function of the mPFC through the inhibition of its neurons by muscimol infusion. Together with the technique of neurometric recordings (spike trains of single sensory neurons; cf. (Stoilova et al., 2019, Stoilova et al., 2019, submitted), the goal was to receive a better understanding about the function and neural location of signal detection and adaptability, "…realiz[ing] Fechner's early dream of 'inner psychophysics'–relating neuro physiological activity to sensation"; cf. (Stüttgen et al., 2011a, Mountcastle et al., 1990).

3. MATERIAL AND METHODS

3.1. Subjects

At the beginning of the research project, four male Long-Evans rats of the same offspring born eight weeks ahead of training with a weight between 200 and 250g (breeding company Janvier Labs) were trained to successfully participate in a psychophysical decision tasks. The experimental task procedures were controlled by local authorities, "The National Investigation of the state of Rhineland-Palatinate", Germany. The training was conducted on week days, Monday to Friday, during the dark phase of a 12 h light/dark cycle (lights off at 8:00 am – 8:00 pm). Water was restricted throughout and only given during testing and ad libitum on weekends when they were held in a rats' cabinet (Bioscape GmbH) with a constant temperature of 23°C and with a humidity at <50%.

3.2. Training

Besides the training steps, three primary days of handling were included to acquaint the animals to the experimenter. A standard rat behavioral chamber ("Skinner box"; ENV-008, Med Associates Georgia, VT, USA) and further technical devices (amplifier by Cambridge Electronic Design Ldt, UK) were used during the whole training procedure. The training was recorded and evaluated by the computer program Spike 2, Version 7 (Cambridge Electronic Design Ldt., Cambridge, UK). The experimenter weighted the rats before and after each session. In the first step of the training procedure, the animals learned to poke any of the three ports. Poking the center or side ports (=left and right response ports) was associated with reinforcement by collecting water. In each case, 30µl of water was provided at the t the center, right, or left port by activating the water pump for 0.5s respectively. At the same time, poking the left or the right port (=response ports) produced a corresponding sound (left port: low frequent sound of 4,096 kHz; right port: high frequent sound of 16,384 kHz; sound duration of 0.07s). However, random activation of the left and right water pump prevented the animals from exploiting only one of the two ports. Additionally, the experimenter could manually provide or restrict water at a certain port to accelerate the learning process. At the sixth day of training, the second practice step was introduced. Specifically, trial initiation at the center port elicited a low or a high frequent stimulus, while water was delivered only after the animal poked in the associated reward port (= right or left response port). Furthermore, a response was required within 4s after trial initiation; however, poking into the wrong reward port did not terminate the ongoing trial. On the following day, the rodents continued with training step 3, which was identical to step 2, but a delay of 0.1 s from center nose poke to stimulus presentation was added. From the eighth training day onwards, step 4 of the program requested a full single-interval forced choice task, so the rat was only rewarded after a correct response; incorrect responses yielded a time-out punishment, meaning that the subject could not initiate another trial for the next 4s. Furthermore, the introduction of a penalizing sound[19] served as a sensitization for the delay to stimulus presentation.

The results of the first training days showed that two of the rats struggled choosing the correct side after sound delivery, and at least two of them had a strong bias either to the left or the right port. As a consequence, from the twelfth training day onwards, each time the rat chose the wrong port four seconds of time-out (the rat could not activate another trial) hindered the animal from obtaining positive reinforcement. Although all rats slowly increased in performance, on the twenty-second training day correction trials were implemented to accelerate task learning. In fact, for every wrong choice the animal had to correct its responding before the next trial could be activated. As a result, the rodents did not receive as many rewards and were therefore increasingly motivated to choose the right port.

Three of the four rodents behaved as expected and improved their performance. Interestingly, rat number 2 deteriorated in its performance during the repeating trials, so correction trials were stopped after six sessions. In between, rat 1 and 3 moved on to the fifth training step implementing a delay to sound stimulus presentation in steps of 0.1s > 0.25s > 0.4s. Due to a quick performance increase of the three other rats (their d’ was close to 2.0 at that time; c.f. section 2.3.4.) correction trials were discontinued after ten days. At the same time, the performance level of rat 1 and 3 justified to continue with the sixth training step establishing a broader bandwidth to the sound. Three and four days later, subject 2 and 4 also continued with the sixth training step. In discrimination and adaption tasks, the broadening of the sound bandwidth was to implement a noisy background in an experimental procedure. So in the following three weeks the rats learned to correctly discriminate the high and low frequent sound

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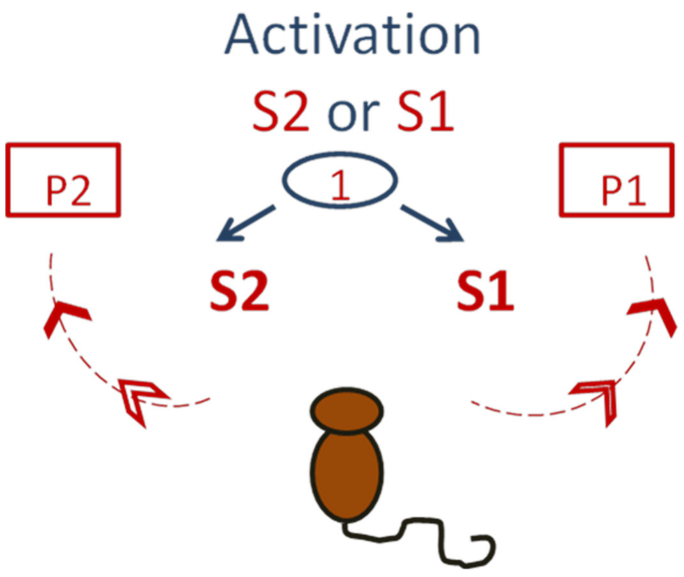
[19] Incidentally the panelizing sound showed not to be an intelligible learning module

within a noisy background. Finally, during the 12th week of training the rats were acquainted to less reward for correct trials (step 7), as with reduced reward rates the animals received less water per unit time and therefore also performed more trials per session The probability rate for rewards was decreased from 1.0 to 0.5. Finally, after about 14 weeks of training the rats were ready to begin with their behavioral experiments. The following chart outlines all training steps.

-Table 4-

Training steps	
Step 1	Get animals to poke and collect water (pump active for 0.5 s; 30ul); in each trial, either a center or a correct side poke will yield reward; side pokes are accompanied by corresponding sounds (low frequent sound: 4096kHz; high frequent sound: 16384kHz; duration: 0.07s; 80dB; band widths: 0.4); left and right water pumps are activated in random sequence to prevent animals from exploiting only one of the two; experimenter may manually provide water now and then; session length 30 minutes
Step 2	Trial initiation in center port elicits a stimulus presentation; water is delivered only after animal pokes in the appropriate reward port; required response within 4s after trial initiation; poking elsewhere does not terminate the trial
Step 3	Introduction of a delay of 0.1s from center nose poke to stimulus presentation; response required within 4s after trial initiation; poking elsewhere does not terminate the trial
Step 4	Full single-interval forced choice task; reward only after correct response (correction forbidden); introduction of a penalizing sound if the rat does not respect the delay (0.1s) while poking center port; after 7 days of training according to script 4, introduction of a time-out punishment (4s)
Step 5	e.g. 0.1s → 0.25s → 0.4s; move on when animal aborts less than 20% of trials
Step 6	Change stimulus composition by broadening its bandwidth; move on when rat performs correctly in >85% of trials across both categories
Step 7	Reduce reward probability to 0.5



-Figure 14-

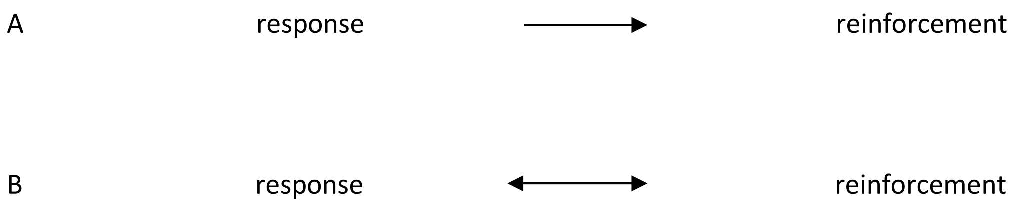
Sketch of behavioral paradigm. The trial begins when the rat initiates stimulus presentation (S1 or S2) by poking into the center port (1). Depending on the sound presented and the rat's perception, the latter responds by going to port 1 or 2 (P1 or P2). If the rat reacts correctly, it will be reinforced with water applied at the correct port. False responses, however, lead to withdrawal of water.

3.2. Behavioral testing

3.2.1. Controlled reinforcer ratio

The first experiment dealt with a controlled reinforcer ratio (CRR), meaning that the activation of one of the two alternatives had to go along with hitting the correct response port (Stubbs and Pliskoff, 1969): activating stimulus S1 requested response R1, activating stimulus S2 requested response R2. Henceforth, only the correct sequence of stimulus and response allowed the subject to finish up the current trial and to begin a new trial. In other words, every time the rat triggered the high- or low-pitched sound the reward was assigned to its particular port (left for the high-pitched sound, right for the low-pitched sound). In this case, the programmed reward contingency matched what the rat obtained (programmed = obtained; c.f. Fig. 15). So the programmed response reinforcer ratio schedule could not deviate from the experienced reinforcer ratio schedule. Additionally, a variable ratio contingency was included to examine the effect of overall reinforcement density. For this, two different variable ratios (VR) were implemented, VR2 and VR6. In VR2, on average reward was provided after every second correct choice. In VR6 the average reward probability was one out of 6 correct responses. Hence, the reinforcement density was three times higher for VR2 than VR6 (c.f. subsection 4.1.1. Fig. 17).

-Figure 15-



- A- Controlled reinforcer ratio (CRR), association of response and reinforcement
- B- Uncontrolled reinforcer ratio (URR), interdependence of response and reinforcement (c.f. 3.2.2)

3.2.2. Uncontrolled reinforcer ratio

The second experiment served to analyze the rats' behavior in an uncontrolled reinforcer ratio (URR) schedule. With URR, the specified reinforcer ratio could deviate from the actual (=experienced) reinforcer ratio. This is what CRR could control (see above).

In contrast to the first experiment (subsection 3.2.1.), the subject was not forced to collect the reward from the assigned response port before a new trial could be activated. Instead the rat could initiate a new trial and with that a new reward allocation to one of the ports. Furthermore, the URR schedule allowed the subject to exploit one of the response ports, e.g. during asymmetric reinforcement (meaning that a correct detection of one of the two stimuli went along with a higher reward magnitude). Hence, in an URR scenario, and for instance due to unequal reward magnitudes for correct responses to different choice alternatives, the animal could favor one response port leading to an extreme bias to either side, c.f. (Stubbs and Pliskoff, 1969).

In other words, the rat behaved in a closed loop as behavioral allocation directly determined reward allocation. As one of the two response port lead to relatively more rewards for a given choice, the subject was motivated to decide for the associated choice alternative more often. Over time, this behavior was a self-supporting system as the more given responses to one of the reward ports subjectively meant a higher reinforcement, and again the rewarding influenced the rat to detect the associated stimuli to this specific reward port (Fig. 19).

3.2.3. Statistical analysis

All analyses were either performed with Excel (Microsoft Office 2010), or Matlab, R2018b (The Mathworks, Natick, MA, USA). Firstly, results were demonstrated via graphs depicting the probability of correct responses to a certain stimulus over more than 20 task sessions, secondly, via t-tests outlining sensitivity and criterion setting, and thirdly via objective reward functions. Optimal response criteria and objective reward functions were calculated and plotted by the supervisor of the project, Maik Stüttgen. The symmetric and asymmetric experiments under muscimol were evaluated through Wilcoxon rank-sum tests. Furthermore, linear regression was used for the purpose of comparison in the discussion part.

3.3. Surgery

Before the surgery, the experimenter cared for a clean cage with stretched out paper towels on the bottom of the cage and a heating pat underneath (plus optionally a heating lamp) to ensure a good post-operative environment for the animal. Additionally, the surgery protocol was filled out with necessary information about the rat's physical status (sex, weight, age), and the type and dosage of medication[20]: 1. Analgesia: Rimadyl (4mg kg^{-1}); 2. The triple-combination anesthesia: Fentanyl (0.005mg kg^{-1}, Medetomidin (0.15mg.kg^{-1}), Midazolam (2,0 mg kg^{-1} plus a supplementary dose as pain reflex is positive); 3. The antibiotics: Baytril (2.5ml 2.5% given pre-operative with the drinking water).

Finally, Bregma[21](B) was determined. It helped to locate the coordinates of the later implanted cannulas (C315G, PlasticsOne, Roanoke, VA, USA, diameter 0.5 mm) in the prefrontal cortex (the following coordinates were chosen: +3.0 mm from Bregma (anteroposterior); mediolateral (ML), ±0.6 mm from the midline, dorsoventral (DV) -3.1 mm below the dural surface. Cannulas were implanted at an outwards angle of 10°.one tube on each cortical side, s. Figure 16A/B, PFC) and the auditory cortex (one double-holed tube on each cortical side, s. Fig. 16B AC; for further scientific results about the functions of the auditory cortex see Stoilova et al., 2019, submitted).

When all preconditions were met the surgeon was ready to start out with the main surgical process: the rat was fastened in a stereotaxic frame (Parallel Rail Stereotaxic Instrument; Stoelting, Dublin, Ireland) and fixed using atraumatic ear bars. Then, the rat was anesthetized through the application of isoflurane 5% solved in pure O_2. Later its head was shaved spaciously, and finally the animal was anesthetized by a triple-combination anesthesia (see above). During the whole surgery the rat was kept warm by a small heating pat, and its temperature was continuously controlled. Its eyes were covered with ocular lubricant. Eventually,

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[20] Medication: 1. Rimadyl is a NSAID (pharmaceutical ingredient of Caprofen) with an antiphlogistic, analgetic and antipyretic effect; 2. Fentanyl, Medetomidin, Midazolam are pain killers belonging to the group of Opiats (Fentanyl), α2-Agonists, and Bencodiacepines; 3. Baytril is an antibiotic medication containing Enrofloxacin (Flourchinolon)

[21] Bregma: is the anatomical point on the skull at which the coronal suture is intersected perpendicularly by the sagittal suture WIKIPEDIA 2016. Bregma.

a negative pain reflex allowed the surgeon to open up the rat’s scalp, apply sore cream (Betaisodona) and clean it with saline afterwards. Then, the calculated coordinates for the cannulas were marked and five or six additional points were selected for stabilization, all being helpful landmarks for the drilling of the holes into the bone. For the purpose of stabilization, little screws were drilled into the skull and glued onto the bone with dental cement. Later the cannulas were inserted into the prefrontal cortex and auditory cortex[22], and also glued onto the bone with dental cement. Before the scalp was sewed together, Betaisodona was spread out and the antagonizing medication Atipamezol (0.75 mg kg^{-1}), Flumazenil (0.20 mg kg^{-1}) and Naloxon (0.12 mg kg^{-1}) was applied, before the rat was carefully transported to the prepared cage.

After surgery, the rat’s body temperature was carefully controlled, and water and food was provided ad libitum. Rimadyl was provided for two more days, glucose (5%, 5ml i.p.) was given if needed. For recovery purpose, the training was paused for 7 days.
One of the rats died after surgery so that the pharmaceutical experiments were conducted with three of the originally four testing subjects (death of rat (AD2): 08/18/16).

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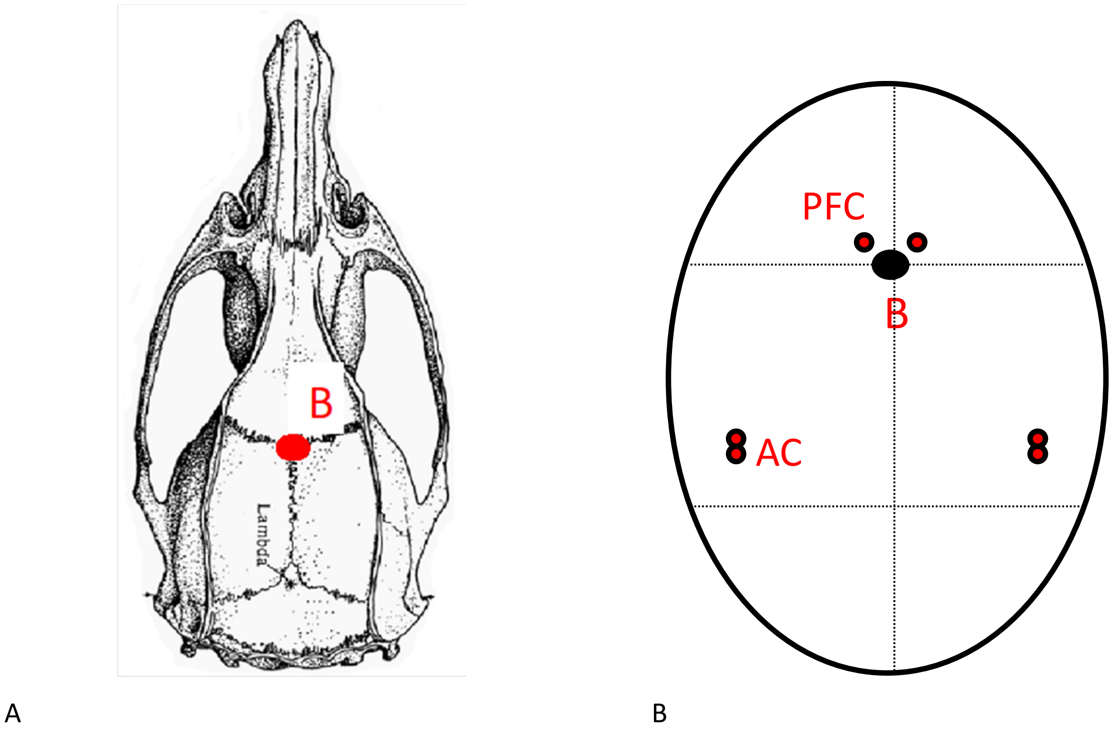
[22] Cannulas were implanted for additional tests which were however not part of the current work, and results are therefore not described; for further scientific results about the functions of the auditory cortex see Stoilova et al., 2019, submitted.



-Figure 16- Location of cannulas

- A (Paxinos and Watson, 1998) skull diagram of a rodent
- B rough implantation plan

For implantation of the cannulas Bregma (B)[21] was determined first, then one tube was implanted in the left and right prefrontal cortex (PFC), respectively. A double-holed cannula was implanted in each auditory cortex (AC), left and right.

3.4. Application of pharmaceuticals

The third experiment will provide new information about the role of the PFC concerning signal detectability. In order to analyze the rats' performance during the blockage of different brain areas[23], the latter are either manipulated with saline or muscimol (Sigma-Aldrich, St. Louis, MO, USA). While saline does not affect the neural processes, muscimol, naturally obtained from the fly agaric mushroom, is a GABA-A-receptor agonist that activates the inhibitory brain systems ((Krupa et al., 1999). Since one found out about the inhibitory effect on the functions of cortical brain areas, Muscimol has often been used to study behavioral patterns as it is able

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[23] Both, the auditory and the prefrontal cortices were bilaterally and unilaterally manipulated

to specifically block neural activity in cortical areas of interest. In the current study it was used to unilaterally and bilaterally block the PFC. The necessary apparatus (Pump 11 Elite, Harvard Apparatus, Holliston, MA, USA).) is a syringe pump that offers the clamping of two 22 or 23 gauge glass-syringes (10µl of volume each), which are connected to very small plastic tubes. These plastic tubes in turn are hooked onto small adapters that are later inserted into the rat's implanted cannulas.

To start out, 70%-ethanol is drawn into a 5ml-syringe. Firstly, the tubes with the hooked adapters are connected to the syringe and flushed until they are completely bubble-free. Then, the glass-syringes are filled with ethanol before they are bound to the tubes. Now the 10µl of ethanol are discarded and 0.5µl of air are drawn in. In the following step the syringe is filled up either with saline or muscimol, so that the small air bubble separates the liquid vehicle and the pharmaceutical (either saline or muscimol). To ensure that the correct amount of either 0.25, 0.5 or 1µl saline/muscimol is applied, the first 1µl is discarded. Finally, the syringes are put into the syringe pump and the adapters are inserted into the rat's cannulas. Then, 0.25 (0.5, 1) µl of saline or muscimol is applied. To ensure that 1µl is correctly injected into the specific cortical area, the experimenter waits about 1 minute (min) before the tubes are removed. After 45 min of resting, the rat starts out with the testing procedure.

3.5. Testing under muscimol

The third and last experiments dealt with the neural mechanisms of reinforced behavior. To investigate the neural function of the mPFC concerning signal detection, the subject`s behavior was observed under muscimol application that inhibited neural activity in covered brain areas. In order to do so, the rats' outcome under muscimol application (brain function was blocked) was compared with that under saline-control (brain function was kept active). The main goal was to analyze the role of the mPFC concerning adaptive behavior for long-term memory through changing stimulus-reward contingencies.

On the whole, the rats were tested under asymmetrical reinforcer schedules first, and later under symmetrical reinforcement contingencies. On top of this, the subjects were analyzed separately under unilateral and bilateral saline and muscimol application.

4. RESULTS

As outlined in the introduction, the main goal of this work was, in a first step, to get a deeper understanding how well non-human animals adapt to changing reinforcer conditions and which theoretical model best reflects the given data. In a second step, the mPFC was examined to get more inside concerning its role for decision making. Therefore, section 4.1. will first characterize the subjects' task performance in two behavioral experiments under changing reinforce conditions. In section 4.2. similar behavioral experiments will be combined with pharmacological tests in order to check the mPFC for its role in adaptive behavior. The following table shortly outlines the task schedules and procedures of the behavioral and pharmaceutical experiments (see also the description of the task structure in section 3.2.).

-Table 5-.
Short outline about the conducted experiments, the procedures, and tasks schedules

<u>1. Controlled reinforcer ratio schedule (CRR)</u>

Procedure:

- the subjects are reinforced for every second/ every sixth correct response like in a variable ratio schedule
- correct S1/S2 responses are alternating reinforced with a probability of 0.25I0.75

Task schedule:

Fig. 17: depiction of S2 responses depending on the reward probability (example given by of one of the four subjects)

Fig. 18: One-sample-t-Test for all four subjects to check their deviation of correct S2 responses and criterion setting from this of an ideal observer

<u>2. Uncontrolled reinforcer ratio schedule (URR)</u>

Procedure: Correct S1/S2 responses are alternating reinforced with a probability of 0.1I0.5 or 0.5I0.9

Task schedule :

- Fig. 19: depiction of S2 responses depending on the reward probability (example given by of one of the four subjects)
- Fig. 20: One-sample-t-Test for all four subjects to check their deviation of correct S2 responses and criterion setting from this of an ideal observer

- Fig. 21: comparison of the empirical (the subjects') criterion shift with that of an ideal observer (according to the ORF)

3. Function of the mPFC

Procedure: Blocking of the mPFC via muscimol

Task schedule:

- Fig. 24/25/26: Bilateral blocking of the mPFC with asymmetric reward schedules (task performance was compared under different muscimol amounts: 0,25/0,5/1µgµl^{-1})
- Fig. 27: Unilateral blocking of the mPFC during a balanced reward schedule

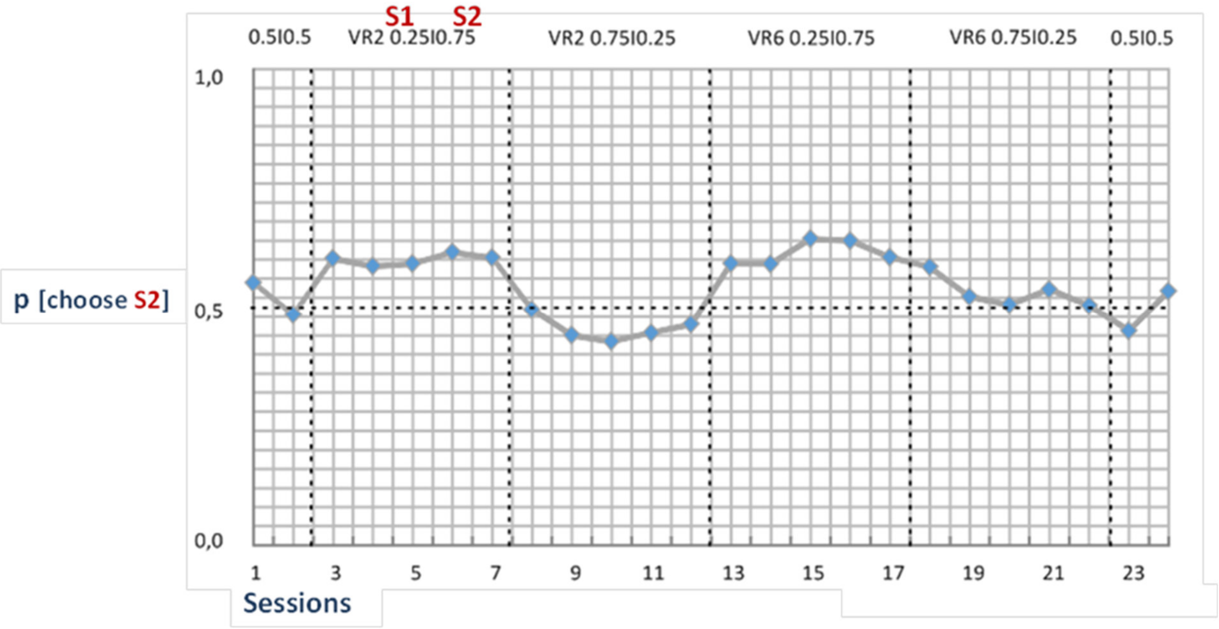
4.1. Behavioral experiments -How well did rats adapt to changing reinforcement contingencies?

Both behavioral experiments investigated whether vertebrates were able to optimally integrate incoming sensory evidence as part of stimulus-reward contingencies, and finally produced goal-directed, adaptive behavior in binary choice tasks. Without anticipating too much beforehand, the following experimental results will show that non-human animals quite optimally integrate incoming sensory evidence as part of stimulus-reward contingencies.

4.1.1. Controlled reinforcer ratio

The following subsection will therefore firstly demonstrate exemplarily through the data of just one rat why optimal behavior in rodents was plausible. Afterwards a second illustration and the comparison with the ORF (see 2.3.) will give evidence that all four subjects tended towards optimal behavior.

The first behavioral experiment therefore dealt with asymmetric reinforcer ratios (except for every first and last couple of sessions that included symmetric reinforcer contingencies to prevent any biasing (Fig. 17).) In a variable ratio scenario the subject had to learn that stimuli S1 and S2 were alternating reinforced with a probability ratio 0.25 and 0.75 (for a detailed task description see 3.2.).



-Figure 17-
In Figure 17 the abscissa contains the session numbers, the ordinate reflects the probability of left (=S2) choices depending on the reward probability provided. The specific reward probability is given on top of the diagram (e.g. 0.5I0.5 for a balanced ratio). The first and last sessions contained a balanced reward schedule (S1 and S2 were equally reinforced) to prevent biased behavior at the beginning and at the end of each testing module. Besides the changing reinforcer ratio, a variable ratio contingency was included (VR2: on average, every second correct choice was rewarded; VR6: on average, every sixth correct choice was rewarded).
Except for the first and last two sessions, asymmetric reinforcement influenced the rat to adapt its behavior. While in sessions 3 to 7 and 13 to 17 the left (=S2) stimulus was rewarded more often, in sessions 8 to 12 and 18 to 22 the right (=S1) stimulus provided more rewards. Exemplarily for all test subjects, the results of the depicted vertebrate obviously adapted its behavior to either side depending on the reward probabilities.

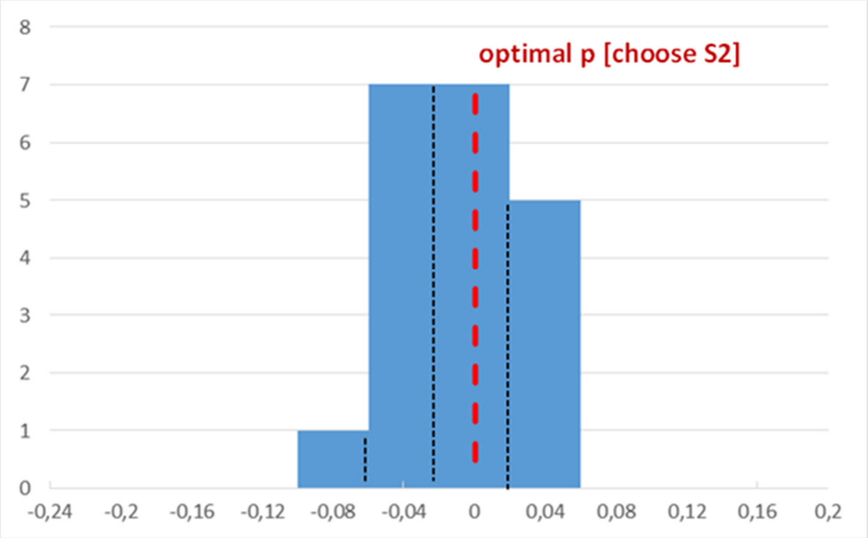
Exemplarily for all four subjects, Figure 17 shows the reaction pattern of one rodent to changing reinforcer conditions. In sessions 3 to 7 and 13 to 17 the S2 stimulus (=left response port, high-pitched sound) was rewarded more often than the S1 stimulus (instructed a response to the right response port), and corresponding with the reinforcer ratio, the subject moved to the left reward port more frequently. A similar behavior was shown when S1 lead to a higher reward probability (Fig. 17, sessions 8 to 12 and 18 to 22); then the animal reacted with a higher frequency of right responses (Fig. 17). Henceforth, the subject varied its behavior depending on the reinforcer ratio.

Remarkably, the subject favored the port with a higher reinforcer ratio during the whole testing procedure; even though the program incorporated a variable ratio schedule. So the rat was not rewarded every time it correctly detected the signal, but depending on the specific variable ratio exemplarily, on average after every second (V2) or sixth correct choice (V6). For that, in the first two testing blocks the subject was rewarded in one out of two correct responses (VR2). In the last two blocks, it only received water in one out of six correct responses (VR6). Ultimately, the variable ratio schedule did not hinder the subject from proper adaption to asymmetric reinforcement as expected from SDT; even though the rat gained generally more rewards for correct answers in two of the four sessions (in other words, the absolute reward amount was higher for V2 than V6). In comparison with the second behavioral experiment an overshooting behavior (associated with a rapidly shifting curve towards extremer values), particularly at reinforcer ratio changes, could hardly be observed (for more see subsection 4.1.2).

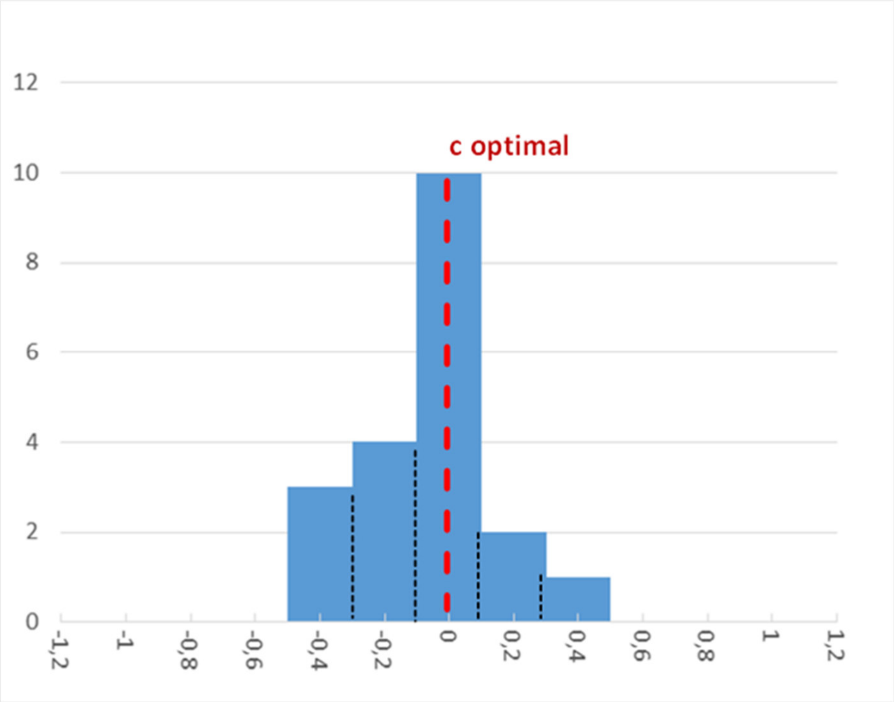
Additionally, one of the goals was to find out whether the animal behaved optimally referring to SDT. In order to do so, the One-sample-t-Test was used to mathematically check whether and how extreme the mean of the empirical observers' outcome deviated from that of an optimal observer (subsection 2.3.): for that, the relative response ratios for S2 (=p [choose S2]) of all test objects (rats AD1 to AD4) of the last two sessions were compared with the perfect observer's optimal p [choose S2] rate for all four changing contingencies. That is shown in Figure 18A, whereby the x-axis reflects the deviating probability of S2 responses across all four subjects from the perfectly allocated responses (dashed red line defined "optimal") of an optimal subject in a discrimination task. The y-axis shows how often and in which direction from the optimal allocation the rats tended to one or the other alternative. Over the whole task and across all rats, the graphical outcome of panel 22A demonstrates that the rats' choice allocation deviated from 0 by -0.1 and maximally by +0.1. The mean deviation from the perfect observer over all sessions and across all rats was -0.010. The results of the Wilcoxon-Sign-Rank-Test with T(19)= 1.5 and p= 0.263 showed that there was no significant difference between a perfect observer`s performance and the vertebrates' outcome of this study.

To evaluate how well the subjects adapted their behavior in order to maximize reward, empirical criterion setting was compared with that of an ideal observer (SDT allows to exactly determine optimal criterion setting in order to maximize reward under changing reinforce conditions). Figure 18B shows that the rats deviated from the ideal observer's outcome by minimally -0.5 and maximally by +0.5. The mean deviation of the animals' criterion setting compared with an optimal subject deviated by 0.0! The Wilcoxon-Sign-Rank-Test confirmed with T(19)= -1.4 and p = 0.167 that there existed no major difference between a perfect subject's adaption process and this of four trained rodents.

In general, in both graphs (Fig. 18A and B) to classify a response to a certain unit, first the deviation of responses compared with this of a perfect subject was evaluated. Then equal units were established to categorize each response. The taller a bar was, the more often a response was classified to the specific unit.



-18A- Comparison of the subjects' (AD1-AD4) p [choose S2] and p [choose S2]-optimal



-18B- Comparison of the subjects' (AD1-AD4) p[c] and p[c]-optimal

-Figure 18-

In 18A the horizontal axis shows the rats' deviation of p [choose S2] from the optimal probability of S2 choices given by an optimal observer (dashed red line). The vertical axis reflects the absolute number of sessions, collapsed across all four rats. In general, the rats showed differences in their choice allocation by minimally -0.1 and maximally by +0.1. Similarly, panel B compares the rats' criterion setting (blue bars) with that of an optimal observer (dashed red line). The rats' outcome only deviated by minimally and maximally +0.5 and -0.5. The Wilcoxon-Sign-Rank-Tests for both data groups confirmed that there was no major difference between a perfect observer's responses and these of trained animals.

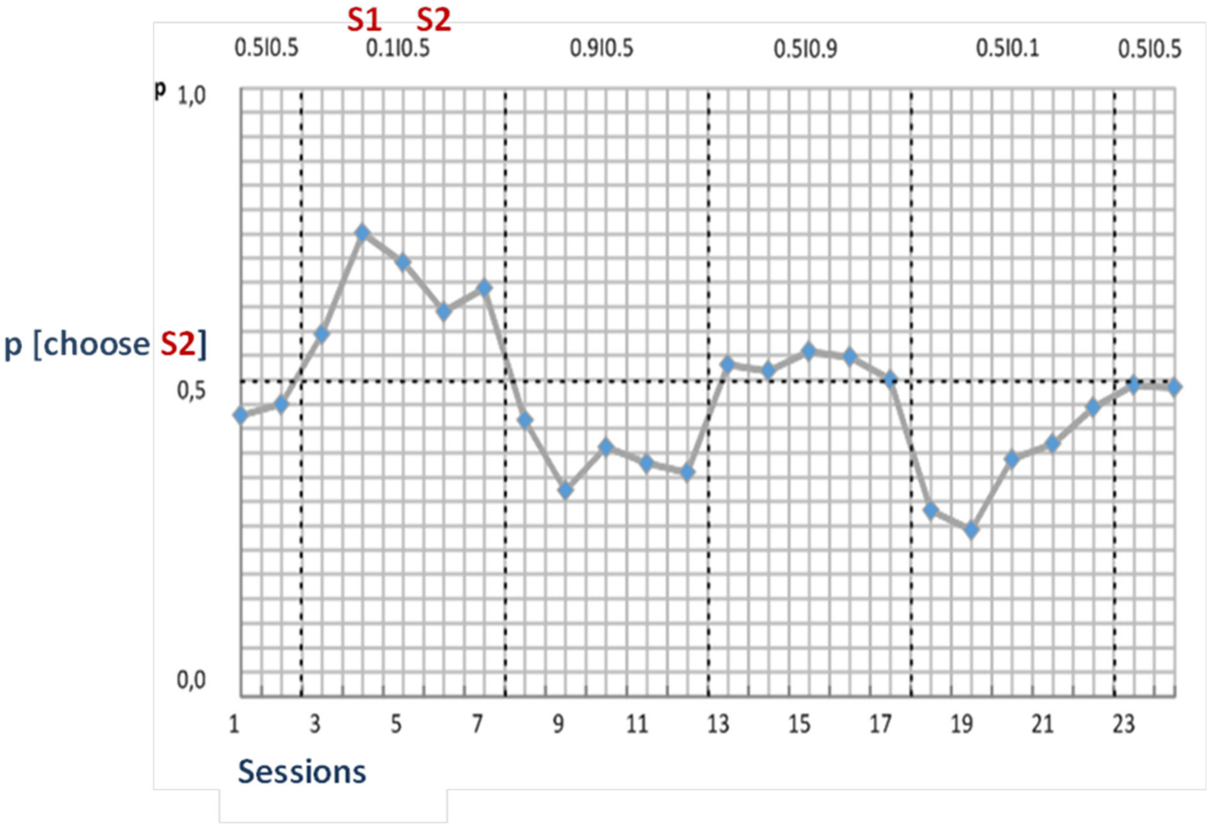
4.1.2. Uncontrolled reinforcer ratio

The general question of the second behavioral experiment was identical to the first testing procedure (subsection 4.1.1.) as its main function was to further investigate whether non-human animals, in terms of SDT, optimally react to incoming sensory stimuli in changing stimulus-reward-contingencies. However, the testing procedure was slightly rearranged, so that this time the reward was not assigned to a special response port and even after an incorrect response a new trial could be initiated (for more information, see 3.2.2.)

The first graph again reflects on the basis of just one experimental subject (AD4), the reaction to changing reinforcement conditions of all four subjects. Later on, the outcome will be further verified by comparing the subjects' outcome to that of an ideal observer and in correspondence to the ORF (subsection 2.3.)

Figure 19 shows the session numbers on the x-axis and the probability of correct left (=S2) choices on the y-axis. Since the experiment dealt with asymmetric reinforcer ratios the specific reward probabilities for S1 (=right, low-pitched)-stimuli and S2 (=left, high-pitched)-stimuli are plotted on top of the diagram. The first and last sessions were conducted with symmetric reinforcement (Fig. 19, 0.5I0.5), however, the main focus was on the four groups of asymmetrically reinforced sessions in order to analyze the rat's (AD4, Fig. 19) behavior under different reinforcer contingencies.

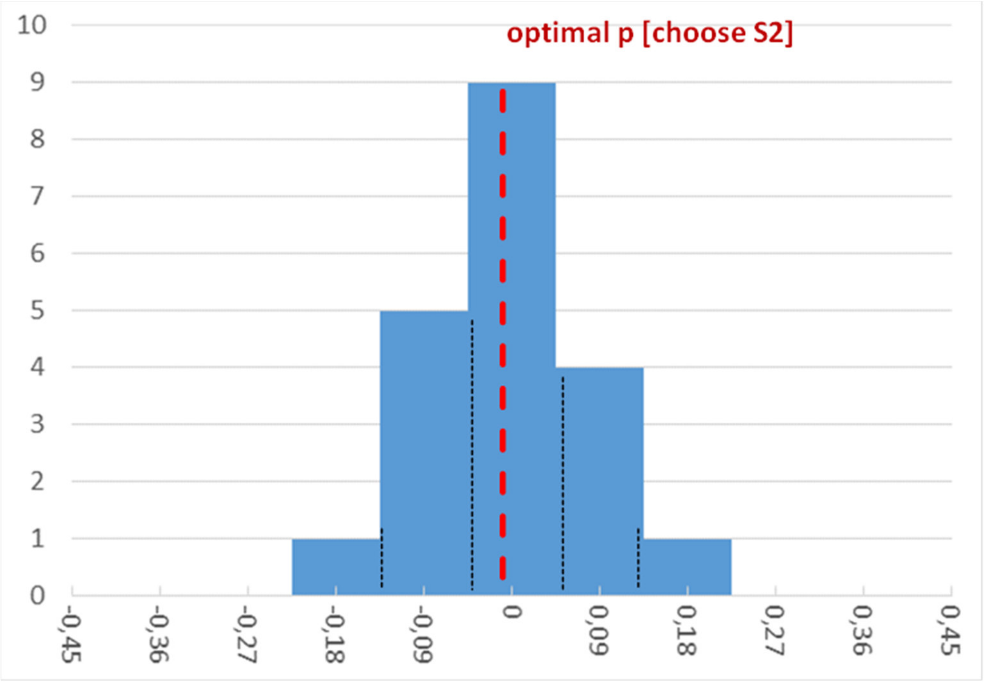
Similar to the first behavioral experiment, during sessions 3 to 7 and 13 to 17 S2-stimuli (=left, high-pitched sounds) were rewarded more often than S1-stimuli (right, low-pitched sounds), and corresponding with the reinforcer ratio, the rat moved to the left side more frequently. A similar behavior was shown when S1-stimuli lead to a higher reward probability (Fig. 19, sessions 8 to 12 and 18 to 22); then the subject answered with a higher frequency of right responses (Fig. 19). Similar to what could be seen in the first experiment, also in the second procedure adaptive behavior could be observed depending on the reinforcer ratio. Besides a favorite choice allocation on the side of higher reward probability, all of the rats reacted with overshooting behavior at the beginning of ratio changes and later tented towards unbiased reactions, similar to what Stüttgen et al. noticed in their studies (cf. subsection 2.4.). Interesting was that the intensity of the overshooting behavior changed according to the relative reward ratio (Fig. 19; 0.1I0.5/0.5I0.1 or 0.5I0.9/0.9I0.5). In both situations, the absolute contrast



-Figure 19-
The horizontal line contains the number of sessions; the vertical line shows the probability of S2 responses. On the whole, rat AD4 started and ended the experiment with two sessions of a balanced reward probability for stimulus 1 (S1, right, low-pitched sound) and stimulus 2 (S2, left, high-pitched sound). The specific reward probability is given on the top of the diagram (e.g. 0.5I0.5 for a balanced ratio). Except for the first and last two sessions asymmetric reinforcement influenced the rat to adapt its behavior. While in sessions 3 to 7 and 13 to 17 S2 was rewarded more often, in sessions 8 to 12 and 18 to 22 S1 provided more rewards. Exemplarily for all task subjects, the rat adapted its behavior to either side depending on the reward probabilities.

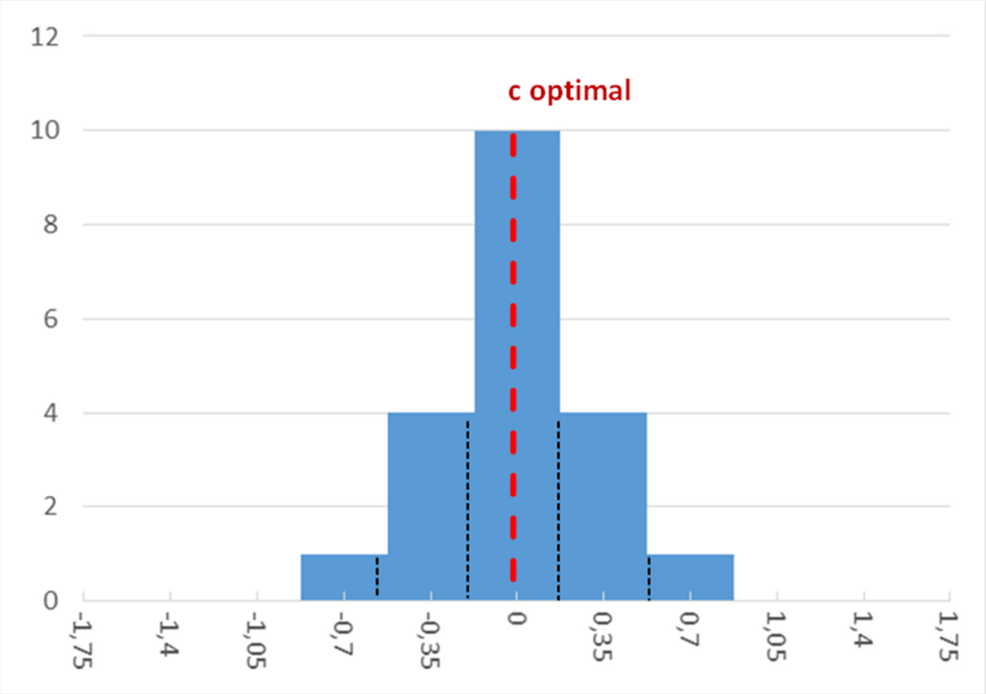
between reward levels was identical, but the relative reward rate and the reward density differed.

Comparable with the illustrations to the CRR experiments, besides adaptive behavior, the main interest was to analyze the rats' ability to react nearly optimally in terms of SDT. Again, the One-sample-t-Test was used to check whether and how extreme the mean of the empirical observers deviated from "optimal". As with CRR, the rats' probability rates for S2 (=p [choose S2], Fig. 20) and their criterion setting (Fig. 21) was comparable to the perfect observer's optimal S2-responses as well as criterion shifting for all four changing contingencies. Over the whole task and across all rats, the outcome of the Wilcoxon-Sign-Rank-Test with T(19)=0.0 and p= 0.601 showed that the rats' choice allocation did not significantly deviated from that of the optimal observer. Additionally, the graphical data demonstrated that their performance differed by minimally -0.18 and maximally by +0.18.



-Figure 20-
The horizontal axis shows the rats' deviation of p [choose S2] from the optimal probability of S2 choices given by a theoretical perfect observer (dashed red line). The vertical axis reflects the absolute number of sessions, collapsed across all four rats. In general, the rats showed differences in their choice allocation by minimally -0.18 and maximally by +0.18.The Wilcoxon-Sign-Rank Test showed that there was no major difference in the outcome of an optimal observer and a trained individual.

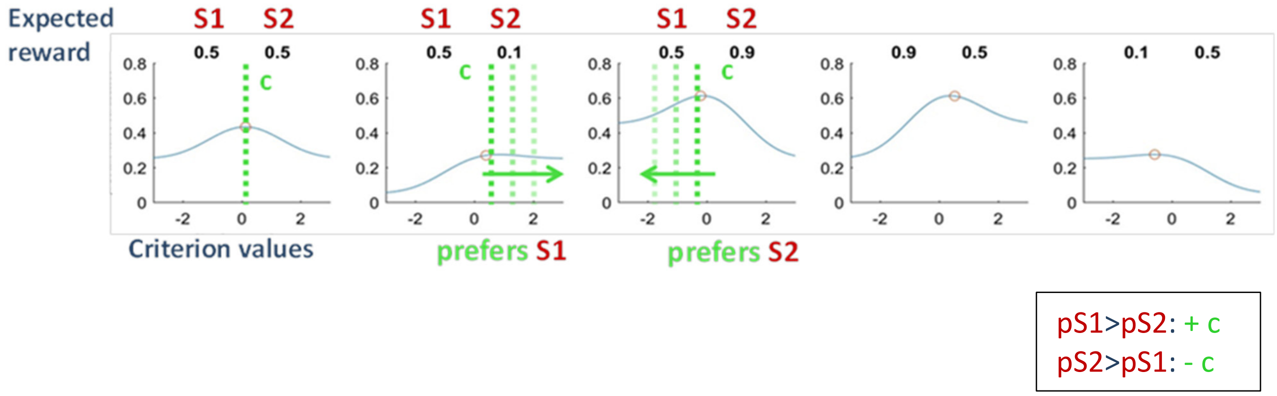
Furthermore, also the criterion setting for URR was observed and compared with an optimal observer, again to check whether the adaption process corresponds towards a maximization of overall reinforcement. Figure 21 shows the deviation of a perfect criterion setting across all reinforcer contingencies, which differed from an optimal observer only by minimally/maximally -/+ 0.7. The outcome of the Wilcoxon-Sign-Rank-Test was T(19)=-0.3 and p= 0.7369.



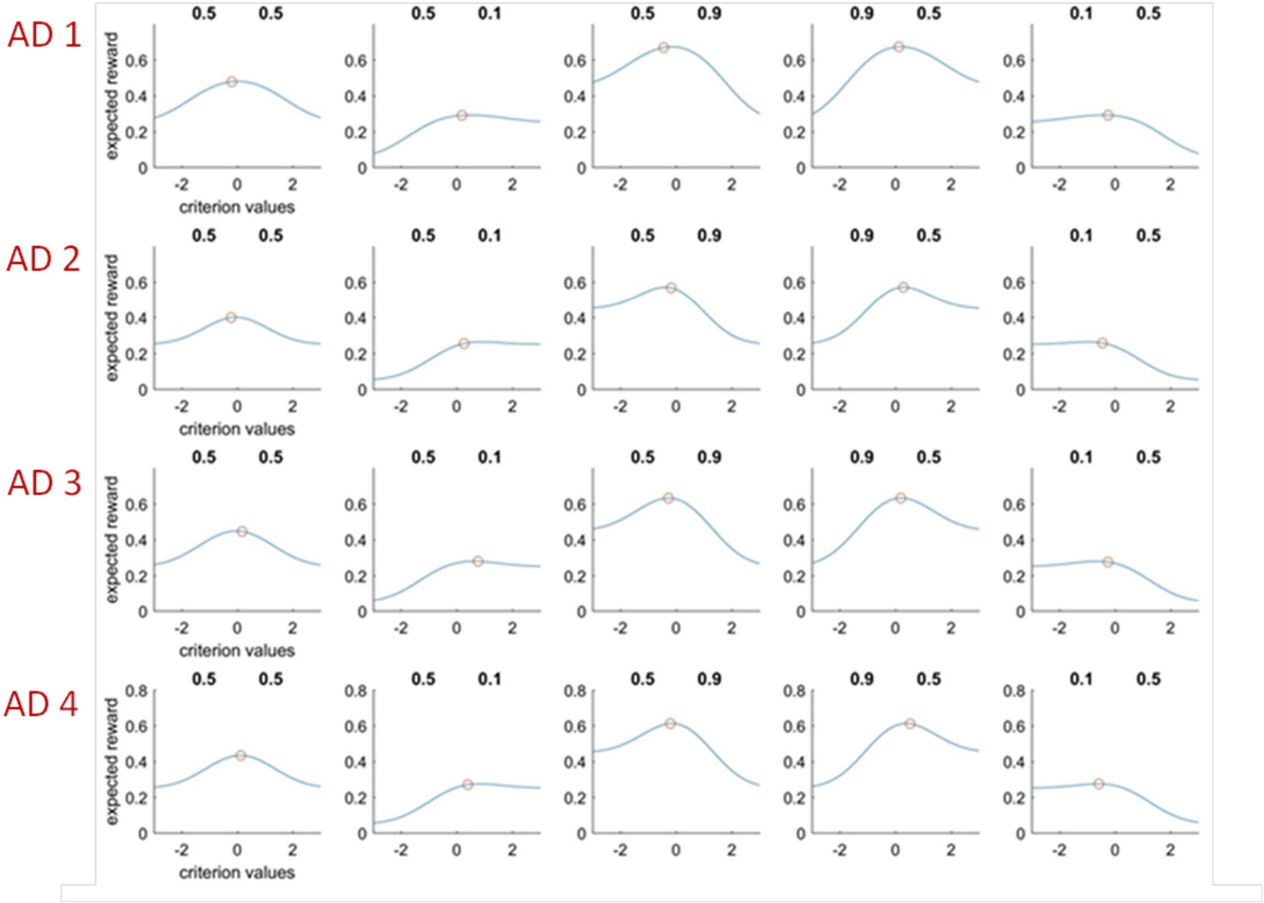
-Figure 21-
The x-axis shows the rats' deviation from the optimal criterion setting of an optimal observer (dashed red line). The y-axis contains the absolute number of sessions, collapsed across all four rats. The subject minimally and maximally deviated their criteria by -/+ 0.7. As before, the data showed that trained subjects of this study behaved equally well as a perfect observer.

According with the first experimental procedure, to find out more about optimal signal detection, the rats' given answers were compared with the ORF (Maddox, 2002) and a perfect subject maximizing the amount of reward during a certain task session (subsection 2.3.). In Figure 22 the x-axis depicts the criterion values for an ideal observer (thin blue curve) and for rat AD4 (thin reddish circle) depending on the reinforcer ratio for S1 and S2 (above the graph). The y-axis contained the expected reward depending on the reinforcer ratio and the criterion setting. The rat therefore obtained most rewards for setting its criterion at the peak of the ORF. In the first panel S1 and S2 were reinforced equally (Fig. 22, panel 1, reinforcer ratio [0.5I0.5]), in this case, criterion setting for an optimal observer coincides with the peak of the ORF at 0. Now, as S1 was reinforced more often than S2 (Fig. 23, panel 2, [0.5I0.1], the criterion value was shifted to the right (in the direction of high-pitched sounds) as the rat gained more rewards for low-pitched stimuli (Fig. 23, dashed green line). The dashed green line represented the shifting of criterion associated with asymmetric reinforcement, while a higher reward ratio leads to a shifting in the opposite direction (Fig. 22, panel 2 and 3).

According with the relative reinforcer ratio, not only the response rate differed, but also optimal criterion setting (compare c for the relative reward rates 0.1I0.5/0.5I0.1 and 0.5I0.9/0.9I0.5, Fig. 22). In panels 3 and 4 the ORF shows a clear peak indicating the maximal reward for optimal criterion setting. In panels 2 and 5, however, the ORF for the greatest gain of rewards is less striking indicating that in terms of SDT adaption towards optimal criterion hardly gains more rewards than unbiased behavior. Nonetheless, even at shallow parts of the ORF the rat optimally shifted its criterion (Fig. 22, panel 2 and 5, compare ORF and blue circle).



-Figure 22-
In all graphs the x-axis contains the criterion value (subsection 2.3.3.), the y-axis is the probability for the expected reward. The blue curve shows depending on the reinforcer ratio the optimal criterion value for the highest amount of rewards. The small reddish circle shows the criterion setting of AD4 for the last two sessions of each contingency (see text for detailed description). In the first graph the objective reward function shows that equal rewarding (0.5I0.5) for S1 and S2 optimally leads to an unbiased behavior that corresponds with the rat's outcome. The second and third graph, however, demonstrate criterion shifting due to asymmetric reinforcement. The small box to the right shows the criterion shift depending on the probability of a given S1/S2 signal as hypothesized by SDT: higher rewarding for S1 stimuli lead to criterion shifting in the opposite direction (to a positive c values), and more rewards for S2 lead to a negative criterion shifting. Ultimately, the subject behaves nearly optimal compared to an ideal observer.



-Figure 23-
Overview of all vertebrates' (AD1 to AD4) outcome about criterion setting in an asymmetric reinforcement task. The x-axis contains the range of criterion values, the y-axis shows the expected reward probability depending on the reinforcer ratio for S1 and S2. For the panel description see Fig. 23.
Generally, all rats nearly optimally arranged their internal criterion (thin reddish circle) as their shifting of criterion almost matched this of an ideal observer's outcome, represented by the maximum value of the ORF (ORF=thin blue curve). The differences to the optimal criterion values range between -0.3 to + 0.3.

We can therefore conclude that in both behavioral decision tasks all four subjects adapted their behavior according to changing reinforcer conditions (cf. Fig. 17, 19) and, talking about SDT, they showed nearly optimal behavior under asymmetric reinforcement (Fig. 18, 20, 21, 22). It is especially remarkable that the subjects adapted their behavior according to SDT even when this brought about barely more rewards (cf. shallow parts of the ORF in Fig. 23).

4.2. Neural mechanisms of choice behavior in a psychophysical decision task based on the prefrontal cortex

The final experiments dealt with the neural mechanisms of reinforced behavior. To investigate the neural effects of the mPFC on signal detection, during the testing procedure the subjects' behavior was compared under muscimol[24] application that inhibited neural activity in covered brain areas, and with that under saline-control (cf. 3.3.-3.5.). By doing so, the role of the mPFC concerning adaptive behavior could be analyzed for varying stimulus reward contingencies.

On the whole, the laboratory animals were tested four weeks in partly symmetrical and partly asymmetrical reinforcement schedules. Additionally, both hemispheres were tested under unilateral and bilateral muscimol doses: in the first three weeks the subjects' behavioral patterns were analyzed under different bilateral muscimol doses, in the last week of testing unilateral blocking was intended to examine whether adaptability can be undertaken by just one hemisphere.

4.2.1. Psychophysical decision task with asymmetric reinforcement

At first, the rats were tested with a dose of 1µgµl^{-1} muscimol during an asymmetrically reward schedule of the following probability ratio: 0.5I0.5 – 0.05I0.95/0.95I0.05 – 0.5I0.5 (Fig. 24).
All three subjects (as mentioned before, one testing object unfortunately died after surgery, cf. 3.3.) showed a similar outcome: they were not able to distinguish SN and N, but were extremely biased to one side (to receive water, they exploited only one water port without adapting to the specific reinforcer ratio). One testing object did hardly react at all. Their d' (see 2.3.4) dropped to 0.5 (Fig. 24) and the subjects' criterion setting, optimally being about 0 for balanced reinforce ratios, or optimally shifting to the opposite side of the reinforced stimulus in asymmetric reinforcer contingencies, was not perfectly shifted in accordance to SDT.
As expected, the same dose of saline did not change the rats' behavior: they reacted as usual and recognized SN and N with a satisfactory sensitivity (d'~1.6).

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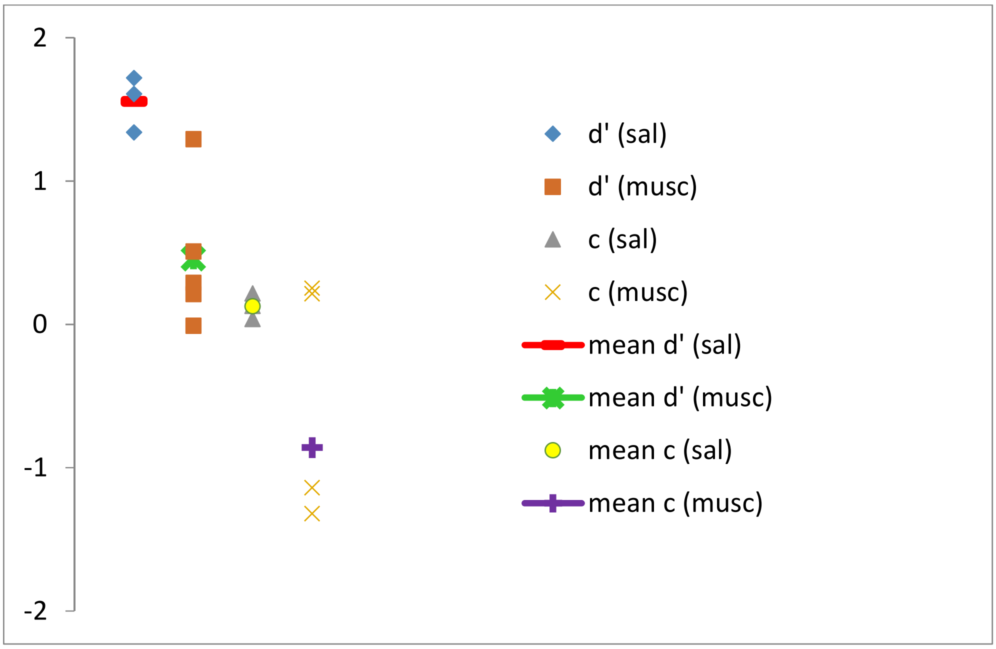
[24] Muscimol is a GABA-A-receptor agonist that activates the inhibitory brain systems. It blocks the neural activity of specific cortical areas.



-Figure 24-

Bilateral blocking of the mPFC with 1µgµl^{-1} muscimol. The diagram shows the absolute values of d’ and c’ under saline control (sal) or muscimol (musc). Also, the mean values for all subjects together are marked. Comparing the average d’ under saline-control and muscimol (1µgµl^{-1}), the rats’ performance clearly dropped as they lost their ability to distinguish SN and N.

The Wilcoxon-Ranksum-Test for d’ with the following data sets

x = [1.7199,1.6091,1.3407]

y = [0.51,1.294,0.29024,-0.0080544,0.21263],

whereby x stands for the subjects’ performance under saline-control, and y stands for the subjects’ performance under muscimol influence. The ranksum [W] was p = 0.0357 meaning that the 0-hypothesis could be rejected with α=0.05, which clearly showed that the performance under 1ugul^{-1}muscimol was much worse than under saline influence.

The Wilcoxon-Ranksum-Test for c with the following data

x= [0.130559324,0.037077556,0.217556278]

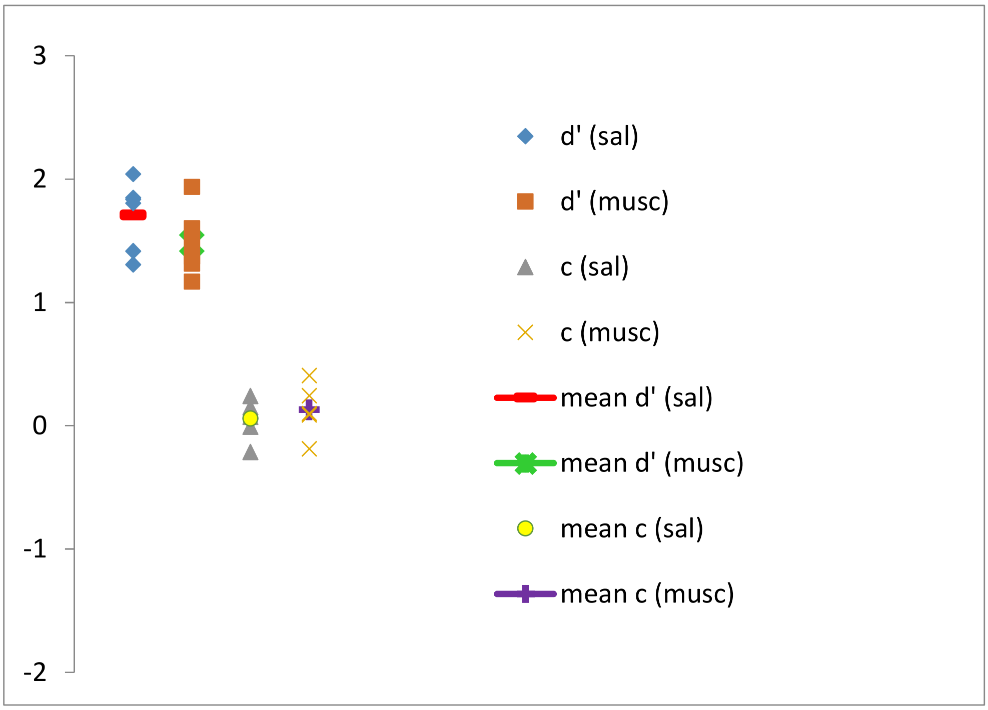
y= [-2.3,-1.139132833,0.253375101,-1.319337021,0.213639764]

gave W=16 and p = 0.5714 meaning that statistically there was no major difference in the vertebrates’ behavior under saline or muscimol.

4.2.2. Psychophysical decision task with symmetric reinforcement

In the second week the subjects' behavior was observed under the influence of 0.25 µgµl^{-1} muscimol in a symmetrical reinforcement schedule (0.5I0.5 for either side port). In comparison to the same dose of saline, the rats' sensitivity (d' (sal) ~ 1.7; d' (musc) ~ 1.4) and criterion setting (Fig. 25) was nearly identical for muscimol and saline injection as the calculations of the Wilcoxon-Ranksum-Test confirmed (W[d']=46, p[d']=0.310; and W[c]=36, p[c]=0.699) showing that the sensitivity as well as the criterion setting under saline and muscimol did hardly differ.

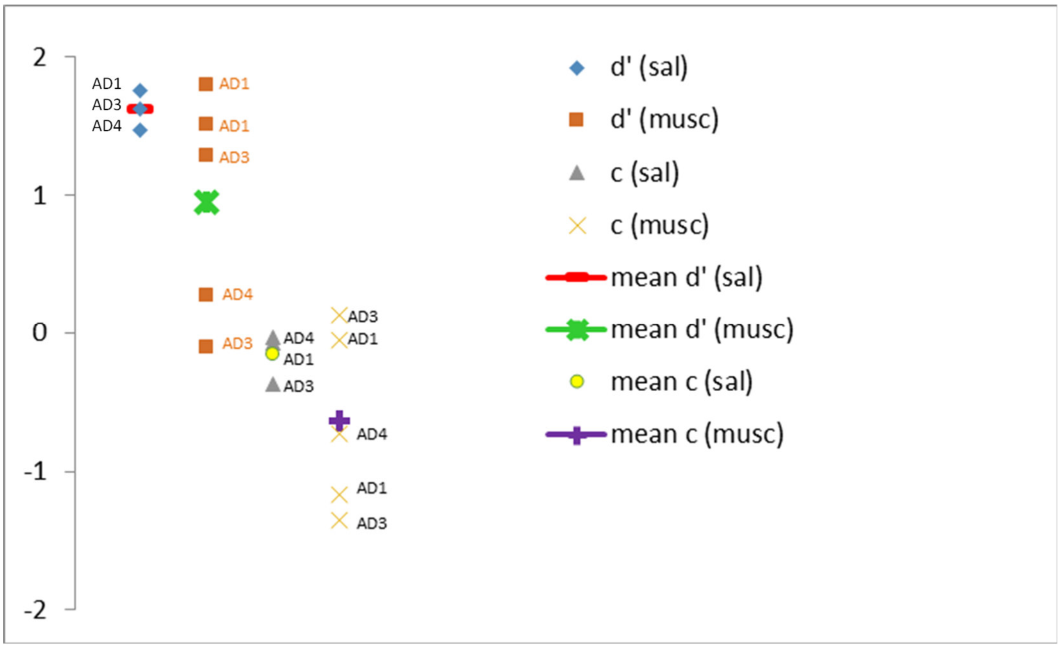
Noticeably, this outcome contradicts with what Lagler et al. describe in their recent paper (Divisions of Identified Parvalbumin-Expressing Basket Cells during Working Memory-Guided Decision Making, (Lagler et al., 2016) concerning muscimol injections. Although they bilaterally injected just 0.125 µgµl^{-1} muscimol into the rats' cortex they reported, "prelimbic cortex reversibly impaired task performance" (Lagler et al., 2016). Also, Stoilova et al. found inconsistent doses concerning the blocking of the mPFC (Stoilova et al., 2019). Possible individual influences of muscimol amounts or other reasons of the described inconsistent reactions to muscimol doses will be discussed later.



-Figure 25-
Bilateral blocking of the mPFC with 0,25 µgµl^{-1} muscimol (cf. Fig. 24 for the description of the diagram). Obviously the dosage of 0.25 µgµl^{-1} muscimol caused no major effect on the subjects' sensitivity as well as criterion setting compared with saline injection (d' (sal) ~ 1.7; d' (musc) ~ 1.4).

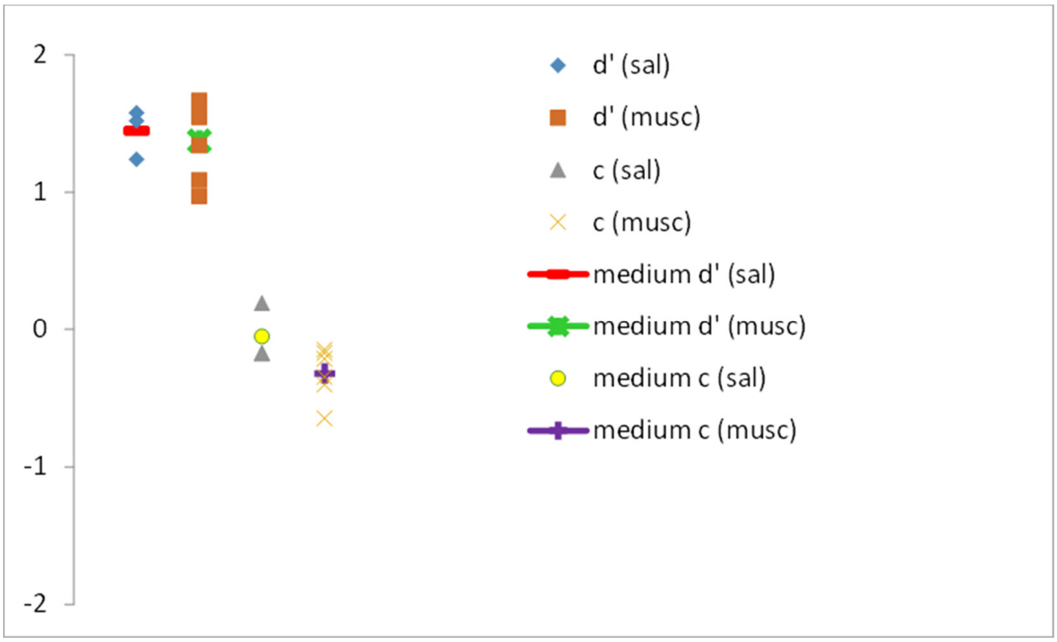
Lastly, a bilateral amount of 0.5µgµl^{-1} muscimol was injected for the last symmetrical reinforcer schedule (0.5I0.5 for either side). Interestingly, all three rats showed different behaviors. One rat performed similar to the saline application (Fig.26, AD1), one behaved slightly worse than under saline application (Fig.26, AD3), the third rat could not distinguish the two alternative stimuli at all (Fig.26, AD4). The Wilcoxon-Ranksum-Test, however, demonstrated that the average sensitivity and criterion setting of all vertebrates was similar under saline or muscimol influence (W[d']=17, p[d']=0.393; W[c]=23 p[c]=0.556).

Adding up all of the rats' sessions, a tendency of performance and bias is still recognizable: under the influence of saline the rats performed with an average d' of 1.6; the application of muscimol lowered the great-point average of d' to 0.9. Additionally, muscimol biased the rats more to the left side compared to saline injection (c(musc) ~ -0.6,   c(sal) ~ 0.2; Fig. 26).

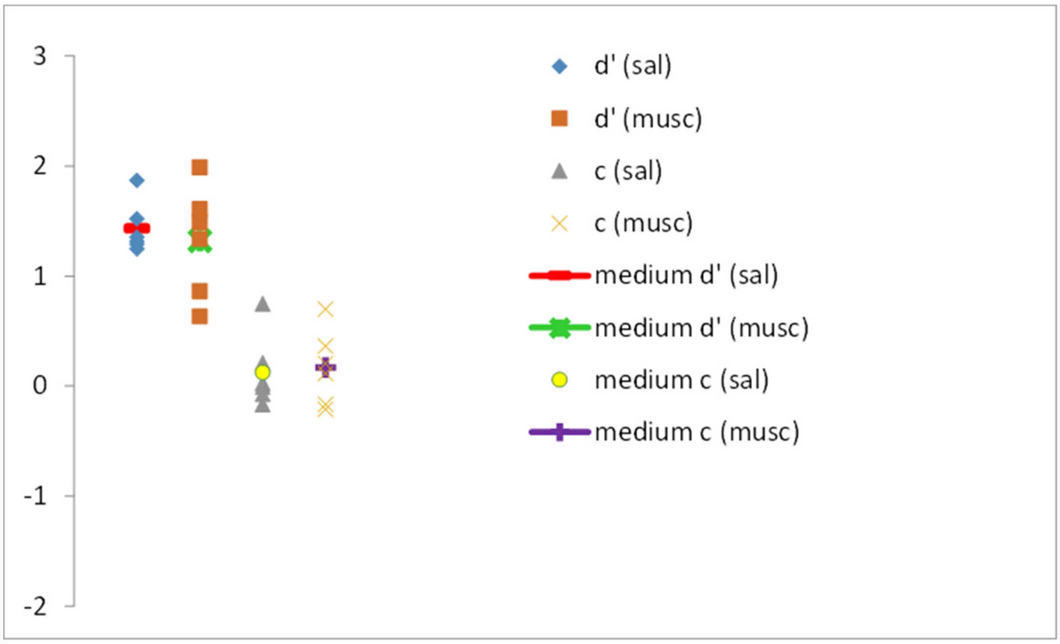


-Figure 26-
Bilateral blocking of the mPFC with 0.5 µgµl^{-1} muscimol (cf. Fig. 24 for the description of the diagram). Remarkably, the dose of 0.5µgµl^{-1} muscimol seemed to block neural mechanisms of the mPFC with an intensity between the higher (1µgµl^{-1}) and the lower (0.25µgµl^{-1}) dosage. The medium d' dropped down from 1.6 under saline infusion to a great-point average of 0.9 under muscimol application. Additionally, muscimol caused a stronger bias than under saline-control ((musc) ~ 0.6, c(sal) ~0.2). As mentioned above, all tree vertebrates showed a different behavior to the same amount of muscimol.

Finally, choice behavior was studied under unilateral injection of 0.5µgµl^{-1} in a symmetrical reinforcer schedule (0.5I0.5 for either side). Unilateral injection either on the right or left prefrontal cortex lead to a similar reaction under saline or muscimol infusion. In both cases, they showed a satisfactory outcome of d' ~1.4 and they were hardly biased to either side (W[d' right]=15 p[d' right]=1; W[c right]=23 and p[c right]= 0.556). A similar outcome was seen when only the left mPFC was blocked: W[d' left]=39 p[d' left]=1; and W[c left]=38 p[c left]=0.937.



A) Unilateral blocking right



B) Unilateral blocking left

-Figure 27-

Unilateral blocking of the mPFC with 0.5 µgµl^{-1} muscimol (cf. Fig. 24 for the description of the diagram). Overall, unilateral blocking seemed to have no major effect on sensitivity (d') and criterion setting: performance under saline control and muscimol barely differed.

Referring back to the main questions of this work, the outcome of the behavioral experiments produces more evidence that non-human animals are very well capable to almost optimally react to changing reward conditions and, in the long term, adapt their behavior in order to gain the greatest amount of reinforcement. Additionally, the blocking procedures of the mPFC provide further indications about its major role for the integration of sensory evidence as well as adaptive behavior during stimulus reward contingencies. The following section will therefore discuss the current findings about non-human detectability in terms of SDT and the TT.

5. DISCUSSION

The present research project underlay the goal to find out more about adaptive behavior under changing reinforcer contingencies. In practice, rats functioned as experimental subjects to get a better idea how human and non-human animals generally adapt their behavior to changes in their environment in order to optimize everyday life necessities as foraging or mating to preserve homeostasis; cf. (Stüttgen et al., 2011b, Keramati and Gutkin, 2014). In 1980 Graham H. Pyke, amongst other scientists, showed through his detailed observations in bumblebees that animals adapted their behavior for optimal foraging (Pyke, 1980), while M. Keramati and B. Gutkin stressed that for these homeostatic conditions "two brain circuits", "the hypothalamic homeostatic regulation system" and "the cortico-basal ganglia reinforcement learning mechanism", must work in concert (Keramati and Gutkin, 2014), cf. (Mowrer, 1960, Yeo and Heisler, 2012). One of the most plausible theories describing adaptive behavior is SDT, which was therefore examined in depths by this paper. Just lately, Bohil et al. clarified its meaning up until today: "The techniques provided by SDT have found wide application, including domains such as radiology, assessment of memory in clinical populations, and many kinds of monitoring tasks. In general, any categorical decision or diagnostic task can be evaluated using SDT…" (Bohil et al., 2015).

Although, the main purpose of this paper was not to get a deeper insight into the human behavioral mechanisms, throughout its completion it was still striking to understand the similarity of adaptation processes in humans and vertebrates (Alsop, 1998): in both situations the subjects managed a two alternative forced choice task with auditory stimuli. So the initial situation and the task of distinguishing two different alternatives were comparable. Ultimately, also the fundamental question was the same for both, human and non-human animals, when talking about signal detection: how did subjects accomplish to solve decision problems, and which theory would explain it best. Primarily for practical reasons and a broad agreement about the similarity of vertebral and human sensory systems the use of non-human animals were generally favored (cf. (Alsop, 1998).

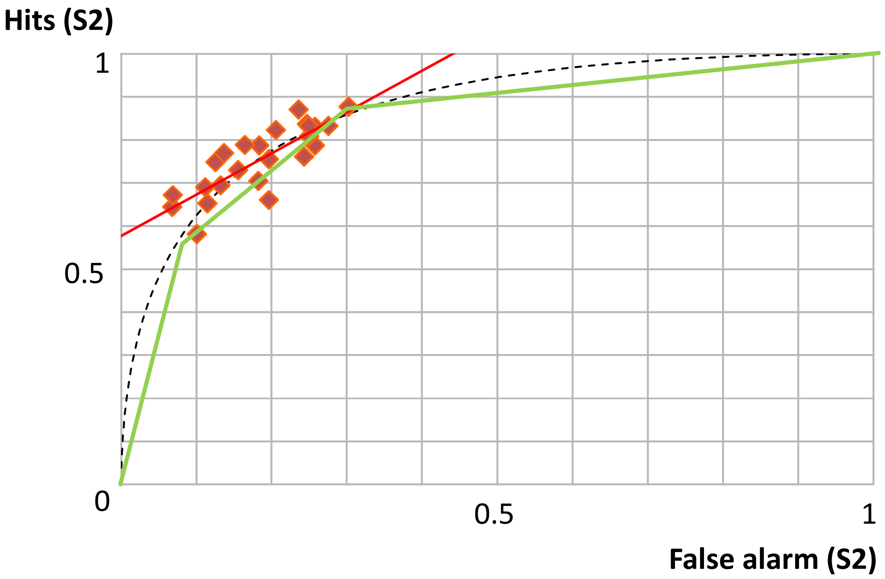
For that, the subjects' task performance was observed under changing reinforcer contingencies in order to derive a model that described best whether and how experimental objects adapted their behavior due to changing reward conditions (Sutton and Barto, 1998). The Literary debate served to introduce possible theories to explain human and non-human animals' behavior in adaptive choice tasks. This chapter will therefore serve to examine which of these theories best described the outcome of the experimental results with a primary focus on SDT as key model for optimization and a detailed comparison to the competing TT.

Considering optimization – discussion about continuous and discrete theoretical models to best describe adaptive behavior in vertebrates

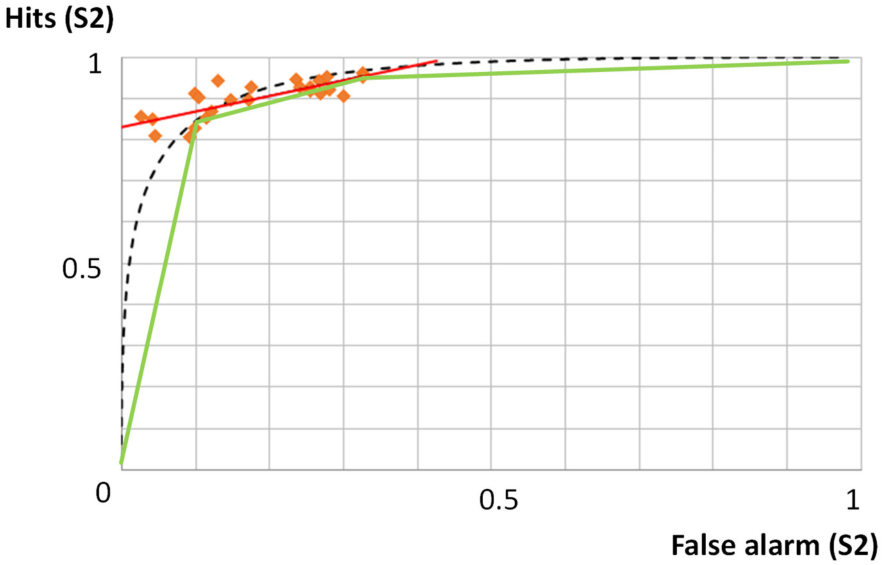
In the first place, the main question was whether optimization could be considered at all. A quite simple way to get an initial assessment was to graphically compare the current outcome with those given by scientists favoring SDT. The beginning chapters thoroughly explained how performance could be measured in terms of signal detectability. A good way to do so was the ROC that graphically reflected the subject`s performance depending on correct responses (hits) and false responses (false alarms) (s. Fig. 8 of chapter 2.3.5. The ROC comprised the effect of an individual's performance through d' and the shifting of criterion as reaction to changing reinforcement (s. 2.3.3., 2.3.4.). Practically, the better the performance, the higher was d', the steeper was the ROC, and the better was the subject's distinguishability of two different signals. Whilst differences in performance levels created two separate ROC-curves (Fig. 8), equal performance levels but changes in criterion setting (Fig.8 yellow cross "S" for a strict criterion and blue cross "L" for a lax criterion) resulted in the same ROC. Hence, the individual performance level as well as a changing environment was depicted by the ROC with its curvilinear shape as John T. Wixted shortly summed up in his paper comparing SDT with a dual-process detection model (Wixted, 2007), oppositely to a linear curve favoring principles of the TT (Wixted, 2007). Henceforth, Wixted highlighted the differences to the classical threshold model with a discrete and fixed line that neither varied from trial to trial nor did it incorporate environmental changes during the testing session. In the 1960s when SDT was heavily debated amongst scientists in the field of neuropsychological processes, in his paper "Is there a Sensory Threshold" John A. Swets pointed out "…that sensory excitation varies continuously and that an apparent threshold cut in the continuum results simply from restricting the observer to two categories of response" (Swets, 1961), see subchapter 2.2. In the same paper he introduced the classical TT and further advancements as the HTT, the LTT, and the Two-Threshold Theory (subchapter 2.2.). The quintessence of his complex projects were his comments concerning rating experiments that consisted of a yes-no procedure while the observer additionally had to specify how likely the stimulus was, given a six category likelihood scale (Swets, 1961)). Interesting was that the human subject was at least capable of distinguishing six different categories of sensory excitation (Birdsall, 1955) contradictory to any limitary threshold model of less than at least six categories. On top of that, there was enough evidence that not even a limit of six categories correctly reflected the human capacity of distinguishability, hence favoring a continuous sensory theory like SDT. In the same paper Swets further examined Green's idea of a Two-Threshold Theory with three categories (see subchapter 2.2.). Swets agreed that three categories better fitted to the observer's outcome than the classical threshold line. Nonetheless, even back then he was quite sure that "…a three-category theory…is inconsistent with the six categories of sensory excitation indicated by the rating data" (Swets, 1961).

<u>SDT vs. TT - the given results support SDT as best fitting theory for adaptive behavior in vertebrates</u>

In the current study, all of the four subjects' session points formed slightly different ROCs (two of the four ROCs are shown in Fig.28). Of course, it was quite expectable beforehand that each individual would show a different performance level, since they all differed in performance level and individual adaptability. However, with only a few exceptions, all four test objects showed nearly perfect behavior as their outcomes resulted in steeply rising curvilinear ROCs depicting what Wixted's described as a graded, instead of discrete, sensory ability. In detail, Figure 28 shows the data of rat AD2 and AD4 (each orange dot stands for the result of one experimental session) demonstrating their decent performance, whereby rat AD4 performed even better than rat AD2, resulting in a steeper rising ROC. The dashed black curve showed a curvilinear ROC by principles of the SDT, whereas for comparable purposes, the red line stands for a typical threshold line and the green curve depicts only a non-mathematical approximation of a discrete Two-Threshold assumption. At least the graphical comparison of Figure 28 between a signal detection and threshold models clearly favored SDT as best fitting approach of adaptive decision making. Only a quick glance on the different ROCs therefore gave a first hint to further follow the optimization track as possible theory behind adaptive behavior.



Experiment 1: subject AD 2



Experiment 1: subject AD 4

- Figure 28-

Outcome of experimental sessions under CRR for subject AD2 (panel at the top) and AD4 (panel at the bottom). Each orange dot stands for the outcome of one session. In both graphs, false alarms are plotted on the abscissa and the hits are plotted on the ordinate. The orange dots stand for the results of each conducted session. The dashed black curve shows the ROC under SDT, whereas the red line depicts a classical threshold (=linear regression of x/y values) to the conducted experiment and the green linear line shows a theoretical approximation of a Two-Threshold Theory (c.f. “Is there a Sensory Threshold”, Swets, 1961, Fig. 6). Even the graphical comparison shows quite impressively that the ROC under SDT gives a very good approach to the single results of each session, while both other theories less fit the rat’s individual data.

Now, coming to the behavioral experiments in detail, it was to analyze both behavioral experiments individually to check the rats' adaptability through changing reinforcer contingencies and deduct the most fitting theory to the outcomes of all conducted experiments. In fact, besides two different behavioral set-ups, changing reinforcer schedules (cf. chapter 3.2.) were used to explicitly study the association of given stimuli, varying payoff matrices, and the final given choice; cf. (Feng et al., 2009).

Besides the ROC, the main question was whether human and non-human sensory distinguishability was generally rather graded or discrete. Whilst proponents of the TT favored a discrete model for sensory detection, supporters of SDT were convinced that sensory perception could be best portrayed as continuous Gaussian distribution function, whereas stimuli detection depended not only on signal strength but on internal and external influences, theoretically represented by a varying c (see 2.3.3) as contrasting tool to the threshold line of TT. In the first experiment, the subjects followed a CRR (see 3.2.1.) with asymmetric reinforcement (ratio of S1 and S2: 0.25I0.75 and 0.75I.0.25). Figure 17 impressively showed that the rat favored the side port of higher reward probability in all four blocks of ratio changes. The latter observation could be supported by Feng's experiments with monkeys that obviously avoided the side with increased punishments (Feng et al., 2009). As mentioned before, not even the variable ratio schedule influenced the observer to give up perfect side movement in asymmetric reinforcement, although the variable ratio schedule implied that the subject was only rewarded every second correct answer or even just after every sixth correctly given choice (see 3.2.1. and 4.1.1. VR 2 and VR6). To strengthen the first assumption of optimal adaption ability in vertebrates, in the same chapter the One-sample-t-Test was used to compare the rats' outcome of c and p[choose S2] with an ideal observer. The results presented in Figure 18 could clearly underline that the subjects' performances did not significantly differ to that of an ideal observer. The minimal deviations to optimal behavior therefore allowed to further pursue the theory of optimal adaptive behavior to asymmetric response tasks in vertebrates and to support the low evidence base on asymmetric response studies Stüttgen mentioned in 2011; "While most research employing SDT employs balanced payoff matrices, equal reinforcement…for correct answers is the exception rather than the rule in natural environments…" (Stüttgen et al., 2011b); cf. (Feng et al., 2009). Giving credit to Stüttgen's research activities concerning adaption processes under asymmetric reinforcement, the outcomes of his pigeon studies very much reflected the results of the experiments of this study. Whilst Stüttgen's experiments of 2013 rather suggested non-optimizing theories (see subchapter 2.4.) the majority of his studies clearly supported optimal behavior in terms of SDT, which will soon be discussed.

Before that, the second URR experiment served to further check whether SDT also held truth for a second and different decision task. While in the first "controlled" experiment the reward was always assigned to one port making it easier to follow the programmed task; in the second uncontrolled procedure after each trial the reward was newly allocated and the subject was therefore not forced to the programmed side port (see 3.2.2.). Nonetheless, also in the second behavioral experiment the subjects adjusted their side movements according to the probability ratio: when the reinforcer rate was higher for the left port, the object moved more often to the corresponding side and vice versa (Fig. 19, Fig. 23). Even more remarkable was their nearly optimal criterion setting, even in trials when unbiased criterion shifting lead to slightly more payoffs, which further suggests the principles of SDT. Namely, not only the graphical data confirmed ideas of SDT (Fig.19, 20), also for the second uncontrolled task the One-sample-t-Test was conducted to statistically check whether non-human subjects tended towards perfect behavior. Indeed, the comparison for criterion shifting and correct side movement with dependence on asymmetric probability changes supported the first experiment's outcome of perfect signal detection.

A central parameter of this paper and difference of the two competing theoretical models was the static criterion as for the TT and a continuous criterion shifting for SDT. Henceforth, it was interesting to have a closer look on criterion movement in order to give further proof to one or the other model. So the experiments served to evaluate what Stüttgen et al. saw in their pigeon studies and strengthen the theory about a continuously shifting criterion as to optimize rewarding during asymmetric reinforcement; cf. "Shifting the decision criterion in a signal detection or discrimination task from a neutral location can be beneficial when the payoff matrix is asymmetrical [see introduction]. Exact placement of the optimal decision criterion depends on the ratio of reinforcement for the two alternatives and can be derived from a SDT-based model fitted to individual birds' data."(Stüttgen et al., 2011b). Stoilova et al. could also show in their latest study that criterion setting depending on the asymmetric reinforcer schedule helped the vertebrates gaining >97% rewards. Additionally, they gave more evidence that criterion updating was rather influenced by reinforcement than negative feedback in error trials (Stoilova et al., 2019, submitted).

Despite critics like Killeen et al. that questioned whether criterion setting due to asymmetric reinforcement could be seen as optimal, (They rather suggested "this deviation is explained in terms of a simplistic error-correction (EC) heuristic by subjects. The payoff matrix is adjusted to permit EC as a sensible…tactic. A closed form approximation of the equilibrium location of the criterion is shown to predict the systematic deviations (conservative adjustment of bias) found in the data, based solely on the detectability index, d'" (Killeen et al., 2018)), having a closer look at Stüttgen's and this study's outcome leading to an even stronger support for the theory of nearly-optimality in non-human animals.

Talking about the results demonstrated in chapter 4, the example of AD4 stood for nearly perfect reactions of all four animals. Rat AD4's performance showed how optimally the rat altered its criterion in order to gain the maximum rewards. The ORF (Fig. 23, Fig.29A blue bold line) graphically represented optimal shifting of criterion, as its peak meant the optimal criterion set point to receive the most rewards for a certain reinforcer contingency. So the closer the blue circle (standing for the rat's individual criterion shift) matched the ORF's peak, the better was the subject's performance. It was especially remarkable that all four testing objects adapted their behavior nearly optimally, even at shallow parts of the ORF when criterion setting to extremer values would hardly cause missing rewards (Fig. 23); cf. "the pigeons, after a period of adjustment, distributed their choices quasi-optimally even though this brought about only a small number of additional reinforcers" (Stüttgen et al., 2011b). Likewise with Stüttgen's outcomes of 2011 similar conclusions could be drawn: first, the pigeons in his experiment also shifted c (Fig. 10, Fig. 29C, bold black line) nearly optimally relating to the ORF (thin black line); second, as mentioned before, the overshooting behavior was larger for extremer reinforcer ratios (see paragraph below). Furthermore, Stoilova el al. could show that the testing subjects were capable of successfully reacting to high frequency of changing reinforcer contingencies as their performance did not significantly differ when reinforcer changes occurred after 20 or 180 min (Stoilova et al., 2019).

Possible limitations of SDT

Killeen, Taylor, and Trevino however criticized that in some of the typical signal detection tasks "punishment for an incorrect response [was] simply omitted reinforcement or a brief time-out. For some animals this [was] negligible, leading…to superstitious responding and persistent unnecessary…responding" (Killeen et al., 2018). Moreover, Stahlman and Blaisdell found that a higher reward magnitude, reward probability, or reward quality resulted in a reduced spatiotemporal behavior[25] (Stahlman and Blaisdell, 2011, Stahlman et al., 2010). Zentall therefore concluded that non-human animals seem to adjust their behavior rather along with successes than with errors (Zentall, 2016), which goes hand in hand with the main statement of the income based model (cf. 2.4.). Indeed, Gigerenzer et al. argued that these observations might generally question a complex explanation for signal detection, but instead considered a trial-and-error model for non-human animals; "Decision making under uncertainty may be more parsimoniously, accurately, and informatively predicted by simple processes—heuristics such as "titrate against errors"—than by global optimization models" (Killeen et al., 2018); cf. (Gigerenzer and Brighton, 2009), (Gigerenzer and Selten, 2001).

Contrarily with their postulations were the presented results of this study as the subjects quickly adjusted to the changing reinforcer ratios during the whole session (cf. (Treisman and Williams, 1984). Unlike a simple trial-and-error reaction, the current results clearly demonstrated that the effect of side movement seemed to be dependent on the absolute reinforcer ratio as the bias to one side increased when the ratio was 0.1I0.5 compared with 0.5I0.9 (see chapter 4.1.2.).

Contradictory to the current outcomes, amongst others, Jäkel and Wichmann, could show that the applicability of principles stated by SDT highly depended on the overall scientific question as well as situational circumstances. In laboratory settings and the possibility to work with highly trained non-human animals, the original idea, restated by Blackwell (Blackwell, 1952), to most efficiently and adequately compare the subjects outcomes with the ideal observer in two-interval-forced-choice[26](2IFC) tasks should be re-questioned for rather untrained task subjects. Particularly, Jäkel and Wichman could show that naïve objects had the lowest thresh-

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[25] Observed behavior relating to both, space and time: The experimental subjects' shown behavior within their training surroundings in a given time period.

[26] Two-interval-forced-choice task: task procedure of two intervals, whereby the subject has to decide whether the signal was presented in the first or second interval

old for four-alternative-forced-choice (4AFC) tasks; “Naive observers…performed worst during 2-IFC, in terms of both reliability and sensory determinacy, and they performed best for spatial 4-AFC” (Jakel and Wichmann, 2006). In general, Yeshurun et al. collected published data about the IFC tasks and could show that some of the early stated principles of SDT about forced choice tasks, i.e. ruling out bias for interval-forced-choice jprocedures in order to eliminate the role of the individual decision criterion (Green and Swets, 1966), did not account for many of the re-analyzed studies as well as their own conducted experiment; “In conclusion, we [found] large interval biases in all of these studies. Across studies we found biases that favored either the first or the second interval” (Yeshurun et al., 2008), cf. (Frund et al., 2011). Although, many scientists based their research on the original ideas of SDT Jäkel’s, Wichmann’s, and Yeshurun’s findings showed that it is justifiable to re-question some of the originally stated factors. Stüttgen briefly summarized their detailed analysis: “…their data [did] not allow a clear interpretation of how the psychometric functions from the different tasks relate to each other, the authors speculate that extra-sensory factors, like sensory memory and spatial attention,[had] different effects in different tasks. It is noteworthy that these extra-sensory effects[were] ignored in SDT” (Stüttgen et al., 2011a). In fact, more recent studies of Frund et al., M. Lages, M. Treisman, and T.C. Williams focused on these extra-sensory factors concerning the influence of behavioral improvement through learning and the influence of motivation and attention throughout a task session (cf. (Frund et al., 2011);(Lages and Treisman, 1998); (Treisman and Williams, 1984)) as well as reward expectations highlighted by Stoilova et al. (Stoilova et al., 2019, submitted).

Frund and his colleagues found out that for drawing correct psychometric functions in SDT extra-sensory factors happing throughout each trial and session need to be considered, “we performed a large number of simulations to investigate the effects of non-stationary behavior on estimation of psychometric functions. The effects of non-stationarity on the estimated credible intervals could not be neglected” (Frund et al., 2011). On the whole, they criticized that too often, both, in single-interval tasks and also in forced-choice tasks, stationary cognitive performance was assumed and used for the fitting of psychometric functions, although their own complex studies showed non-stationary cognitive conditions in experimental subjects and therefore an underestimation of psychometric data sets. In fact, they presented evidence that a large amount of trials could not correct that bias; “we performed a large number of simulations to investigate the effects of non-stationary behavior on estimation of psychometric functions. The effects of non-stationarity on the estimated credible intervals could not be neglected. When psychometric functions were estimated from non-stationary data, the credible intervals for threshold as well as width were much too small. Even worse, the typical strategy that is used to deal with corrupted data is to simply collect more data. This strategy does not work here: More bad data will not lead to good inference.(Frund et al., 2011). Also Bohil et al. criticized that "even stimuli known to vary along multiple dimensions are frequently collapsed onto a single evidence axis" (Bohil et al., 2015, Swets, 1995) suggesting to extend the classical signal detection model to a multidimensional model that allowed to choose from stimulus dimensions instead of particular signals (cf. "general recognition theory" (Ashby and Townsend, 1986). Similarly, Parasuraman, Masalonis, and Hancock developed a model that allowed one event to be represented in both categories, even though to different degrees (cf. "fuzzy signal detection theory" (Parasuraman et al., 2000). For the sake of completeness, it must be said that despite these extensions to the classical SDT, the outcomes of all these experiments showed similar results concerning the key factors of d' and c (Stafford et al., 2003).

Nonetheless, recent studies of Harris et al. further limited some of the principles of SDT as they showed the significance for decision making of inter-stimulus-intervals in forced-choice tasks. The longer the interval between two stimuli the more decrease in performance could be observed; "One stimulus can be accurately compared with the memory of a previous stimulus if they engage overlapping representations, but activation of the common cortical territory by an interpolated stimulus can disrupt the memory trace" (Harris et al., 2001). While most authors admit that extra-sensory effects play a role in signal detection, some, as earlier mentioned, demonstrated that long-term experiences influenced the subject's behavior, others, like Stewart et al. obtained evidence for a direct impact of previous stimuli in decision making; cf. (Stewart et al., 2005). Generally, Wolfe et al. gave evidence that many detection theories reached limits for rarely presented stimuli, "Heuristics that produce acceptable performance over a wide range of target prevalence may betray us at low prevalence" (Wolfe et al., 2005).

Overall, amongst many others, Frund et al. Treue and Martinez (cf. (Treue and Martinez Trujillo, 1999)), as well as Stüttgen et al. admitted that extra-sensory factors as motivation and attention manipulated data in terms of SDT, therefore suggesting to control these fluctuations by establishing correction factors.

Further observed fine behavioral patterns whilst testing for optimization

Similar to the overshooting behavior, more current scientists started out to address fine behavioral patterns. Amongst them were Teichert and Ferrera who tested for optimal criterion shift for asymmetric reward likelihoods instead of reward magnitude. Firstly, they found that for the latter condition criterion shifting was not optimal in terms of SDT; secondly, instead of over-adjustment the subjects showed under-compensation in asymmetric reward likelihoods, „In the magnitude bias condition subjects shift their decision criterion too far, i.e., they overcompensate. In contrast, they do not shift their decision criterion far enough in the likelihood bias condition, i.e., they under-compensate.“ (Teichert and Ferrera, 2010). Remarkably, these observations contradicted what was seen in human beings before. For non-human objects they therefore postulated „that differences in reward magnitude [were] more salient than differences in reward likelihood: reward size is experienced immediately while reward probability emerges over multiple trials” (Teichert and Ferrera, 2010). In contrast to SDT, Bohil et al. postulated that vertebrates might be able to “learn within one trial”, since they over-estimated one category at the beginning of reinforcer ratio changes and later narrowing down to neutral responding (Bohil et al., 2015, Hoffman and Fiore, 2007). Other observations were made by Stoilova et al. that response bias was less extreme than required for optimal performance (Stoilova et al., 2019, submitted).

Having mentioned them before, Killeen, Taylor, and Trevino (Killeen et al., 2018) conducted experiments to find out more about fine behavioral patterns during signal detection tasks. Amongst other detailed behavioral patterns, they could show that behavioral variability and also response errors increased as the reward probabilities or magnitude decreased (cf. (Capaldi et al., 1997, Rose et al., 2009).

Overshooting behavior – a newly found phenomenon

Remarkably, the described observations went hand in hand with what Stüttgen et al. saw in their 2011 conducted pigeon studies (Stüttgen et al., 2011b). Even the mentioned stronger overshooting effect for extreme probability ratios as well as the return to shallow parts were comparable; „changes in choice allocation [were] more pronounced for the more extreme reinforcement contingencies" (Stüttgen et al., 2011b). In fact, why the subjects showed this overshooting reaction has not been understood so far and needs more investigation. Generally, the phenomenon of overshooting reactions in vertebrates was a new observation of Stüttgen and a few more scientists in the field of adaptive behavior. Presumably, earlier research rather focused on steady-state behavior or just shorter task periods missing out the over-adaption; cf. (Stüttgen et al., 2011b). For example, Corrado et al. set up relative reward-baiting probabilities with only a constant length of 50 to 300 trials reporting about a "…[quick adaption] to changes in the environment at block boundaries."(Corrado et al., 2005), not mentioning a strong over-reaction as currently seen, similarly to further experimental set ups with a shorter block period of constant probability ratios; cf. 50 trials per condition in (Davison and Baum, 2000), 121/125 trials per block in (Lau and Glimcher, 2005).

Nonetheless, the reason for an overshooting behavior seen in the current study as well as Stüttgen's and a few other studies (Feng et al., 2009, Killeen et al., 2018)) need to be further examined (cf. (Teichert and Ferrera, 2010) "In the asymmetric reward magnitude condition, monkeys over-adjusted their decision criterion such that they chose the highly rewarded alternative far more often than was optimal")). One possible explanation could be that as soon as the probability ratio changed to either side, the vertebrates tried to gain as many rewards as possible in a short time period, however, as the session block continued they realized that although rewards were mainly allocated to one side, they would lose rewards by completely missing out the contrary port. Stüttgen himself suggested "[a] potential reason for this overshoot may be that the differential choice allocation to options differing in reinforcement density is dependent on the discriminability of these reinforcement densities—in effect, a psychophysical problem: the discrimination of marginally different reinforcement frequencies for the two options." (Stüttgen et al., 2011b). Teichert and Ferrera could show that the over-adjustment was not due to a lower discriminability for biased conditions as similar effects were also shown for neutral reward ratios, "… the observed overcompensation cannot be attributed to reduced stimulus discriminability in the biased condition." (Teichert and Ferrera, 2010). However, in their experiments the subjects lost more rewards due to the over-shooting behavior (on average 6%) than reported in earlier studies (1-2%, cf. (Feng et al., 2009)) (Teichert and Ferrera, 2010). Additionally, they found out that human and non-human animals seem to react differently when maximizing pay-off. Their experimental outcome justified the question whether different utility functions[27] led to different behavioral patterns. Like Kahneman and Tversky (Kahneman and Tversky, 1979) as well as McCoy and Platt (McCoy and Platt, 2005) they had evidence that "…humans rather tended to concave and non-human animals to convex utility functions…" value[ing] big rewards relatively less, and the shift which optimizes expected utility [being] smaller than the one that optimizes expected reward" (Teichert and Ferrera, 2010). Nonetheless, so far the overshooting behavior cannot be explained through SDT or any optimization theory and needs more investigation.

Summarizing assessment and further ideas

Having contrasted two major theories in the context of adaptive behavior, SDT and the TT, recent scientists, amongst them was David Kellen, looked again closer at former variations to the classical threshold models focusing on Luce's in 1963 postulated one-category LTM (cf. 2.2.). Kellen and similar minded scientists did not only question a truly continuous model as SDT for the subjective representation of stimuli, they were eager to incorporate non-sensory states to their examinations; "…even though the model [LTM] only assumes two sensory states, other non-sensory states affect their disposition toward each of the available response options, enabling their occurrence with some probability. Presumably the non-sensory states are independent of whatever states are relevant for the decision to be made, and therefore influence the performance in recognition memory tasks in the same manner as in sensory tasks." (David Kellen, 2016). Since Luce believed in non-sensory influences, i.e. motivation and experience, that lead to decision making, the model allowed the subject to decide for "yes", stimuli present, when the signal was not detected. However, as mentioned in the beginning, even Luce admitted that "the most obvious misfit of the LTM to the data comes from the predicted 'corner'…of the two ROC segments" (David Kellen, 2016). Figure 28 demonstrated that one-category threshold models as well as multiple-category threshold models at least did not fit to the collected data of the present study. For the sake of completeness, the same would account for high threshold models belonging to two-category models demonstrated in chapter 2.2. (cf. (Nachmias, 1981, Laming, 2013)).

Although most scientists in the field of signal detection showed in their conducted experiments that SDT gave the most fitting explanations for their data, followers of the multiple

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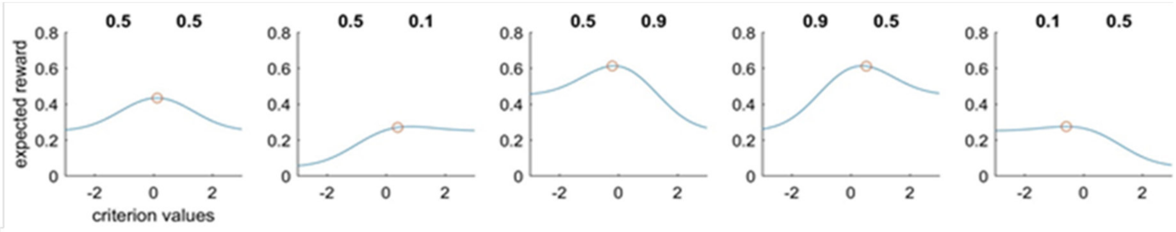
[27] Utility functions help to determine preferences according to a set of different alternatives

threshold models still argued that in many studies threshold models equally fitted to the same scientific results (Dube et al., 2012). Even scientists favoring optimization had to admit that certain threshold models they used for comparison reflected their data almost as well, “Consistent with this assumption, the fit results showed that both models fit the group data closely, with a slight edge for the SDT model” and “One interpretation of these results is that both models perform adequately”; cf.(Kellen and Klauer, 2014, Broder and Schutz, 2009), (A. Chechile, 2013), (Province and Rouder, 2012, David Kellen, 2016). Independent of the present study and the outlining of the multiple ideas for the best fitting model to signal detection tasks, many scientists agreed that threshold theories encountered their limits in “conditions in which performance is virtually perfect” (David Kellen, 2016), already mentioned by D.H. Krantz in 1969 as “super-detection state…in which the individual is absolutely certain that the item was previously studied” (Krantz, 1969).

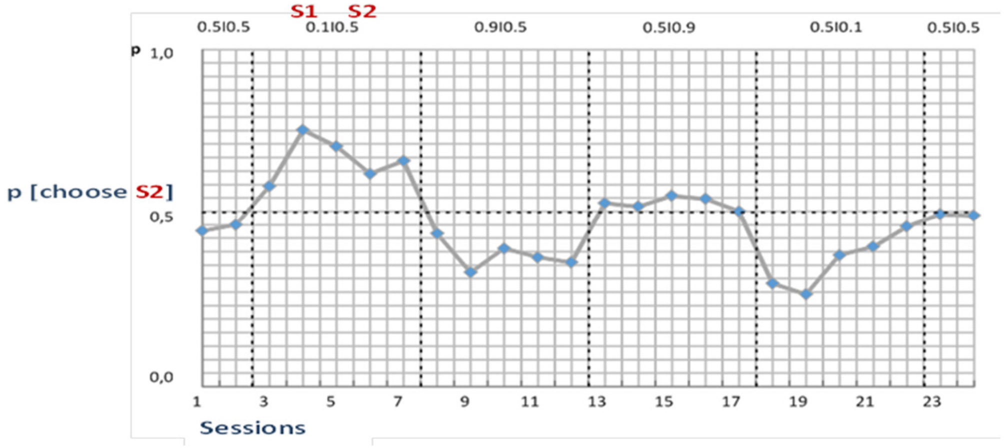
As mentioned at the beginning of this chapter, both behavioral experiments investigated whether non-human animals were able to optimally integrate incoming sensory evidence as part of stimulus-reward contingencies in their long-term memory.

Despite the ongoing discussion about the most fitting theoretical model concerning signal detection, SDT describing nearly optimal reactions to changing stimulus-reward contingencies, gave a reasonable approach to the outcome of both studies (the current study as well as Stüttgen et al’s study in 2011). In fact, both tasks dealt with asymmetric reinforcement; however, setting up two different task procedures gave an even stronger evidence for one or another theory in adaptive choice behavior. Nonetheless, as thoroughly discussed in section 2.4., even Stüttgen and his colleagues later had to admit that other non-optimizing theories, as the income based model, better fit to their data as what previously expected by SDT (Stuttgen et al., 2013) (cf. 2.4).

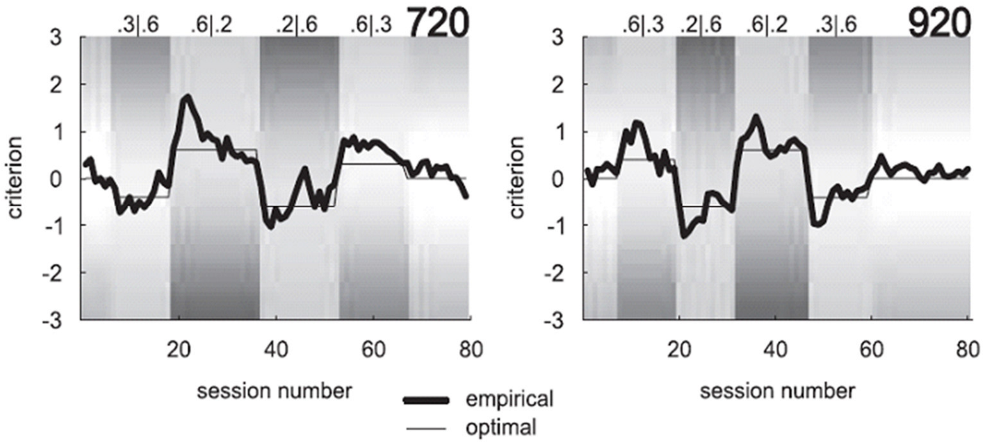
Henceforth, only considering SDT or the TT would not be sufficient enough to explain the broad process of decision making and the adaption to changing life events. As discussed earlier, the threshold model reduces decision making to a small possible number of fixed states (cf. section 2.2.) that would not wholly represent human and non-human animal’s capacity of distinguishing between at least six different categories (cf. see upper paragraph of this section). Nonetheless, also SDT theory lacks certain circumstances that would fully describe how non-human animals react to changing life events, i.e. non-sensory states; also it cannot be



A Uncontrolled reinforcer ratio (URR), p [choose S2]



B Uncontrolled reinforcer ratio (URR), p [choose S2]



C Outcome of Stüttgen's pigeon studies in 2011 (Stüttgen et al., 2011b)

- Figure 29 –
Comparison of Stüttgen's pigeon experiments with outcomes of this study. For panel description see sections 3.2.2. (panel A, B) and 2.4. (panel C). Responding behavior of rat AD4 (panel A and B) and pigeons 720/920 (C) emphasized the approach of SDT: first, the subjects clearly adapted their behavior to changing reinforcer ratios, represented by the shifting of c (panel A: the empirical criterion setting, red circle, matches the peak of the ORF, blue thin line; panel C: criterion setting follows this of an optimal observer, black thin line). Second, as they reacted to changing reinforcer conditions the probability of reward maximization increased (panel B). Additionally, the overshooting behavior was evident in both studies.

applied to untrained, naïve observers in unknown situations; and many more, (cf. upper paragraphs).

The mPFC – as one component for proper decision making in a complex nervous system

After receiving more information about how non-human animals tackle decision tasks, the final challenge was to examine which brain areas mostly organize and control the ability for almost perfect decision making. In this study the prefrontal cortex was primarily studied while my colleague in a later experimental set-up focused on the auditory system (Stoilova et al. 2019, submitted). Besides the mPFC the PFC contained the orbitofrontal cortex, the dorsolateral PFC, and the ventrolateral PFC.

It was well known that the process of decision making in human and non-human animals was constructed of a complex network of neural mechanisms; first within the peripheral and central nervous system that needed to be perfectly coordinated, second as inter-hemispheric and inter-cortical functionality, and third on a single-to-single neural level. Fortunately from the beginning on, men have always been interested in the human mind and were therefore eager to find out about the cortical functions and their locations. Ultimately, there was sufficient evidence that the prefrontal cortex played a remarkable role for a functioning decision process; "Notably, the mPFC has emerged as a crucial neural substrate of social cognition and behaviors in humans (Ko, 2017, Dolan, 2002, Bicks et al., 2015), as well as cognitive flexibility like reversal learning as Stoilova et al. could show in their recent paper (Stoilova et al., 2019). Despite this fact, only a few studies examined non-human animals concerning the impact of the prefrontal cortex within the complex process of decision making and its direct role in optimal signal detection (Ko, 2017, Yizhar et al., 2011, Yizhar, 2012). Additionally, only a few research projects really examined the animals' behavior before and after knocking out exactly one cortical region. So the focus of this study was to go down to the neural level by blocking the neural function of the prefrontal cortex through the inhibition of its neurons by muscimol infusion (Stoilova et al., 2019). Together with the relatively new technique of neurometric recordings (spike trains of single sensory neurons) the goal was to receive a better understanding about the function and neural location of signal detection, "…realiz[ing] Fechner's dream of 'inner psychophysics'–relating neuro physiological activity to sensation"; cf. (Stüttgen et al., 2011a, Mountcastle et al., 1990).

As mentioned before, in the past many scientists could show that the mPFC played a crucial role for decision making (section 2.5.). This study concentrated on a specific field within decision making, namely the role of the mPFC for the adaption to changing surroundings via varying reinforcer ratios. For that, unilateral and bilateral blocking of the mPFC was intended to give answers to this question. Furthermore, the following outline will show that decision making and specifically adaptation cannot be reduced to one single cortex, but a whole sensory system. Because of this, the intention was to describe the function of the mPFC as well as its broader intercortical role for adaption processes.

Despite the importance of a single neuron’s power that can be analyzed by neurometric recordings, this study mainly examined the role of one complete cortex for signal detectability. In the first experiment the prefrontal cortex of both hemispheres was blocked with 1µgµl^{-1} and the subject had to follow an asymmetric reinforcer ratio schedule (0.5I0.5 – 0.05I0.95/0.95I0.05 – 0.5I0.5). As mentioned before, the rats were not able to optimally respond in order to gain most rewards compared with their reaction during saline infusion. More important, in the direct comparison to saline infusion, it was obvious that the blockage of the prefrontal cortices hindered the subjects from optimally adapting their behavior to changing environments. Importantly, not only in experimental procedures with time-out punishments, Stoilova et al. could show that punished responses (through foot-shocks as punishing instrument) significantly decreased during saline infusion (Stoilova et al., 2019). Interesting was that the dosage of muscimol seemed to have an important impact of how well the objects performed. Bilateral blocking with 1µgµl^{-1} muscimol wholly prevented any satisfying reaction as the vertebrates were strongly biased to one side of the water ports. These results go hand in hand with the observations made by Yong Sang Jo and Sheri J.Y. Mizumori in their recently published study “Prefrontal Regulation of Neuronal Activity in the Ventral Tegmental Area”, (Jo and Mizumori, 2016). Their rats were trained to use either arm of a T-maze set-up. After the bilateral injection of 1µgµl^{-1} muscimol, however, they consistently ran up to only one of the arms.

The second and third experiment gave more evidence for the dosage-dependent behavioral performance. The subjects were tested in a symmetric reinforcer ratio schedule (0.5I0.5) for both side ports whilst the muscimol dose was firstly reduced to 0.25µgµl^{-1} and later increased to 0.5µgµl^{-1}.

Whilst the lower dosage of 0.25µgµl^{-1} muscimol did not have a great effect on the subjects' performances (d' and c did not significantly differ (see subchapter 4.2 and Fig. 25)), the higher muscimol dosage of 0.5µgµl^{-1} impaired the rats in different ways. Figure 26 demonstrated that all three subjects showed different performances under the medial dosage of 0.5µgµl^{-1} muscimol leaving the question whether the dosage of muscimol was highly individual in the case of neural impairment. At least, Lagler and his colleagues used as part of their recent paper ("Divisions of Identified Parvalbumin-Expressing Basket Cells during Working Memory-Guided Decision Making" (Lagler et al., 2016)) a bilateral amount of 0.125µgµl^{-1} muscimol and reported that this dosage, oppositely to the current study's dosage, already hindered the subjects from optimal decision making (Lagler et al., 2016). Lagler's observation went hand in hand with Krupa et al. who reported about a dosage of 0.150µgµl^{-1} abolishing neural activation, cf. (Krupa et al., 1999). Nonetheless, more studies under muscimol would be needed to find out whether muscimol infusion lead to a rather similar or individual reactions in vertebrates (Stoilova et al., 2019).

In the last neural experiment unilateral blocking of one of the two hemispheres did not have an effect on the rats' performances (Fig.27). On the whole, this outcome supported what most former studies postulated: optimal behavior was possible with the function of one hemispheric mPFC. Though, due to their analyzation, some scientists speculated that the right and left mPFC might be in charge of slightly different behavioral functions(Lee et al., 2016).

Overall, referring to the introductive goals, the results of this work gave additional evidence that the mPFC had a major role in adaptive behavior during stimulus-reward contingencies ("…inactivation of medial prefrontal cortex with muscimol strongly affected both discrimination performance and criterion setting, Stoilova et al., 2019, submitted). So its known function of integrating sensory evidence and putting it to long term memory could be supported through my pharmaceutical experiments.

Over decades, many scientists understood that the pure focus on one single cortex was not sufficient to describe decision making; not even the adaption process was fully represented by just one brain cortex. Although, it had so far been difficult to precisely associate certain sensory functions with particular brain areas, it could be undoubtedly stated that sensory information was restored, connected, and encoded within a complex network amongst multiple brain areas; “both the normal encoding of tactile information and the process of injury-dependent plastic reorganization depend on system-wide interactions that involve many brain structures and can only be fully reconstructed (or decoded) by examining the simultaneous dynamic interactions between populations of cortical and subcortical neurons” (Krupa et al., 1999). For instance, Krupa et al. studied cortico-thalamic feedback mechanisms to find out that an inactivation of the somatosensory cortex lead to an immediate change of the ventroposterior medial thalamic neural activation (cf. (Krupa et al., 1999, Kaas et al., 1984, Merzenich et al., 1983)) as well as further subcortical levels (cf. (Nicolelis et al., 1993, Faggin et al., 1997)). Consequently, the present study’s results of the mPFC having an impact within the broad process of sensory integration, analyzation, and encoding can be seen as one further element in order to understand the complex sensory network.

Similar with the present study, Rorie et al. drew their attention to the location of brain areas responsible for decision making. Electrophysiology helped them to find out that “single neurons in cortical area of the Lateral Intraparietal Cortex (LIP) [were] known to carry information relevant to both sensory and value-based decisions that [were] reported by eye movement“ (Rorie et al., 2010), cf. (Roitman and Shadlen, 2002, Huk and Shadlen, 2005). Other scientists found out that LIP neurons were further necessary to interconnect between the broad sensory network in order to understand stimulus probability or rewarding, cf. (Gold and Shadlen, 2001, Gold and Shadlen, 2007) for optimal decision making. A rather new detection within the LIP was its most likely neural role as “salience map” ((Rorie et al., 2010, Gottlieb et al., 2009),(Goldberg et al., 2006, Ipata et al., 2009) for new, unknown, or sudden stimuli.

However, so far research had mainly shown that the sensory system was a huge system of interconnecting pathways, whereby very similar sensory functions seemed to even overlap in different brain areas; cf. (Rorie et al., 2010), (Platt and Glimcher, 1999, Lau and Glimcher, 2005, Kiani and Shadlen, 2009, Klein et al., 2008). The outcome of the present pharmacological experiments with muscimol gave strong evidence that also the mPFC played a major role in many of the mentioned sensory functions. The results clearly showed that proper decision making was not possible while blocking the mPFC of both hemispheres. Consistent with the function of the mPFC, also Rorie et al. and .Feng et al. (Feng et al., 2009) demonstrated that the LIP was responsible for optimal decision making in terms of SDT during asymmetric reward contingencies. Besides these observations, Rorie et al. also reported about changing reactions to asymmetric reinforcement as earlier discussed: in their experimental studies, asymmetric reward rates lead to strong bias toward the higher reinforced stimulus while they, consistent with the recent outcome of the present study, observed some kind of overshooting behavior what they reported as “mechanistic effect of biasing the starting point of the motion integration process“ and “as the motion epoch developed, however, the representation of both relative and absolute value faded” (Rorie et al., 2010). In former scientific data, the two-staged behavioral reaction for asymmetric reward contingencies, the overshoot at the beginning, and the balancing out over time, was described by Dietrich and Busemeyer as “two-stage processing hypothesis” (Diederich and Busemeyer, 2006) what they associated with an accumulation of signal input at the beginning of signal presentation and a ceasing of accumulation when the accumulator reaches a stationary boundary (Rorie et al., 2010). In general, the later noted that studies about behavioral adjustment to asymmetric reward contingencies might have a longer history than always believed. Earlier scientific reports dealt with similar problems, however grouping it to rubrics of attention (Maunsell, 2004). So it would be useful to investigate former literature about that topic to gain further evidence of behavioral adjustment and optimization to asymmetric reward tasks. The overshooting aspect was discussed in earlier paragraphs of this chapter, and since the reason for this overreaction has not been understood so far, its neural cortical representation would be pure speculation.

Besides the LIP, Thomas Z. Luo and John H.R. Maunsell found out that also the Lateral Prefrontal Cortex (LPFC) had a major impact for proper signal detection. To get a deeper understanding about the main tools of SDT, they were eager to get a deeper understanding whether the LPFC influenced both, sensitivity and criterion setting in signal detection “the distinction between criterion and sensitivity [was] crucial because [as explained in the beginning parts of this work] any improvement in an observer’s hit rate [could] be equivalently brought about by a decrease in c or an increase in d’” (Luo and Maunsell, 2018). Luo and Maunsell themselves (Luo and Maunsell, 2015) recognized that some cerebral regions might be only engaged with sensitivity (i.e. the visual cortical area V4), and others primarily with criterion setting (cf. (Sridharan et al., 2017, Cavanaugh and Wurtz, 2004, Zénon and Krauzlis, 2012) like the superior colliculus. Their most recent paper, however, revealed that the LPFC seemed to have an impact for both, sensitivity and criterion setting; “firing rate modulations related to the two behavioral changes were highly correlated on a cell-by-cell basis. This finding suggests that Δc- and Δd’-related modulations arrive in a common signal in LPFC. However, it is also possible that Δc- and Δd'-related signals have separate origins, and that a mechanism within LPFC restricts the extent to which individual cells are modulated by either signal. " (Luo and Maunsell, 2018). In general, they finally considered whether any of the examined regions were really just responsible for one or the other tool of SDT or whether all of these cerebral structures had at least a small impact in signal sensitivity and criterion setting, "…it [was) possible that that no brain structure [was] entirely associated with only criterion changes" (Luo and Maunsell, 2018). Luo and Maunsell summed up that among other engaged cerebral regions, i.e. the superior colliculus and thalamus (cf. (Goldberg and Wurtz, 1972, Briggs et al., 2013, McAlonan et al., 2008), sensory attention was represented by the visual, parietal, and prefrontal cortex (cf. (Luo and Maunsell, 2018, Lynch et al., 1977, Moran and Desimone, 1985).

The outcomes of this paper supported the more recent perceptions that tools of SDT, both c and d', were controlled by neurons of the mPFC (amongst neurons of many other cortical regions). Additionally, just lately Liang and his colleagues discovered "Neuroligin-2 [as] an inhibitory synapse-specific cell-adhesion molecule that was recently implicated in synaptic inhibition in the mPFC… [that was] essential for the long-term maintenance and reconfiguration of inhibitory synapses in the mPFC". The authors hypothesized that the behavioral phenotype was produced by dysfunction of a peculiarly plastic subpopulation of inhibitory synapses in neuroligin-2-KO mice. These studies illustrate the idea that various synaptic signaling and adhesion pathways operating in the mPFC contribute to the initiation, maintenance, and/or modulation of social behaviors (Liang et al., 2015, Ko, 2017). It appeared that the current scientific discussions were just the starting point for a more detailed view on social behavior and its cortical representation and origin. The knock-out experiments for this work therefore served to approve existing assumptions about the key role of the mPFC within social adaptation in non-human animals.

Limitations of knock-out experiments

At last, a limiting factor about the knock-out experiments was that the neural function and mechanisms could not be observed and measured during activation but that two states of consciousness – neural activation and knocking-off – were directly compared, therefore favoring neurometric recordings for direct neural deduction (Parker and Newsome, 1998). Additionally, the neurometric recordings gave evidence about the great power of single neurons of vertebral sensory systems, and revived older psychophysical threshold theories as the Lower Envelope model (LEM) questioning whether stimulus detection was represented by one single neuron. “Sensory thresholds are set by the class of sensory unit that has the lowest threshold for the particular stimulus used and are little influenced by the presence or absence of responses in the enormous number of other neurons that are less sensitive to that stimulus” (Barlow, 1995). Together with the knowledge about SDT, scientists in the field of neurometric psychology believed that one neuron or a small neural unit could stand behind the detection of stimuli, depending on further internal and external circumstances the subject was exposed to. “They employed signal detection theory to compute the minimal detectable increment in contrast or spatial frequency that could be signaled reliably by V1 neurons across a range of base contrasts and spatial frequencies. These increment thresholds were then compared to the increment thresholds of human and monkey observers measured psychophysically across the same ranges of contrasts and spatial frequencies. Their plots showed that the best V1 neurons matched psychophysical performance closely, consistent with the lower envelope principle for relating neural activity to behavior” (Parker and Newsome, 1998), cf. (Geisler and Albrecht, 1997).

Furthermore, it needs to be noticed that the responsible laboratory technician falsely prepared the vertebrates’ brain slices in order to confirm the correct placement of the brain tubes for the knocking-out experiments. However, since the experimental tests and more important, the surgical procedures, were conducted in the same laboratory and with equal standards as those of Stoilova et al. (Stoilova et al., 2019), correct location of the brain tubes can be assumed.

6. CONCLUSION

Firstly, this work’s intention was to find answers about how well non-human animals adapt to changing environments by implementing asymmetric reinforcement to adaptive choice tasks, and secondly, get answers about which cortical areas are involved in doing so. Until now, many scientists used principles of SDT (Signal Detection Theory) or TT (Threshold Theory) to explain perceptual decision making. The current intention was to compare both theories and finally give a tendency which postulations are more plausible representing the outcome of this work. The first question about non-human animals’ performance concerning adaptive behavior could be quite easily answered: likewise with former scientists, this work showed that rats were well capable of reacting to asymmetric reinforcement, and even more, their performance almost matched that of ideal observers. In two experiments featuring different sets of reinforcement contingencies, the animals showed nearly optimal behavior, leading over to the question what theoretic background could best describe the shown behavior. While the literary debate described in detail that SDT stood for a continued shifting of criterion independent of a subject’s sensitivity to a signal, the TT was represented by static thresholds limited by the idea of one or more thresholds as e.g. postulated by LTT (low threshold theories) or HTT (high threshold theory). The results of this study showed that the subjects’ continuously shifting of criterion together with their almost perfect sensitivity to the given stimuli meant a maximization of rewards going along with what SDT postulated, and disagreeing with the idea of a static threshold as favored by TT. Nonetheless, current studies suggest that other non-sensory factors have to be further examined to wholly describe adaptive behavior.

Finally, the pharmacological experiments clearly showed that the mPFC (medial Prefrontal Cortex) played a major role in this task, however, there is more and more evidence that cortical areas do not solely represent certain behavioral traits, but that adaptive behavior is the outcome of many interconnecting neural systems and cortical regions. Therefore, much effort is needed to really get behind the fine neural networks representing the diversity of behavior, if yet possible.

Zusammenfassung

Diese Dissertationsschrift wurde verfasst, um erstens das Anpassungsverhalten von Versuchstieren bei asymmetrischem Belohnungsverteilung zu untersuchen, und desweiteren Informationen über die kortikale Repräsentation dieses adaptiven Verhaltens zu erhalten.
Im Rahmen der Literaturrecherche zeigte sich, dass bis dato zwei wesentliche Theorien genutzt wurden, um zielgerichtetes Verhalten in perzeptuellen Entscheidungsaufgaben zu erklären: einerseits die Signalentdeckungstheorie und andererseits die Schwellentheorie. Es machte also Sinn beide Theorien zu vergleichen und die wesentlichen Unterschiede herauszuarbeiten, um dann anhand der Versuchsergebnisse des im weiteren Sinne „Ja/Nein-Aufgabentyps" eine Tendenz über das theoretische Modell hinter adaptiven Verhaltens aufzuzeigen. Diese Versuchsergebnisse bestätigten die in kürzerer Vergangenheit durchgeführten Studien mehrerer auf diesem Forschungsgebiet tätigen Wissenschaftler, nämlich das durchweg sehr gute Anpassungsverhalten der Versuchstiere auf asymmetrische Belohnungsverteilungen. Schaute man sich die Reaktionen der Tiere genauer an, fiel auf, dass diese im Sinne der Signalentdeckungstheorie ihr Entscheidungskriterium je nach Belohnungsverteilung kontinuierlich veränderten, ihr Verhalten also nicht nach Schwellenwerten ausrichteten. Dies wiederum führte dann auch zu der in der Signalentdeckungstheorie beschriebenen Belohnungsmaximierung. Auch wenn die Ergebnisauswertung dieser Dissertation zur Signalentdeckungstheorie tendiert, konnte diese nicht alle beobachteten Verhaltensweisen der Versuchstiere erklären (z.B. das „Overshooting" Verhalten, s. Text). Es ist also davon auszugehen, dass weitere, nicht-sensorische Faktoren, wie z.B. Motivation, für adaptives Verhalten mit verantwortlich sind.
Die zweite Fragestellung beschäftigte sich mit der kortikalen Repräsentanz adaptiven Verhaltens. Mithilfe von Muscimol, einem GABA-A-Rezeptor Agonist, konnte die Funktion des medialen präfrontalen Kortex selektiv geblockt und so dessen Rolle im Hinblick auf adaptives Verhalten näher beleuchtet werden. Hierbei zeigte sich, dass der mediale präfrontale Kortex das Anpassungsverhalten der Versuchstiere durchaus beeinflusst. Aktuelle Studien machen allerdings deutlich, dass Verhaltenseigenschaften immer durch mehrere Kortizes – nicht nur durch einen einzigen - abgebildet werden. Es bedarf also eingehender Forschungen, um die komplexen Zusammenhänge tierischen Anpassungsverhaltens grundsätzlich zu verstehen.

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