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(Things you do not expect happen more often than  
things you do expect) Plautus (ca 200(B.C.)

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IST - Priority 2

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Learning-Induced Plasticity in Cortical Receptive Fields

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| PP  | Restricted to other program participants (including the Commission Services)          |   |
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## D4.3 LEARNING-INDUCED PLASTICITY IN CORTICAL RECEPTIVE FIELDS

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***Abstract:***

The aim of this deliverable was to address the problem that in the literature two different forms of learning-induced retuning of neurons in auditory cortex have been reported: best frequency shifts and local spectral sensitivity enhancements. A rationale was developed to dissociate the functional implications of these two forms of learning-induced plasticity and an experiment was designed to test the specific hypothesis that best frequency shifts are particularly suited for retuning cortical neurons in detection tasks and local spectral sensitivity enhancements for retuning the neurons in discrimination tasks. First experimental results in accord with this hypothesis are presented and discussed.

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## 1. Introduction

The aim of this deliverable is to report on the development of a rationale and experimental approach to address the phenomenon of task-specificity of learning-induced plasticity in receptive fields of cortical neurons. Work in DIRAC focuses on this problem as it represents an example of "top down" processing, an element of "cognitive loops", as introduced in DIRAC's general framework. The work reported here is based on technical developments achieved in workpackage 2 (see deliverable D2-2) and provides the basis for the treatment of physiological correlates of rare event processing on the "microscopic scale" as will be conducted in workpackage 5<sup>1</sup>.

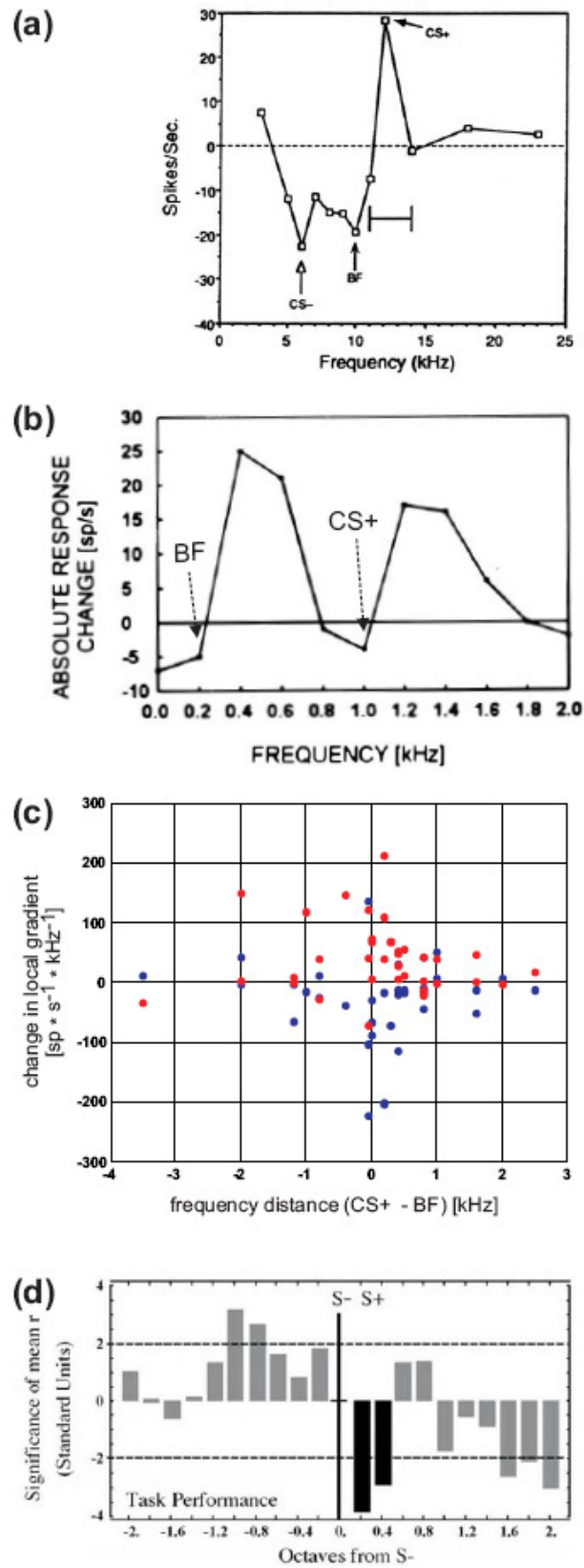
## 2. Background

In the early 1980s it was generally assumed that the tuning characteristics of primary auditory cortical neurons, while being adaptive during development, were stable and unmodifiable in the adult brain. This view was part of more general, usually implicitly held, conjecture about the physiological correlates of learning and memory and the brain: It was believed that physiological mechanisms underlying learning and memory are located in "higher centers" of the brain and operate (among other things) on "sensory representations", the latter being conceived as faithful representations of physical stimulus parameters and provided to the rest of the brain by primary sensory cortices. It was one of the major discoveries in sensory neuroscience that stimulus representation in the primary sensory cortices in the adult brain is in contrast modifiable as a consequence of either altered input, e.g. by injury of peripheral structures of the sensory system (compensatory plasticity) or by processes that alter the subjective relevance of certain sensory inputs (learning plasticity). For the case of learning-induced plasticity this was achieved by metabolic labeling techniques (Gonzalez-Lima and Scheich 1986) and electrophysiological recording (Weinberger and Diamond 1987).

The major result at this time was that when an animal learned about the special relevance of a selected tone frequency using a standard conditioning paradigm a subset (40% - 60%) of units showed a partial or complete shift of their best frequency (the tone frequency that elicited maximum firing rate) to this training frequency occurred. This result is exemplified in Fig. 1a, where the difference of tuning functions (post-training minus pre-training) of cortical unit is demonstrated (from Edeline and Weinberger 1993). This unit had a pre-training best frequency of 10 kHz and was conditioned to a 12 kHz tone. Apparently, training led to a frequency-specific increase of firing probability for the training frequency and much smaller increases or decreases at all other frequencies including the pre-training best frequency. This phenomenon, called the best frequency shift, has been considered the physiological correlate in sensory cortex of the learning about a special relevance of a pure tone frequency (Weinberger 2004).

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<sup>1</sup> In the first 18 months, workpackage 5 deals with correlates of rare event processing on the so-called "mesoscopic scale" (cf. Freeman 2000) represented in neurophysiological research by electroencephalographic and local field potential data.



**Figure 1.** Different forms of frequency-specific learning-induced tuning changes in auditory cortical neurons reported from several laboratories. (a) Change of firing rate as a function of pure tone frequency of a unit in guinea pig auditory cortex after tone–shock frequency. Retuning resulted from

maximally increased firing probability at the training frequency (CS+) and less increased or decreased firing probability for all other frequencies (including a test CS- frequency) (after Edeline and Weinberger 1993). (b) Change of firing rate as a function of pure tone frequency of a unit in gerbil auditory cortex after a multiple frequency discrimination experiment. Training involved presentation of one reinforced frequency (CS+) and all those frequencies that were used for the construction of the tuning function as CS- frequencies thereby (i) controlling for contextual effects on tuning measurement that are induced by separation of training sessions and measurement sessions and (ii) allowing for non-stationary effects seen in prolonged measurements of receptive fields. In the shown unit, firing probability at the CS+ frequency and BF were hardly affected, but significant increases of firing rate occurred in the high- and low-frequency neighborhood of the CS+ frequency, placing the CS+ frequency in a local minimum of the response change curve (redrawn from Ohl and Scheich, 1996). (c) Enhancement of sensitivity for frequency changes in a population of units as a result of the type of retuning described in (b). Plotted are training-induced changes of the local slopes of the tuning function in the low frequency neighborhood (blue) and the high frequency neighborhood (red) of the CS+ frequency versus the frequency distance between the CS+ frequency and the best frequencies (BF) of the units. The predominantly negative and positive slope changes in the low and high frequency neighborhood of the CS+, respectively, indicate enhanced sensitivity for frequency change in accordance with the type of retuning exemplified by the response change curve in (b). Higher absolute values of slope changes on the ordinate for smaller frequency distances on the abscissa reflect a larger 'dynamic range for change' near the best frequency of a unit. Across the population of units the described enhancement of sensitivity for frequency change was generally found to be independent of the magnitude and direction of response changes at single frequencies. (d) Retuning statistics from an experiment by Witte and Kipke (2005), see text. From Ohl and Scheich (2005).

In the 1990s a second type of learning-induced retuning of receptive fields of auditory cortical neurons was described by Ohl and Scheich (1996, 1997). This study was designed to better control fulfillment of stationarity conditions required for testing learning-induced changes of firing probabilities against trial-to-trial variability of firing rates as well as long-term stability of firing rate estimates obtained in consecutive stages of experiment as is typically done in this type of training experiments. The major result was that in individual units different forms of retuning occurred altering the local slope of the tuning function in the spectral neighbourhood of the training frequency, while not necessarily changing the tuning function at that frequency itself (Fig 1b). A population analysis revealed that whatever the specific form or retuning was for an individual unit, an increase of the tuning gradient in the local spectral neighbourhood of the training frequency was an invariant result of it (Fig. 1c). A similar type of retuning was recently described from auditory cortex of cats trained to detect deviance of two tone frequencies (S+) from a fixed target frequency (S-). In Fig. 1d significances of mean correlation coefficients ( $r$ ) are plotted between neuronal activity evoked by frequencies in the two-octave neighbourhood of the fixed target frequency S- and the behavioural frequency discrimination threshold. The distribution of mean correlations indicates that improved discrimination performance was paralleled by reduced firing probability at the S+ frequencies and increased firing probability for frequencies below S- (Witte and Kipke 2005).

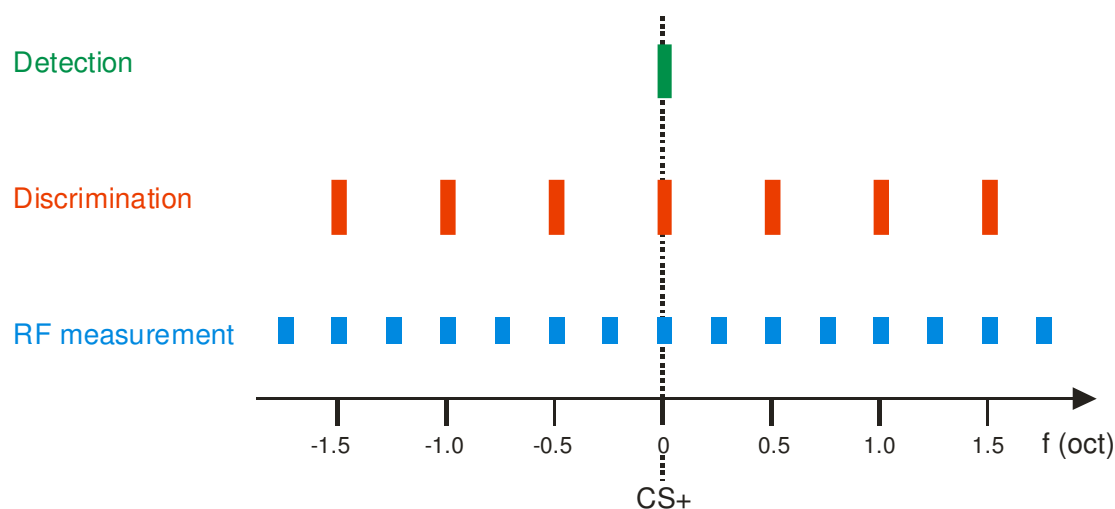
Hence, two different forms of learning-induced changes of receptive fields of neurons in auditory cortex have been described. The first type is a learning-induced shift of a cortical neuron's best frequency towards a frequency that has gained behavioral relevance in a classical conditioning task (for overview see Weinberger 2004). The second type is a local increase in tuning curve slope, i.e. spectral sensitivity, in the spectral neighbourhood of the conditioned frequency (Ohl and Scheich 1996). Previous work has indicated that detection-like and discrimination-like tasks lead to different forms retuning (Ohl and Scheich 1996, Fritz et al. 2005), and more generally that specific task demands of simple and higher forms of learning (Ohl et al. 2001) determine the precise form of retuning behavior.

### 3. Dissociating the Functional Implications of Best Frequency Shifts and Local Spectral Sensitivity Enhancements

Both types of learning-induced changes of cortical receptive fields have been discussed with respect to the functional concept of contrast enhancement. In relation to the best frequency shift type of receptive field reorganization, the concept of contrast enhancement is realized by the idea, that such a retuning facilitates neuronal responses to the tonal conditioned stimulus at the expense of other frequencies (Weinberger 2007)<sup>2</sup>.

From a theoretical viewpoint it has been argued (Ghose 2004) that at least under the assumption of a decision model in which discrimination is based on the comparison of a sum of neuronal responses such a type of receptive field retuning would reduce discrimination performance. This is because a tuning curve has zero slope at its peak, i.e. is least sensitive to changes in frequency. In fact, similar to previous findings in auditory cortex (Ohl and Scheich 1996, 1997), orientation discrimination training in the visual system has led to local steepening of orientation tuning curves in units of V1 (Schoups et al. 2001) and V4 (Raiguel et al. 2006), i.e. to a selective increase of discriminability around the trained orientation.

Therefore, somewhat contrary to the above sketched conceptualization associated with the best frequency shift, a suppression-based model of perceptual learning was proposed (Ghose 2004) that can account for both the selective slope increases and the findings of little changes, or reduced response strengths of neurons for trained stimulus parameters that have been reported in visual (e.g. Ghose et al. 2001) and auditory (Ohl and Scheich 1996, 1997; Beitel et al. 2003; Witte and Kipke 2005) experiments. Mechanistically it is not clear for any of these forms of retuning how modulated excitatory or inhibitory synaptic mechanisms are responsible for the observed effects, although several studies implicate the modulation of inhibitory systems (Ohl and Scheich 1996, 1997; Fritz et al. 2003, 2005); for a recent review of this issue see Irvine and Wright (2005).

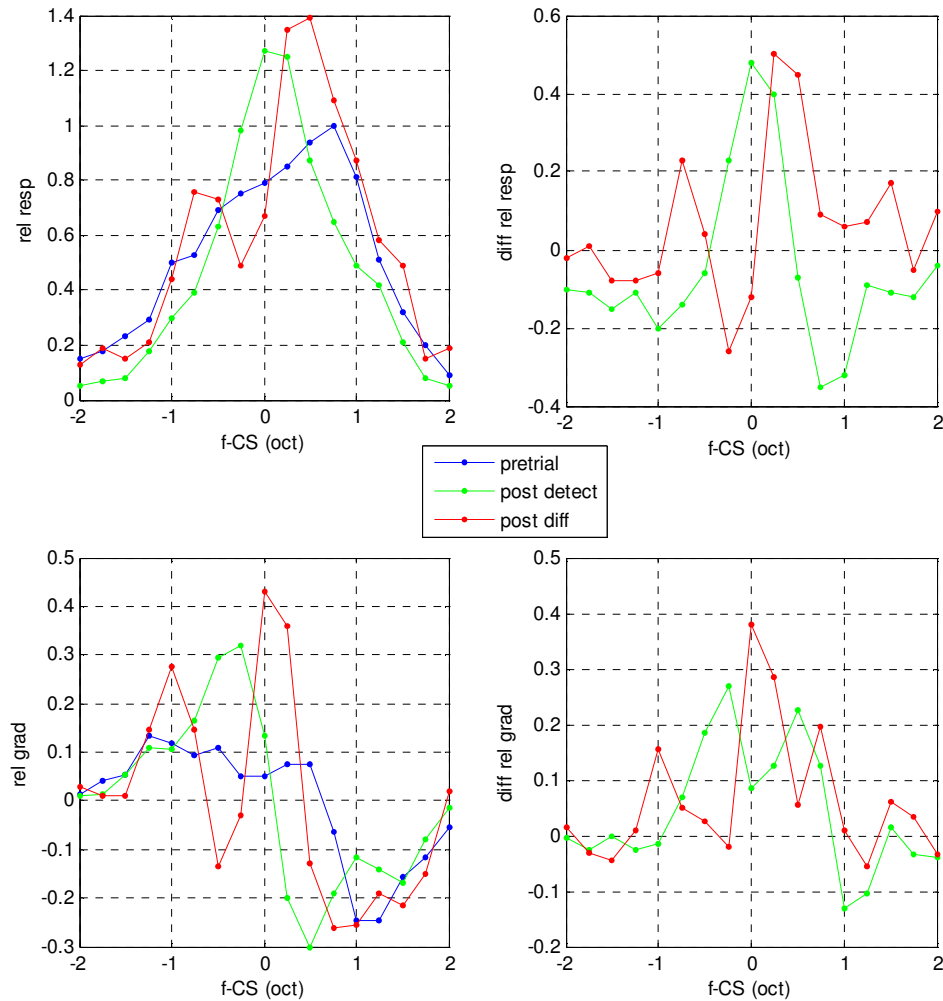


**Figure 2.** Stimulus design. After the best frequency of the unit was determined, a CS+ frequency was selected within its 1 octave neighbourhood. This frequency was used as the CS+ frequency in both the detection experiment (green) and the discrimination experiment (red). The discrimination experiment involved 6 additional CS- frequencies symmetrically arranged around the CS+ frequency in 0.5 octave steps. Prior to training the receptive field was characterized as an iso-intensity spike count

<sup>2</sup> A similar argument is used (Weinberger 2007) to interpret the functional relevance of increased map representations that were found in experiments with perceptual discrimination learning. See Irvine and Wright (2005) for overview and critique.

function measured at 15 frequencies symmetrically arranged around the CS+ frequency in 0.25 octave steps.

To directly test the hypothesis that detection learning and discrimination training would lead preferentially to best frequency shifts and local spectral sensitivity enhancement, respectively, we have performed a pilot experiment with two animals, each one implanted with a single electrode for chronic stable recording over several days. The relevant parameters of the experiment can be taken from Figure 2.

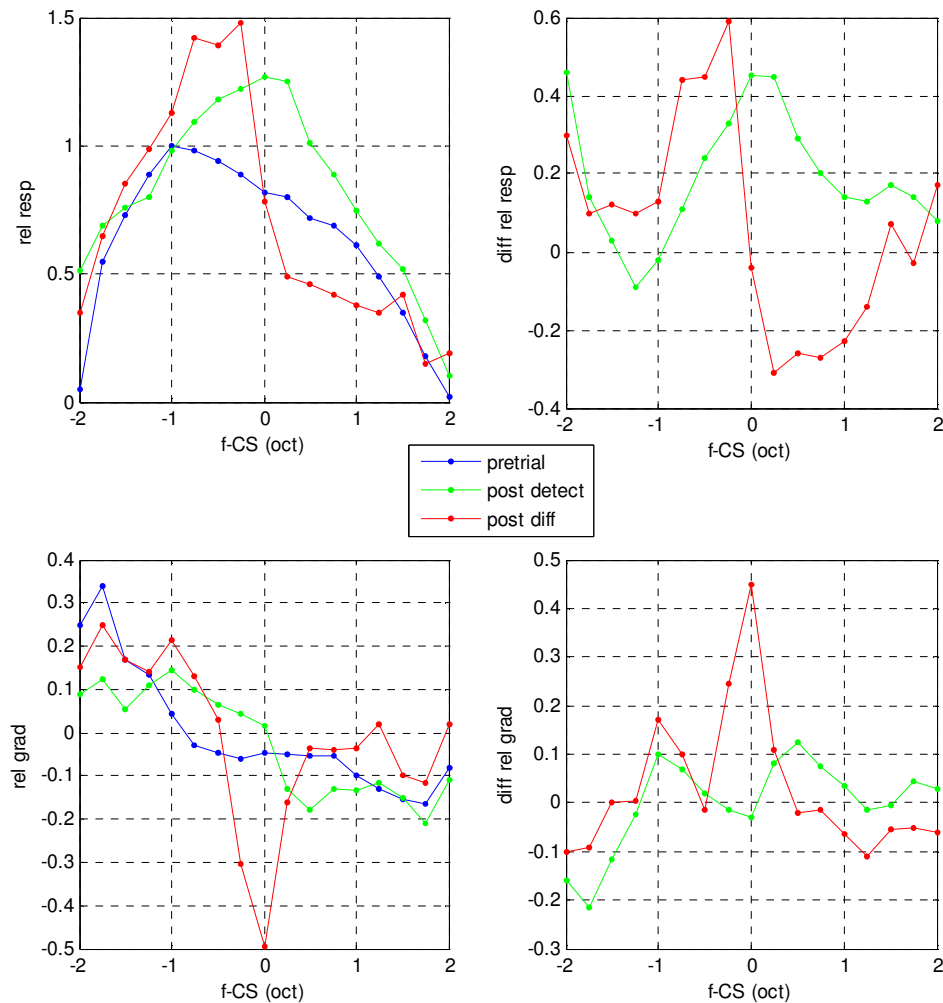


**Figure 3.** Experiment A. (Top left) Iso-intensity response functions ("tuning curves") prior to training (blue), after detection training (green) and after discrimination training (red). (Top right). Changes in firing rate (posttraining minus pretraining) after detection training and discrimination training, respectively. (Bottom left) Local spectral gradients of tuning curves. (Bottom right) Learning-induced changes in local spectral gradients of tuning curves. Tuning curves were normalized to firing rate elicited by the best frequency. Frequency is expressed as spectral distance to the CS+ frequency in octaves.

The first animal (experiment A) was first trained on a detection task using a GO/(NO-GO) procedure in a standard active avoidance shuttle box paradigm; see Ohl et al. (2001) for details of this procedure. After 8 sessions of training this animal was scheduled on a discrimination task which involved 8 sessions of training of a GO response on the same



training frequency (CS+), but 6 additional frequencies (CS-) to which NO-GO responses were required. False alarms (GO responses toward any of the CS- tones) were punished by mild foot shocks to the animal. In accordance with our previous studies, both behaviors were effortlessly learned. Figure 3 illustrates the result of the electrophysiological characterization of the recorded unit prior to recording (blue), after detection training (green), and after discrimination training (red). The top left panel shows that detection training indeed led to a maximally increased firing rate in this unit at the CS+ frequency and smaller increases or decreases of firing rate at other frequencies.



**Figure 4.** Experiment B. Panels as in Fig. 3. In this experiment the animal was first trained in the discrimination paradigm and subsequently in the detection paradigm. The results are similar to experiment A.

Discrimination training, in contrast, produced increased firing at a frequency 0.5 octaves above the CS+ frequency with rather modest effects on firing rate at the CS+ frequency and the unit's best frequency. This can be seen directly in the top right panel which shows the changes in firing rate as a function of frequency. The retuning after discrimination training must also be considered "specific" to the CS+ frequency, however, as the local tuning gradient ("slope of the tuning curve") has been maximally increased in the direct neighbourhood of the CS+ frequency. This can be seen in the bottom panels which show the

gradients (bottom left) and the training-induced changes in gradient (bottom right), respectively.

Figure 4 illustrates the results of experiment B, in which another animal was first training on the discrimination task and subsequently on the detection task. The dissociation between a best frequency shift towards the CS+ frequency after detection training and increased local spectral sensitivity after discrimination training, respectively, is again evident in the data.

While more cases are required for a more detailed statistical analysis these pilot experiments are in accordance with the posed hypothesis.

#### 4. A Further Issue Derived from Information-Theoretic Considerations

Implicit in the discussion about physiological correlates of learning in sensory systems are assumptions about the different roles of "tuning" and "tuning slope" for "coding" of sensory information. Using information theoretic approaches (e.g. Butts and Goldmann, 2006) it is possible to demonstrate that the mean specific information of a response can have local and absolute maxima both over the peak and slopes of the tuning curve, depending on the variance of the response. This can be seen by studying the stimulus-specific information  $i_{SSI}(s)$  as a function of stimulus parameters for various values of the response variance. The  $i_{SSI}(s)$  is derived from the specific information of a response  $i_{sp}(r)$  which is the difference between the entropy of the stimulus ensemble  $S$

$$H(S) = -\sum_s p(s) \log p(s)$$

and the entropy of the stimulus distribution conditional on a response  $r$

$$H(S | r) = -\sum_s p(s | r) \log p(s | r)$$

i.e.

$$i_{sp}(r) = H(S) - H(S | r).$$

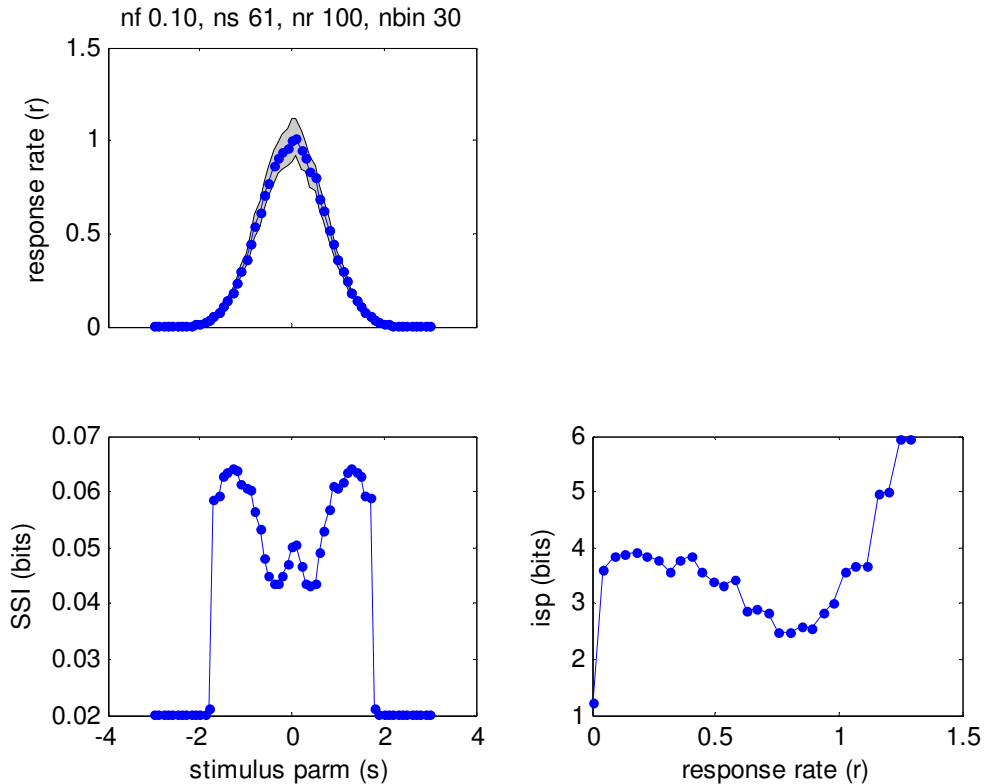
The  $i_{SSI}(s)$  is then the average specific information of a response when the stimulus  $s$  is present:

$$i_{SSI}(s) = \sum_r p(r | s) i_{sp}(r)$$

Figures 5 and 6 show the result of a numerical simulation of a Gaussian shaped tuning curve and 100 repetitions of tuning curve "measurement" with low variance (Fig. 5) and high variance (Fig. 6). Variance of the "measured" responses were controlled by a noise factor  $nf$  that introduced normally distributed noise to a hypothetical noise-free response  $r_0$  yielding a noise-contaminated response  $r$

$$r = r_0 (1 + nf \cdot randn)$$

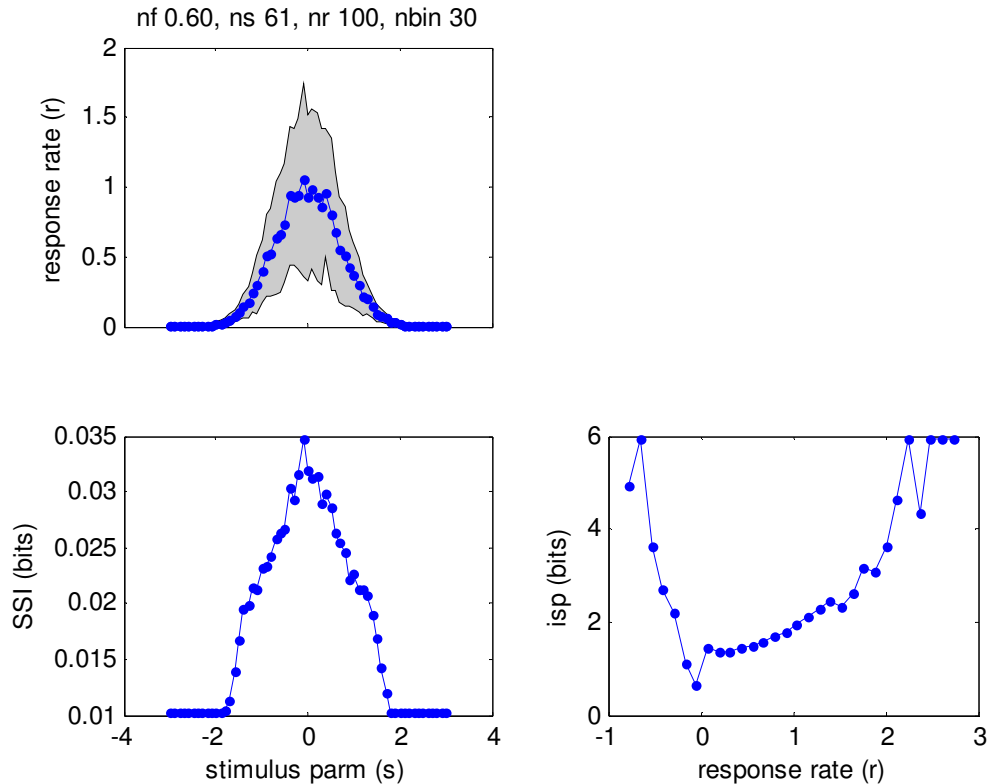
in which  $randn$  is a Gaussian random variable with zero mean and unit variance.



**Figure 5.** Specific information of tuned neuronal responses. (Top) The panel shows a simulated tuning curve (average normalized response rate, blue) and standard deviation of responses (grey) using a noise factor of  $nf=0.1$ . (Bottom left) Average specific information in that case. (Bottom right) Specific information as a function of normalized response rate. The absolute maximum occurs for relative response rates  $> 1$  as they are most likely caused by stimuli close to  $s=0$ .

As is intuitively evident, the average specific information is maximal at high slope regions of the tuning function when noise is small ( $nf = 0.1$ ). When noise is increased, the peak of the average specific information over the tuning curve peak is more and more increased and the peaks over the tuning curve's slope are decreased until the central peak becomes the absolute maximum of  $i_{SSI}$ .

Such behaviour is quite robust among many noise models (Butts and Goldman 2006).



**Figure 6.** Experiment B. Panels as in Fig. 3. In this experiment the animal was first trained in the discrimination paradigm and subsequently in the detection paradigm. The results are similar to experiment A.

## 5. Conclusion

Current theoretical concepts about the nature and precise forms of cortical receptive field retuning (for discussion see Ohl and Scheich, 2005) must be modified to account for the here demonstrated task-dependent effects (Scheich et al. 2007). An improved theoretical framework about the nature and role of cortical receptive field retuning is currently elaborated.

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