DRAC

Detection and Identification of Rare Audiovisual Cues

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DIRAC

Detection and Identification of Rare Audio-visual Cues

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Learning-induced plasticity in cortical dynamics

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D̈RAC

Detection and Identification of Rare Audiovisual Cues

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D4.10 LEARNING-INDUCED PLASTICITY IN CORTICAL DYNAMICS

Leibniz Institute for Neurobiology (LIN)

Abstract:

In the present deliverable we investigated stimulus-related ("bottom-up") and task-related ("top-down") aspects of gamma-band local field potential oscillations in rodent (gerbil) and human auditory cortex. A two-dimensional stimulus set of linearly frequency modulated tones with the dimensions "spectral content" and "modulation direction" was used in an auditory target detection experiment. Both rodent and human data indicate that late (>100 ms) total gamma-band activity (but not early evoked gamma-band activity) induced by a stimulus scales with the similarity of that given stimulus to a trained (rodent) or explicitly denoted (human) target stimulus. The rodent data additionally demonstrate how the relative amplitude of the late total gamma response compared to the gamma activity induced by non-target stimuli grows with acquisition of the learning task from a near-naïve to a well-trained stage of performance.

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1.   Introduction

Stimulus-related cortical activity in the gamma band (>30 Hz) has been described in both
human and animal species, where in the latter case control of non-neuronal bioelectric activity
is easier to achieve (Fries et al. 2008; Yuval-Greenberg et al. 2008). Apart from artefactual or
merely epiphenomenal origins (Jürgens et al 1995), gamma band responses have also been
discussed as potential correlates of information processing and cognition like selective
attention, short-term memory or long-term memory. In order to address the diversity of
proposed functions for gamma-band activity in a more coherent fashion, a framework was
recently proposed (Herrmann et al. 2004) in which two generic processes, (1) the comparison
of stimulus-related information with memory contents and (2) the utilization of signals
derived from this comparison, are considered elemental to various cognitive functions. This
"match-and-utilization model" assumes early (~100 ms) gamma-band activity to reflect
neuronal interaction processes underlying the "match" operation and later (~300 ms)
processes to reflect "utilization"-related operations. It is a prediction of this model that
gamma-band activity would be modulated by the number of features that have to be compared
during successful match-and-utilization operations.
For this deliverable we have carried out a target-detection task in analogous fashion in
animals (Jeschke et al. 2008) and humans (Lenz et al. 2008) to exploit the complementary
advantages of rodent and human subjects, viz. easy intracerebral recording from primary
sensory cortex and monitoring of learning effects on gamma-band activity in the rodent
experiment, and whole scalp accessibility of EEG signals and straightforward instruction of
subjects in the human experiment.

2.   Methods

2.1. Stimuli

As stimuli, both studies employed linearly frequency-modulated tones, because animal lesion
studies have demonstrated that the discrimination of rising and falling frequency-modulated
tones, traversing the same frequency interval is dependent on intact primary auditory cortex
while, for example, discrimination of pure tone pitches is not (Ohl et al. 1999). Furthermore,
in the rodent preparation we aimed at recording and analyzing data from both left and right
auditory cortex as lesion studies in rodents have implied a preference of right auditory cortex
for the processing of frequency-modulated tones (Wetzel et al. 2008). Four linearly
frequency-modulated tones (one being a target) were used as stimuli (Fig. 1). All stimuli were
digitally synthesized (44.1-kHz sampling rate, 16-bit dynamic range) with 5 ms rise/decay
times and presented after digital-to-analog conversion using an analog output card (National
Instruments, Munich, Germany) from a loudspeaker mounted in the middle of the shuttle box
roof at moderate levels of 65 dB SPL.

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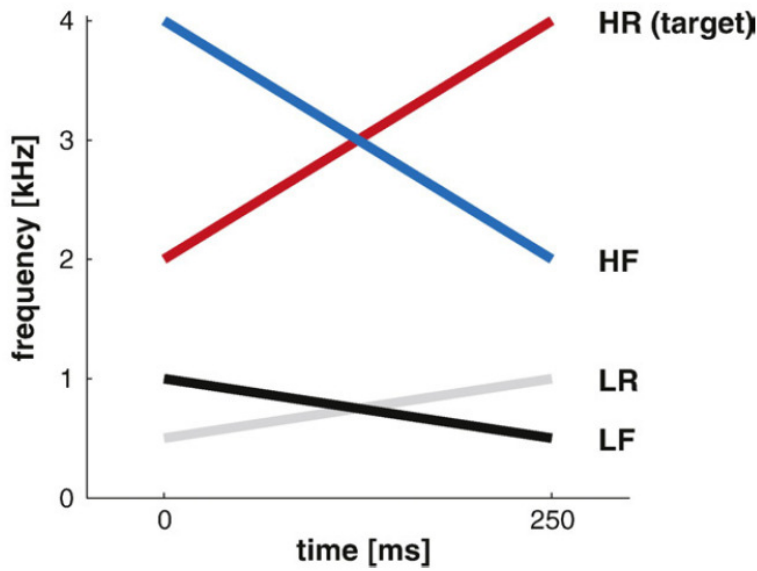things you do expect)   Plautus (ca 200(B.C.)

Figure 1. Illustration of the 4 linearly frequency-modulated tones used as stimuli in the training task. Stimuli traversed either a high (H) or low (L) frequency interval in a rising (R) or falling (F) fashion, and can therefore be identified by the abbreviations (HR, HF, LR, and LF, respectively). Stimulus HR was selected to be the target stimulus. The color code for the stimuli will be used throughout this report.

2.2. Training procedure

Animals were trained in daily sessions on 5 to 7 days a week using a GO/(NO-GO) procedure in a mouse shuttle box (Coulbourn Instruments, Allentown, PA, USA) with a 6-cm-high hurdle between the two compartments. Mild electric footshock (300–500 μA) applied through the grid floor of the shuttle box served as unconditioned stimulus (US). Acoustic stimuli were presented for 6 s as sequences of the individual stimuli (250 ms length followed by 250 ms silence). Presentation of the target stimulus was terminated immediately after the animal switched the compartment (hit). If no hurdle-crossing occurred during the 6-s time window (miss) a US was applied for 6 s or until the animal switched the compartment. If the animal crossed the hurdle during the 6-s time window of non-target presentations (false alarm) the sound was not terminated and a US was applied for 6 s. Each stimulus was pseudo-randomly presented 18 times during a training session, leading to a total of 72 trials in each training session. Conditioned hit rates and false alarm rates were recorded in each training session. Discrimination performance was quantified by the non-parametric sensitivity index SI defined as

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$$SI = \frac{h-f}{2(h+f)-(h+f)^2}$$

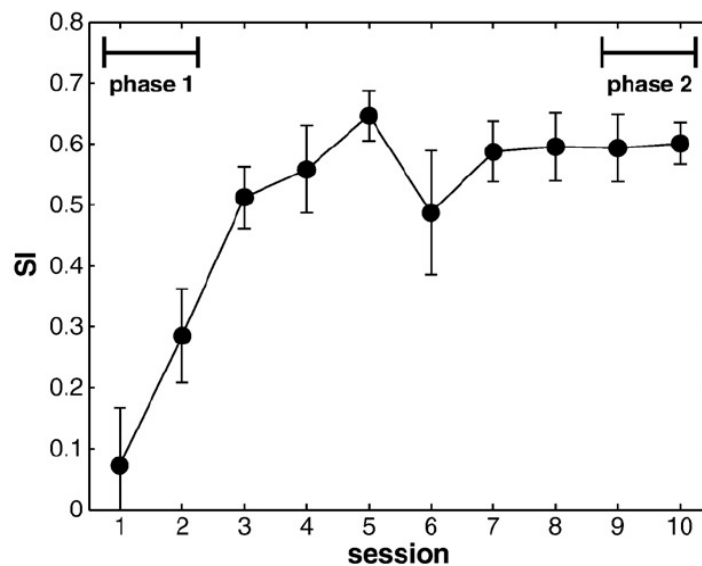with h and f representing hit rate and false alarm rate, respectively.

Figure 2. Development of discriminability index SI for the target discrimination against three non-target stimuli with training. Mean values (±S.E.M.) (n=8) were plotted over training session index. For further analysis, the training sessions are grouped into an early "phase 1" corresponding to gradually increasing target discrimination performance and a later "phase 2" corresponding to asymptotic performance.

3.   Results

3.1. Basic results

Animals (Mongolian gerbils, *Meriones unguiculatus*) were implanted for recording local field potentials from left and right primary auditory cortex and subsequently trained with parallel electrophysiological recording in a two-dimensional auditory target-discrimination task. The task employed four linearly frequency-modulated tones (Ohl et al. 2001) of identical duration (250 ms) and intensity (65 dB SPL). Stimuli varied along the two dimensions "spectral content", specifying the frequency interval traversed by the modulation, which was either "high" (H, 2–4 kHz) or "low" (L, 0.5–1 kHz), and "modulation direction", which could be

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either "rising" (R) or "falling" (F) and are subsequently denoted "HR", "HF", "LR" and "LF",
respectively (Fig. 1). One stimulus (HR) was selected as target and animals were trained in a
GO/(NO-GO) two-compartment shuttle-box task to avoid a mild electric foot-shock via
crossing a low hurdle separating the two compartments in response to presentation of the
target. Misses (NO-GO responses to target stimuli) and false alarms (GO responses to non-
target stimuli) were punished by mild foot-shocks. Stimuli HF and LR share one of the two
stimulus dimensions with the target (viz. "spectral content" and "modulation direction",
respectively); stimulus LF differs from the target in both dimensions.

3.2. Behavioral results

Eight animals were trained to perform in a frequency modulation discrimination task.
Learning performance was assessed by the detectability index SI, which is a non-parametric
variant of the detectability index d' knownfromsignal-detection-theory (Frey and Colliver,
1973) showing higher robustness especially for small conditioned response rates Fig. 2 shows
the development with training of the mean detectability index SI in 8 animals. SI values
reached an asymptotic level of approximately 0.6 after the fourth training session. Learning
speed and asymptotic performance were comparable to previous discrimination experiments.
To dissociate stimulus-related from learning-related modulations of gamma-band activity in
the later analysis, we grouped the training sessions into a "training phase 1" (sessions 1–2),
characterized by a gradual increase in learning performance from a naïve behavioral state, and
a "training phase 2" (sessions 9–10), characterized by asymptotic performance (Fig. 2).
Analysis of the conditioned GO-response rates for the individual stimuli revealed a significant
increase for the target stimulus HR (two-tailed t-test, $p=10-4$) from training phase 1 to
training phase 2 and no significant changes for the other stimuli (HF: p=0.454; LR: p=0.451;
LF: p=0.664). A separate comparison of the change in false alarm rates fromtraining phase 1
to training phase 2 for the three nontarget stimuli revealed no significant differences (2-
factorial MANOVA with factors STIMULUS (HF, LR, LF) and PHASE (sessions 1–2,
sessions 9–10).

3.3. Evoked gamma-band activity

Tightly stimulus-locked gamma-bandactivity ("evoked" gammaband activity) was analyzed
using the wavelet-transform of the event-related potential (ERP). For the statistical analysis,
we used individual peak frequencies of the evoked gamma-band response which varied from
30 to 37 Hz across animals. We also normalized the data for all 4 stimuli with respect to the
maximumevoked gamma amplitude (set to the value 1.0) within each animal to compensate
for individually different average gamma amplitudes. We investigated whether a target effect
on the evoked gamma-band activity known from the human literature (e.g. Debener et al.
2003) could also be demonstrated in the animal experiment. Therefore we compared the
amplitudes evoked by the target stimulus (HR) with the mean amplitudes across the non-
target stimuli. A 3-factorial MANOVA [with factors TARGETNESS (target, non-target),

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PHASE (training phase 1, training phase 2),HEMISPHERE (left, right)] did not reveal significant effects of the factors PHASE [F(1,7)=1.52, p=0.257] and HEMISPHERE [F(1,7)=0.00, p=0.983], but a trend for factor TARGETNESS [F(1,7)=5.45, p=0.052]. No significant 2- factorial or 3-factorial interactions were found. As we have argued above the small number of trials entering the statistical analysis when testing sessions 1–2 vs. 9–10 as phase 1 and 2, respectively, could possibly result in false positive results we additionally tested sessions 1–5 vs. 6–10 as phase 1 and 2, respectively. In this case no significant main effects or 2-factorial or 3-factorial interactions were found indicating that the trend found for factor TARGETNESS during the MANOVA of sessions 1–2 vs. 9–10 might be due to the small number of averages.
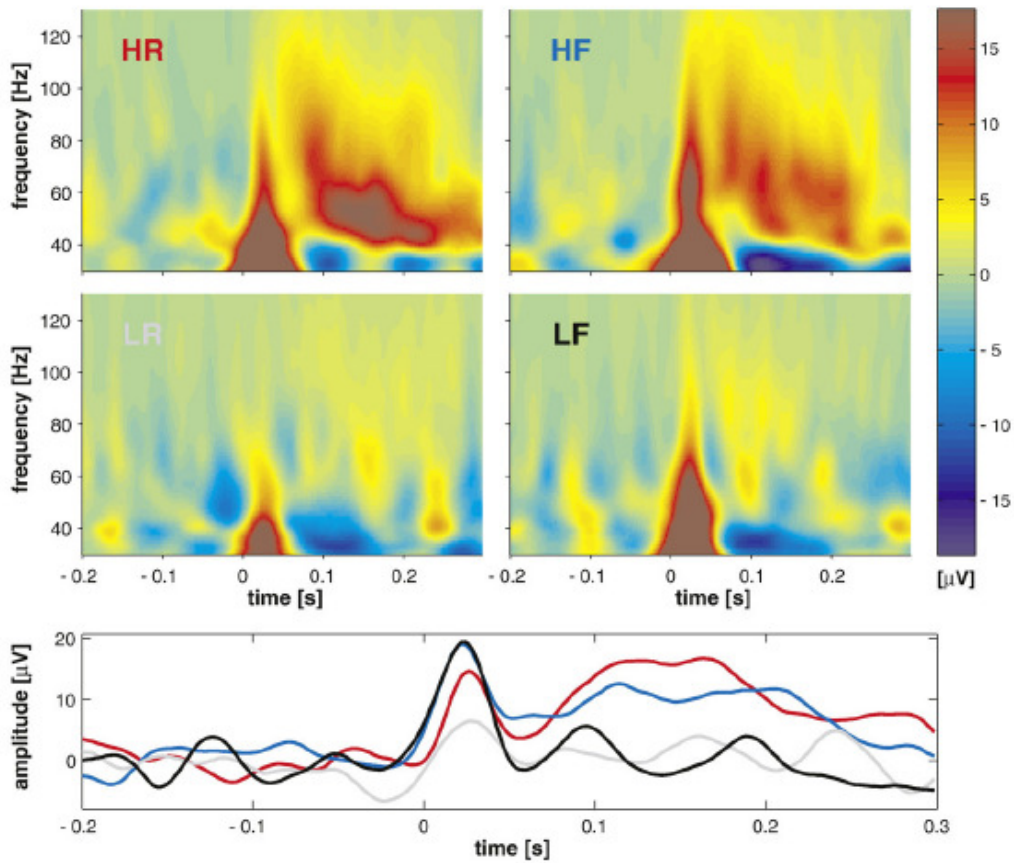

Figure 3. Grand-average of the total gamma-activity. The total gamma-activity was evaluated in the time window of from 100–250 ms post-stimulus. Panels were normalized between the minimum and maximum amplitude within the analyzed time window and across all stimuli. Top 4 panels: Time-frequency planes were plotted for the target stimulus HR and the three non-target stimuli HF, LR, and LF. The target HR and stimulus HF elicited similar total gamma amplitudes in the evaluated time window. Bottom panel: Time course of the grand-average peak. In the evaluated time window presentations of the target stimulus HR led to the strongest gamma amplitude.

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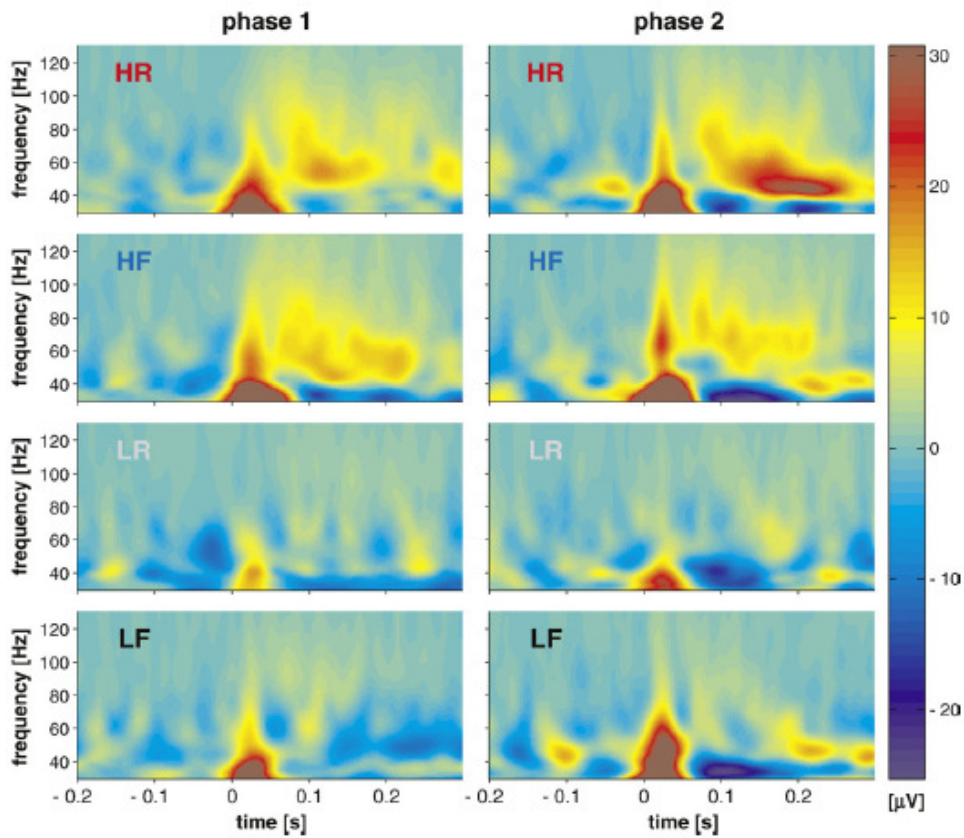things you do expect)   Plautus (ca 200(B.C.)

Figure 4. Illustration of the learning-induced effect on total gamma-band activity. Normalization of the panels were executed as in Fig. 3. In training phase 1 there is only a small difference between HR and HF. Both high frequency stimuli led to stronger total gamma-band activity as the low frequency stimuli. During learning phase 2 the difference between HR and HF was increased resulting in a clear separation of HR and HF.

3.4. Total gamma-band activity

Not strictly stimulus-locked late gamma-band responses were analyzed by averaging the absolute values of wavelet-transformed single-trial local field potentials ("total" gamma-band

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activity). The grand mean averages for the four different stimuli revealed a more or less extended region in the time-frequency plot of pronounced gamma-band activity in a time window of approximately 100–250ms and a frequency interval of 40–100Hz (Fig. 3). Inspection of data from individual subjects revealed that the peak frequency varied from 31 to 74 Hz in the left auditory cortex and from 45–64 Hz in the right auditory cortex. As for the analysis of the evoked gamma-band activity, the animal subjects' individual peak frequencies and normalization across stimuli have been used. In analogy to the analysis of the evoked gamma-band activity, we next investigated whether the total gamma-band activity would show a target effect as was also demonstrated in human experiments (Kranczioch et al., 2006). A 3-factorial MANOVA [factors TARGETNESS (target, non-target), PHASE (training phase 1, training phase 2), HEMISPHERE (left, right)] revealed a significant effect of factor TARGET [$F(1,7)=70.64$, $pb10-3$] and a trend for the interaction PHASE×HEMISPHERE [$F(1,7)=5.08$, $p=0.059$]. Post-hoc comparisons with Bonferroni correction revealed a clear target effect across training phase 1 and 2 (two-tailed t-test, $pb10-4$) with normalized gamma amplitudes elicited by the target stimulus (0.48 ± 0.01) exceeding those elicited by the non-target stimuli (0.19 ± 0.04). The interaction between factors PHASE and HEMISPHERE is given by an increase in normalized gamma amplitude in the left hemisphere between phase 1 and 2 (normalized gamma amplitude in phase 1: right hemisphere 0.31 ± 0.07, left hemisphere 0.13 ± 0.08; phase 2: right hemisphere 0.30 ± 0.07, left hemisphere 0.34 ± 0.05). We next investigated the total gamma activity for the four stimuli separately. This was suggested by the logic of the experimental design invoking four different stimuli expected to activate discernible neuronal populations in the tonotopic map of field AI (Ohl et al., 2000).
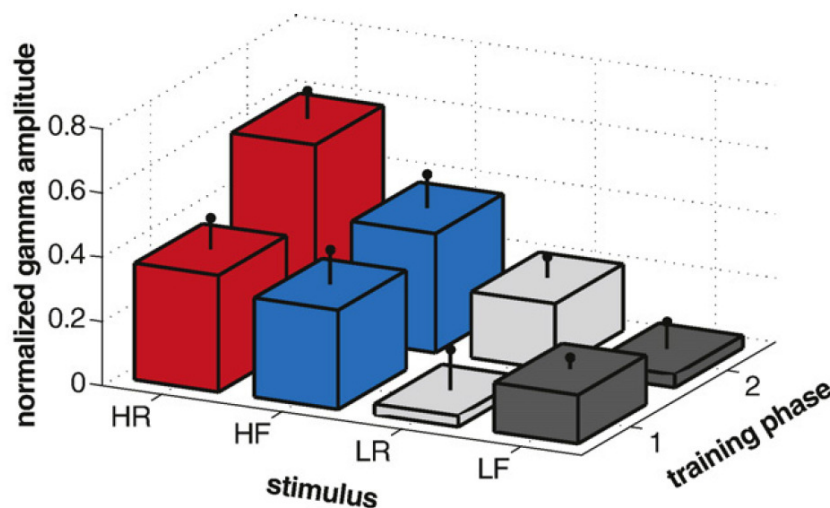

Figure 5. Analysis of total gamma-band activity elicited by the four stimuli in both training phases. The match-and-utilization model predicts that the strength of gamma oscillations depends on the

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similarity of a stimulus with the target. Accordingly, HR should lead to the strongest gamma-band activity, while HF and LR should lead to intermediate levels and LF to the lowest gamma-band activity. This dependence was visible during training phase 2, but not during training phase 1.

A 3-factorial MANOVA investigated the total gamma amplitudes relative to the mean value across all measurements in a given animal [factors STIMULUS (HR, HF, LR, LF), PHASE (training phase 1, training phase 2), HEMISPHERE (left, right)]. The analysis revealed a significant effect for factor STIMULUS [$F_{(3,5)}=70.43$, p b 10−3] and non-significant effects for factors PHASE [$F_{(1,7)}=0.65$, p=0.448] and HEMISPHERE [$F_{(1,7)}=0.81$, p=0.399]. A trend for the interaction STIMULUS×PHASE [$F_{(3,5)}=5.015$, p=0.057] as well as a significant interaction PHASE×HEMISPHERE [$F_{(1,7)}=15.41$, p=0.006] was also found (Fig. 4). Although post-hoc testing of a learning effect on total gamma amplitude separately for the four stimuli did not result in significant changes in gamma amplitude for learning (two-tailed t-test, p N 0.2 in all cases; compare with Fig. 7), it can be seen in Fig. 8 that there seems to be a gradient of gamma amplitudes with decreasing amplitudes the less features are shared by a given stimulus with the target. To investigate this possible dependency we performed a linear regression analysis for each learning phase separately. For phase 2 the regression analysis resulted in a significant relationship between the number of features shared with the target – i.e. stimulus HR shares 2
features with the target, namely modulation direction and pitch, stimulus HF and LR share 1 feature with the target and stimulus LF does not share a feature with the target – and the normalized gamma amplitude [$R^2=0.40$, $F_{(1,30)}=20.23$, p b 10−4]. In contrast no significant relationship was found for phase 1 [$R^2=0.06$, $F_{(1,30)}=2.09$, p=0.16]. Post-hoc investigations on the interaction PHASE×HEMISPHERE revealed a significant difference between the normalized gamma amplitudes observed in both hemispheres only during phase 1 (two-tailed t-test, p=0.048), with larger amplitudes found in the right hemisphere (0.32 ± 0.07 vs. 0.11 ± 0.09). No other significant differences were found across learning phases and hemispheres. Although both hemispheres can not be considered to be different in terms of the observed mean gamma amplitude during phase 2 it is well possible that both hemispheres contribute differently to the gradient of gamma amplitudes across stimuli. We tested possible differences using regression analysis separately for both hemispheres during phase 2. Though a significant relationship between the number of features shared with the target and the normalized gamma amplitude was found for both hemispheres [$R^2=0.31$, $F_{(1,30)}=13.42$, p b 10−3 and $R^2=0.2$, $F_{(1,30)}=7.62$, p=0.01 for the right and left hemisphere, respectively], more variance was explained by the number of features shared in the right hemisphere. In contrast no significant relationship was found during learning phase 1 [$R^2=0.07$, $F_{(1,30)}=2.3$, p=0.14 and $R^2=0.02$, $F_{(1,30)}=0.74$, p=0.4 for the right and left hemisphere, respectively].

4.   Discussion

The target-discrimination task used linearly frequency-modulated tones as stimuli which were varied with respect to two stimulus dimensions, viz. "spectral content" and "modulation

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direction". This allowed construction of non-target stimuli which matched the target stimulus in either one or none of these dimensions. This architecture allowed further testing of a recently suggested framework to address a variety of functions associated with gamma-band activity from a coherent viewpoint (Herrmann et al. 2004). This framework suggests neuronal operations mediating the hypothetical cognitive processes of matching a stimulus with a memory content and using the stimulus according to the result of this match to operate in the temporal regime of the gamma-band. Consequently, one prediction of this framework with respect to the task investigated in the present study is that the amount of gamma-band activity should be maximal during successful processing of the target stimulus, intermediate during processing of non-target stimuli that match the target with respect to only one of the two dimensions, and minimal during processing of the non-target stimulus that match the target in neither dimension.

The analyses of total gamma-band activity revealed that maximum gamma-band amplitudes were induced by the target stimulus, and a learning effect could be observed. Furthermore, we found a linear correspondence between total gamma amplitude and the number of features that a given stimulus shared with the target. This linear relationship developed with learning andwas not found innaïve animals.We interpret these findings as an interaction of bottom-up and top-down factors modulating the total gamma-band activity in a similar way as was described previously for evoked gamma-band activity (Busch et al., 2006). Analyses of variance indicated that the dominant bottom-up effect on total gamma amplitude is contributed by the physical nature of the stimuli. The basic modulation of total gamma amplitude by the stimulus was similar in both hemispheres (Fig. 5) andresembled the amplitudemodulationof thedominant ERP components thus accounting for the target effect found during training phase 1. This result is in good correspondence to studies about the three-dimensional organization (Sukov and Barth, 1998) and cellular mechanisms of generation (Sukov and Barth, 2001) of gamma oscillations in rat auditory cortex which indicate that auditory ERPs and gamma oscillations are produced by a common population of cells. The particular profile of both ERP component amplitudes and gamma amplitudes in the present study can be explained by the positioning of the intracerebral recording electrodes within the tonotopically organized field AI of primary auditory cortex (see Section 3.2). However, this bottom-up effect cannot explainthe significant redistribution of total gamma-band activity in response to the stimuli after the animals have learned the task. This effect was also absent for ERP amplitudes. We suggest that the redistribution of the amplitudes of total gamma-band activity resulting in graded responses accordingto the similarity of the stimuluswith the target represents a top-down effect which was described recently. This interpretation would be in line with that of the companion paperwhere an almost identical experimenthas beencarried out inhumans(Lenz et al., 2007-this issue) as well as with the abovementioned predictions of the match-and-utilization model (Herrmann et al., 2004). Interestingly, the peak frequency of the gamma oscillations showing a graded modulation by target similarity was different in the experiments on gerbil (~40 Hz) and human auditory cortex (Ν100 Hz). Although the two recording setups did not have identical frequency transfer functions, it is unlikely that such a difference has contributed to the differing frequency ranges reported. While different transfer characteristics of the setups would differentiallyweigh different frequency ranges of a signal, they cannot explain that the

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reported modulation of activity by target similarity would occur at different ranges. It is therefore more likely, that species differences account for this observation. Species differences have also been reported for spontaneous EEG (Bressler and Freeman, 1980; Bullock, 2003), their anatomical and physiological causes are not well understood. The observed learning effect might be explained by the behavioral data. During training phase 1 animals still performed suboptimally (cf. Fig. 2) while the performance approached an asymptotic maximum during training phase 2. Thus, one might speculate that animals reveal erroneous behaviour as long as the target stimulus to which they have to react does not induce more total gamma-band activity than the three non-target stimuli to which they do not have to react. The prominence of the linear relationship between number of features shared and total gamma amplitude in the right auditory cortex might be a consequence of a right-hemisphere preference for processing frequency modulated tones as previously demonstrated by lesion experiments in gerbil (Wetzel et al., 1998a) and rat auditory cortex (Rybalko et al., 2006). However, further experiments are needed to clearly disentangle the relative roles of both hemispheres during targetdiscrimination tasks.

5.   Conclusion

The correspondence of the amplitude of total gamma-band activity with behavioral performance status in a target discrimination task during the learning history and the pattern of gamma-band activity with respect to cortical hemisphere convergently imply a functional role of gamma oscillations in cognitive top-down processes recruited during task-discrimination beyond mere stimulus-related bottom-up effects.

6.   Reference

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