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Improving audio-visual temporal perception through training enhances beta-band activity

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A B S T R A C T

Multisensory integration strongly depends on the temporal proximity between two inputs. In the audio-visual domain, stimulus pairs with delays up to a few hundred milliseconds can be perceived as simultaneous and integrated into a unified percept. Previous research has shown that the size of this temporal window of integration can be narrowed by feedback-guided training on an audio-visual simultaneity judgment task. Yet, it has remained uncertain how the neural network that processes audio-visual asynchronies is affected by the training. In the present study, participants were trained on a 2-interval forced choice audio-visual simultaneity judgment task. We recorded their neural activity with magnetoencephalography in response to three different stimulus onset asynchronies (0 ms, each participant's individual binding window, 300 ms) before, and one day following training. The Individual Window stimulus onset asynchrony condition was derived by assessing each participant's point of subjective simultaneity. Training improved performance in both asynchronous stimulus onset conditions (300 ms, Individual Window). Furthermore, beta-band amplitude (12–30 Hz) increased from pre-compared to post-training sessions. This increase moved across central, parietal, and temporal sensors during the time window of 80–410 ms post-stimulus onset. Considering the putative role of beta oscillations in carrying feedback from higher to lower cortical areas, these findings suggest that enhanced top-down modulation of sensory processing is responsible for the improved temporal acuity after training. As beta oscillations can be assumed to also preferentially support neural communication over longer conduction delays, the widespread topography of our effect could indicate that training modulates not only processing within primary sensory cortex, but rather the communication within a large-scale network.

1. Introduction

Our perceptual system constantly receives input from multiple senses and has to combine this information into appropriate representations of the environment. Whether multisensory inputs are integrated into a unified percept or interpreted as separate events, depends on the spatial as well as the temporal proximity between the stimuli (Colonius and Diederich, 2004; Meredith and Stein, 1986; Meredith et al., 1987; Wallace et al., 1992). Research on the temporal bounds of this process has provided evidence for a temporal binding window (TBW) of a few hundred milliseconds during which the joint presentation of stimuli from different modalities results in interactions at the level of single cell activity (Colonius and Diederich, 2004; Meredith et al., 1987), perception (Shams et al., 2002; van Wassenhove et al., 2007) and behavior (Senkowski et al., 2007). The proposed rationale for this temporal variability between the senses is to compensate for the sensory modality-related differences in physical transmission time from source to receiver (Sugita and Suzuki, 2003). The size of this window varies across different stimulus types (Vatakis and Spence, 2010). It also differs between healthy individuals (Stevenson et al., 2012) and is significantly enlarged in people with certain neurobiological disorders (Chan et al., 2015; de Gelder et al.,2005, Foss-Feig et al., 2010, 2005; Hairston et al., 2005; Setti et al., 2011; Yalachkov et al., 2019). Recently, it has been demonstrated that the perception of audio-visual temporal simultaneity is related to pre-stimulus beta- and gamma-band power (Yuan et al., 2016). Interestingly, Powers et al. (2009) have demonstrated that this window can be significantly reduced by providing informative feedback during perceptual training on a simultaneity judgment task.

The neuronal mechanisms underlying this form of perceptual learning (e.g., training) remain uncertain. Previous research on perceptual learning has focused on the perception of simple features of unimodal stimuli (e.g. orientation, contrast, or frequency) and proposed adapted representations in primary sensory cortices (Karni and Sagi, 1991; Pantev et al., 1998; Pleger et al., 2001; Recanzone et al., 1993), an upgraded readout of the sensory information in decision-making areas (Law and Gold, 2008; Dosher et al., 2013; Petrov et al., 2005), or top-down influences (Ahissar and Hochstein, 2004) as potential causes for the learning effects. How these findings can be transferred to multisensory

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learning, such as improving audio-visual temporal perception has yet been rarely examined (Powers et al., 2016). Indeed, Setti et al. (2014) found that extensive training of older adults for five days on a temporal order judgement (TOJ) task did improve the veridical perception of the sound-induced flash illusion (i.e., participants perceived fewer illusory flashes, likely because their temporal binding window narrowed). However, it is important to note that approximately only half of the participants improved in the TOJ task while the remaining half did not improve. Investigating the neural correlates of perception in these tasks can lead to an improved understanding of perceptual training.

An investigation with fMRI revealed that improved post-training performance on a simultaneity judgment task was accompanied by decreased blood-oxygen level dependent (BOLD) signals in the primary visual and auditory cortices and in the superior temporal sulcus (STS; Powers et al., 2012). Dynamic causal modelling showed more distributed effective connectivity between early sensory areas and posterior STS in the post-training compared to the pre-training block. It is important to note that these BOLD activity changes were only found in the conditions where the auditory and visual stimuli were either presented simultaneously or were clearly delayed (by 300 ms). Interestingly, there was no change in BOLD activity in the condition where participants actually exhibited a behavioural improvement. While this study provided important information about the areas in which activity is overall affected by the simultaneity judgment training, the type of information that is transferred between the involved areas remains unknown.

Neural oscillations in the beta and gamma frequency ranges are also associated with multisensory integration. Gamma and alpha/beta power can reflect feedforward signaling of unisensory information and feedback processing in multisensory integration regions, respectively (Balz et al., 2016; Cecere et al., 2015; see Keil and Senkowski, 2018 for a review). Evoked beta-band activity was enhanced by multisensory as compared to unisensory stimulus presentations (Kisley and Cornwell, 2006; Senkowski et al., 2006) and furthermore predicted the shortening of reaction times in response to multisensory stimuli, which suggests a role in multisensory facilitation (Senkowski et al., 2006). Additionally, Kayser & Logothetis (2009) identified bidirectional effective interactions (using Granger causality) between the STS and the auditory cortex in the beta frequency range while monkeys observed audio-visual scenes. The directed interactions from the STS to the auditory cortex contributed to multisensory enhancements in the auditory cortex, suggesting that beta oscillations play a role in inter-areal coupling in the temporal lobe during multisensory processing. Gamma oscillations are likely to be involved in integrating various stimulus features (Engel and Singer, 2001; Singer and Gray, 1995). In line with the finding that the temporal structure of multisensory information determines its integration (Colonius and Diederich, 2004; Shams et al., 2002; van Wassenhove et al., 2007), gamma-band responses were shown to be sensitive to the temporal alignment of multimodal stimulus components with higher multisensory effects for synchronously presented stimuli (Senkowski et al., 2007). Predictive coding, which is involved in the generation of multisensory illusions, is thought to be reflected by low-frequency power increases, e.g. in frontal cortex, and beta-band synchronization between frontal and sensory regions (Keil and Senkowski, 2018). Investigations in multisensory integration by means of perceptual illusions (e.g. sound-induced flash illusion, McGurk effect, rubber-hand illusion) report enhanced gamma-band responses for illusory as compared to non-illusory trials (Balz et al., 2016; Bhattacharya et al., 2002; Kaiser et al., 2005; Kanayama et al., 2007; Shams et al., 2005). More recently, it has been demonstrated that increased pre-stimulus beta-band activity is associated with the likelihood of perceiving the illusion (Keil et al., 2012; Keil et al., 2014a,b), suggesting some sort of top-down signalling. In addition, variations in sensory excitability as reflected by ongoing alpha power fluctuations seem to moderate the perception rate of the sound-induced flash illusion (Cecere et al., 2015; Keil and Senkowski, 2017). Furthermore, audio-visual voice-face integration enhanced coordination between spiking activity in the auditory cortex and gamma oscillatory activity in the STS (Ghazanfar et al., 2008). Indeed, it has been demonstrated in the macaque that there are early feedback and feedforward projections from the visual cortex to early auditory processing stages (Schroeder and Foxe, 2002).

More recently, the canonical microcircuit theory of predictive coding proposed that the brain is organised in templates (Arnal and Giraud, 2012; Bastos et al., 2012) with beta-band (12–25 Hz) oscillations delivering template information and gamma-band (>30 Hz) oscillations delivering prediction error information. It is hypothesized that informative perceptual training will reduce the number of prediction errors. Increases in gamma-band activity will represent updating of the template, accompanied by a decrease in beta-band activity (see Keil and Senkowski, 2018 for a review). However, once the template has been updated there should be a reduction in gamma-band activity. At the same time, training should improve the template for temporal binding that participants have for integrating audio-visual information. This should be evidenced by an increase in beta-band activity.

In this study, we exploited the high temporal resolution of magnetoencephalography (MEG) to record neural activity changes related to training on a simultaneity judgment task, comparing three different audio-visual onset asynchronies (0 ms, 300 ms, and the Individual Window, i.e., each participant's point of subjective simultaneity) before and one day after training. We hypothesized that participants will exhibit a narrower TBW following feedback training (post-training), compared to before training (pre-training). This perceptual improvement will be coupled with increased beta power in the post-training session. While we expected that the training should also comprise an increase in gamma-band power, this should occur during the training session, and not during the post-training assessment. Analysis of spectral power changes in the gamma (30–120 Hz) and beta (12–30 Hz) frequency bands, which are assumed to reflect feedforward- and feedback-signalling, respectively (Arnal and Giraud, 2012; Bastos et al., 2012; Bastos et al., 2015), should provide important indications about the direction in which information transfer in the sensory hierarchy is modulated by training.

2. Materials and methods

2.1. Participants

Twenty healthy adults (12 females, 20–38 years old) took part in the study. Four participants did not return for the post-training session and another was excluded due to behavioral performance at chance level, resulting in sixteen participants included in the behavioral analyses. For analysis of the MEG data two further subjects were excluded due to artefacts (i.e. excessive head movements). Thus, fourteen participants (10 females, 4 males) aged between 20 and 25 years were included in the final MEG analyses. All participants were right-handed and self-reported to have normal hearing and normal or corrected-to-normal vision. Participants were screened for MRI/MEG compatibility and written informed consent was obtained prior to the experiment. The experimental procedures were approved by the ethics committee of Goethe University Medical Faculty.

2.2. General procedure

The experiment took place over two consecutive days. On both days, participants performed a 2-interval forced-choice (2-IFC) audio-visual simultaneity judgment task (SJ) outside the MEG scanner to assess the size of their individual temporal binding window (TBW). After each behavioral assessment, participants performed the same task in the MEG scanner, but with only a subset of SOAs (including their 'Individual Window') to maximize the number of repetitions per condition. Following the first MEG session (pre-training; day 1), participants performed a single-bout training session. The following day, another behavioral assessment was performed. This was done to reassess their individual TBW. Following that, the second (post-training) MEG session

took place. See Fig. 1A for a timeline of the task order. Behavioral training was performed outside the MEG scanner for practical and financial purposes. However, we aimed to ensure that participants had similar viewing conditions (e.g. stimulus size, sound intensity, etc.).

2.3. Estimation of the individual window size

The 2-IFC audio-visual SJ task was adapted from Powers et al. (2012). In this task, participants indicated in which of the two intervals the audio-visual stimulus pair was presented synchronously by pressing either button 1 or 2 on a response pad (Cedrus RB-730). Behavioral testing took place in a dark and sound-attenuated chamber. Visual stimuli were displayed in the center of a computer monitor (Dell UltraSharp 1905 TFT display; resolution: 1280 × 1024 pixels, refresh rate: 60 Hz; response time: 20 ms; vertical scan range: 56–76 Hz) at a viewing distance of 50 cm. Auditory stimuli were presented to both ears via closed-back headphones (AKG K271 MK2) at an approximate sound pressure level of 60 dBA. Stimulus presentation was controlled using the Presentation software package (Neurobehavioral Systems).

A white fixation cross was presented against a black background in the center of the screen throughout the trial. The visual stimulus was a white annulus, surrounding the fixation cross, at 8.8° of visual angle. The auditory stimulus was an 1800 Hz tone burst. The duration for both the visual and auditory stimuli was 16 ms. The SOAs were all visual-leading

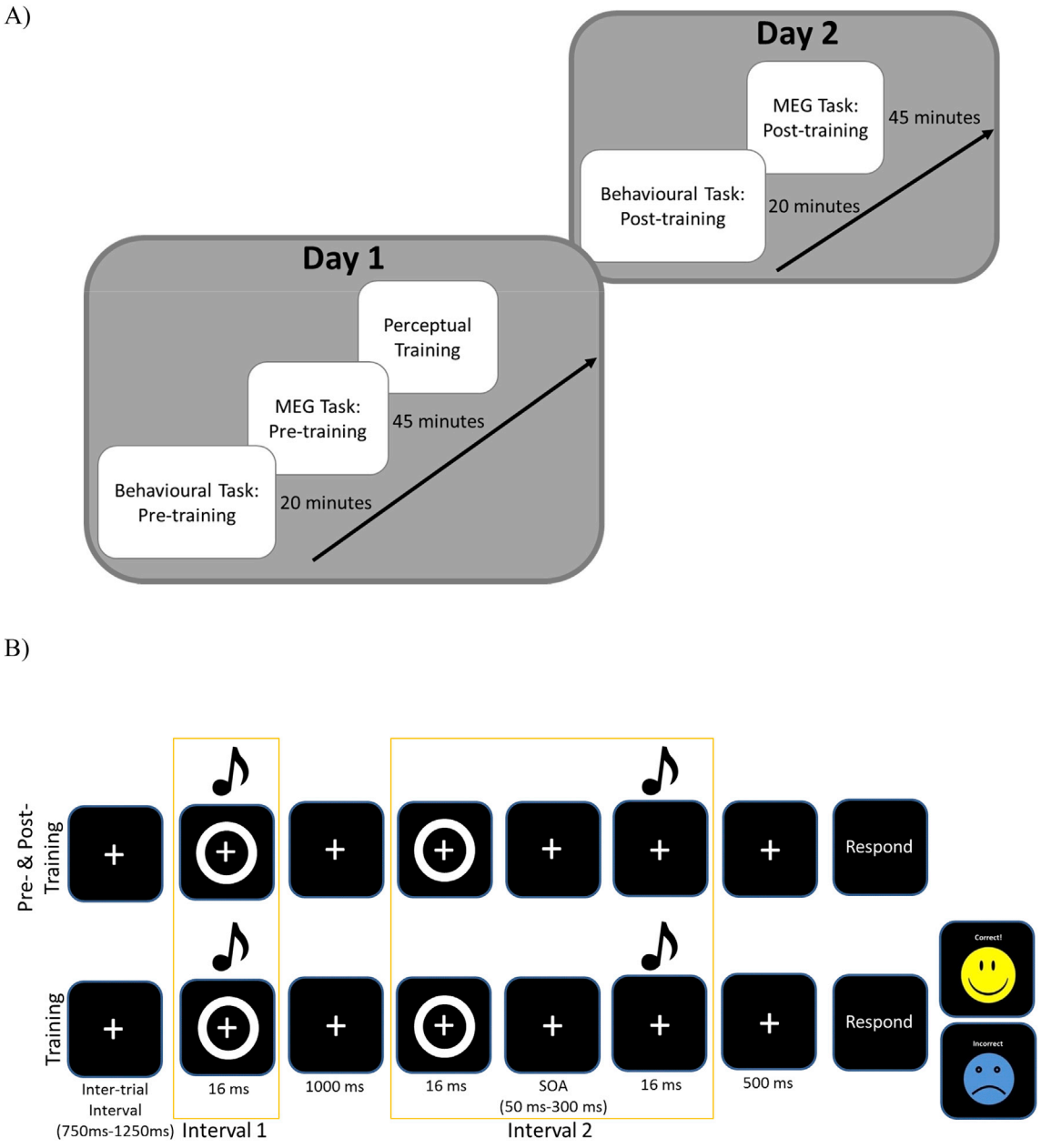


Fig. 1. A) A graphical depiction of the experimental time course and approximate duration of each task. B) Representative trial sequence of the 2-IFC task in behavioral assessments and training. Depicted is a 2-IFC trial with the synchronous pair in interval 1. One audio-visual stimulus pair was always presented simultaneously (SOA = 0 ms), while the other audio-visual pair was separated by an SOA ranging between 50 and 300 ms. In the asynchronous pair, the visual stimulus was always presented first. A condition whereby simultaneously presented stimuli occurred in both intervals, was not presented in the behavioural-only testing. Participants were asked to respond after every second interval to determine which of the two prior intervals contained the simultaneous pair (top). Training involved the same task but included feedback about the correctness of the participant's choice. Correct responses were followed by yellow faces, incorrect responses were indicated by blue faces (bottom).

and ranged from 50 to 300 ms in 50 ms increments. Auditory-leading stimuli were not presented because it was demonstrated previously that the TBW for those stimuli is not reduced by behavioral training (Powers et al., 2009). Intervals 1 and 2 were separated by a delay of 1000 ms and the inter-trial interval was jittered between 750 and 1250 ms in 250 ms steps. The response screen appeared at 500 ms following interval 2 and displayed the question "Welches Paar war synchron?" (German for "Which stimulus pair was synchronous?") for a maximum of 2000 ms or until the participant responded, whichever came first. The simultaneous pair was equally likely to occur in the first or second interval. A condition whereby simultaneously presented stimuli occurred in both intervals, was not presented in the behavioural-only testing. Each SOA condition was randomly permuted and repeated 24 times. The presentation order (synchronous pair in 1st or 2nd interval) was randomized, preventing predictions about upcoming trials.

The raw data from each individual were used to calculate the mean accuracy at each SOA for both the pre- and post-training behavioral assessments. Individual mean data were fitted with a sigmoid curve (Weibull-model). The size of each participant's TBW was defined as the SOA at an accuracy level halfway between the individuals' lowest accuracy point at the behavioural assessment and 100%. Decreases in mean window size across participants were evaluated using a paired-samples *t*-test. In order to analyse how training affected performance in the different SOA conditions, we conducted a 2×6 repeated-measures ANOVA with the factors Training (pre- and post-training) and SOA (50 ms, 100 ms, 150 ms, 200 ms, 250 ms, 300 ms) with accuracy being the dependent variable. In order to test if the interval at which the asynchronous pair was presented affected accuracy, a $2 \times 2 \times 6$ repeated measures ANOVA was conducted with Training, Interval (1st and 2nd), and SOA as factors.

During the training session participants performed the same 2-IFC task but their responses were followed by informative feedback about the correctness of their choice. Fig. 1b depicts a timeline of each trial. Correct responses were indicated by a yellow happy face combined with the visual phrase "Richtig!" (German for 'correct') and incorrect responses were followed by a blue sad face combined with the visual phrase "Falsch" (German for 'incorrect'). These faces were displayed centrally for 500 ms. The training session included only the 50–250 ms SOA conditions. In the experimental session, each condition was repeated 40 times in a randomized order. The total session lasted approximately 30–35 min.

2.4. Behavioral control experiments

To ensure that improved behavioral performance on day 2 was not simply due to stimulus exposure, two additional behavioral control experiments were separately conducted. In the first control experiment, 16 participants (10 females, 19–32 years old) practiced the SJ-task according to the same training protocol but did not receive informative feedback. In the second control experiment, an additional 16 participants (10 females, 20–30 years old) were passively exposed to the audiovisual stimuli while performing a visual oddball detection task (10% oddballs: red instead of white annulus). In this experiment, participants pressed a button when a red annulus occurred. The same SOAs between the auditory and visual stimuli used in the previous experiments were also used in both control experiments. The effect of the training regime (Feedback, No Feedback, and Exposure) on behavioral performance was analyzed using a one-way between-subjects ANOVA.

2.5. MEG data acquisition and stimulus presentation

MEG was recorded continuously using a 275-channel whole-head system (CTF-Omega 2005; VSM MedTech Ltd., BC, Canada) in a synthetic third order axial gradiometer configuration (Data Acquisition Software Version 5.4.0, VSM MedTech Ltd., BC, Canada) with a sampling rate of 1200 Hz. Signals were bandpass filtered at 0.01–600 Hz. Behavioural responses were recorded using a fiberoptic response pad (Lumitouch, Photon Control Inc., Burnaby, BC, Canada) connected to the stimulus PC and the MEG acquisition system as an additional channel. Participants were seated in an upright position. Before and after each run, the participant's head position relative to the gradiometer array was evaluated using coils located at the subject's nasion and 1 cm anterior to the tragus of the left and right ear. Runs with a head movement exceeding 7 mm, in any direction, were discarded. MEG procedures and analyses were in accordance with the good-practice guidelines (Gross et al., 2013; Keil et al., 2014a,b; Rousselet et al., 2016).

Visual stimuli were displayed in the center of a translucent screen at a viewing distance of 53 cm and 8.8° of visual angle. The stimuli were projected onto the screen by an LCD projector (Sanyo xp41) outside the magnetically shielded chamber via two front-silvered mirrors. Auditory stimuli were generated by a computer sound card (Creative Labs; Audigy 32) before going through sound conducting tubes into the MEG chamber where they were connected to ear plugs (ProPlugs, Doc's ProMould). The stimulus protocol was run by Presentation software (Neurobehavioral Systems, Version 11).

The pre-training MEG session comprised three SOA conditions: The simultaneous SOA (0 ms), 300 ms, and the SOA with the duration of each participant's individual TBW estimated in the pre-training behavioral assessment (IWpre). In the simultaneous SOA condition, the auditory and visual stimuli are presented simultaneously, in both intervals. This was done to check for response bias. The post-training MEG session included a fourth SOA representing each participant's individual TBW measured on the second day (IWpost). Each SOA-condition was repeated 150 times, resulting in a total of 450 trials in the pre-training session, and 600 trials in the post-training session. Participants responded by pressing button 1 or 2 with their right index or middle finger, respectively. They were instructed to respond as quickly and accurately as possible after seeing the response screen. Depending on the SOA condition and reaction time, one trial took approximately 3–3.5 s.

2.6. Analysis of behavior during MEG recordings

We evaluated the influence of training (pre-training, post-training) and SOA (0 ms, IWpre, 300 ms) on reaction times in a 2×3 ANOVA. Only correct trials were included in all analyses. The impact of training (pre-training, post-training) and SOA (IWpre, 300 ms) on accuracy was tested in a 2×2 ANOVA (as the 0 ms condition does not allow correct/incorrect judgments). The average numbers of included trials for each condition were: Pre-training: 300 ms = 121; IWpre = 102; Simultaneous = 147; Post-training: 300 ms = 118; IWpre = 110; Simultaneous = 171.

2.7. MEG data preprocessing

MEG data were analyzed using Matlab R2012b (Mathworks) and the Matlab toolbox Fieldtrip (http://fieldtriptoolbox.org/). Trials were classified according to the SOA conditions. The time-of-interest was defined as 400 ms preceding the visual stimulus to 500 ms following the auditory stimulus of the *asynchronous* audio-visual pair. The asynchronous pair could appear either in the first or second interval of the trial (referred to as I1- and I2- trials). As the data from I1- and I2-trials of each SOA-condition was later pooled for analysis, we chose a common baseline. For both I1- and I2-trials the baseline was defined from −500 to −400 ms with respect to the auditory stimulus in I1.

Data epochs containing the time-of-interest and the baseline were selected for pre-processing from the continuous recording. Data epochs contaminated by eye blinks, muscle activity, or jump artefacts were excluded using automatic artefact detection and visual rejection routines provided by the Fieldtrip software. Eye blinks were filtered using a Butterworth filter (4th order) within the frequency band 1–15 Hz with a Hilbert envelope. The filtered data within each trial was converted to z-score and samples with a z-score greater than 10 standard deviations

were rejected. Muscle artefacts were filtered using a Butterworth filter (4th order) within the frequency band 110–140 Hz with a Hilbert envelope. The filtered data within each trial was converted to z-score and samples with a z-score greater than 5 standard deviations were rejected. In order remove jump artefacts a median filter (9th order) was used. The filtered data was then converted to z-score. Trials where segments exceeded 20 standard deviations were rejected.

The baseline and the time-of-interest of I2-trials were concatenated such that their timeline was identical to the timeline of I1-intervals. This created the impression of a phase reset. We restricted our analyses to the time window after this artefact. Trials were demeaned and detrended. A low-pass filter (240 Hz) and notch filters (15.4–17.4, 49.2–51.2, 99.4–100.6, 149.4–150.6, 199.4–200.6 Hz) were applied to the dataset. These frequencies were removed to eliminate artefacts from powerlines as well as electrical noise emanating for a nearby street tram.

2.8. Analysis of spectral power changes

Time-frequency representations (TRFs) were computed by means of Hanning windows with a width of 100 ms at frequencies between 2 and 60 Hz, in 2 Hz steps. Hanning windows were moved in 10 ms time steps. Additionally, broad-band signals from 60 to 120 Hz were multi-tapered in steps of 2 Hz with a width of 5 cycles per time window. A multi-taper time-frequency analysis was performed for higher frequencies in order to realize higher frequency smoothing, as recommended for the analysis of electrophysiological signals above 30 Hz (Mitra and Pesaran, 1999; Percival and Walden, 1993). Statistical analysis was applied to restricted frequency bands (12–30 Hz, 30–60 Hz, and 60–120Hz) because we had a-priori hypotheses about training effects on beta- and gamma oscillatory activity. Additionally, it is possible that changes in gamma-band activity can cross the boundaries traditionally classified as low and high gamma-band activity (Castelhano et al., 2017); therefore a single analysis that incorporated 30–120 Hz was also conducted. Data were normalized using a relative baseline correction before computing grand averages over all participants.

2.9. Statistical analysis of MEG data

Training effects on spectral power in the beta (12–30 Hz), low-gamma (30–60 Hz) and high-gamma (60–120 Hz) frequency bands were evaluated by separate 2×3 repeated measures non-parametric ANOVAs with the factors 'Training' (pre, post) and 'SOA' (0 ms, 300 ms, IWpre). The spectral power was averaged across each frequency band of interest for each time point within each condition, and for each participant, before the analysis was performed. To account for multiple comparisons in space (i.e., channels) a cluster-based permutation test (Monte Carlo simulations) was conducted (Maris and Oostenveld, 2007). Clusters were defined as adjacent grid points whose F-values exceeded a critical threshold corresponding to an uncorrected alpha level of 0.05. For these clusters we defined cluster values as the sum of F-values in a particular cluster. Cluster values were tested against the distribution of cluster values obtained from 2000 permuted data sets. Significance was assessed based on an alpha value of 0.05. Special care was taken to define the appropriate permutations for a factorial design (see Anderson and Ter Braak, 2003 for methods; Suckling and Bullmore, 2004). To avoid confounds due to the within-subject factor when estimating main effects, observations for both levels of within-subject factors were kept together for each subject. Only whole participants were allowed to be exchanged during the permutation procedure. No exact permutation tests, based on the F-statistic, exist for the interaction effect, since restricting permutation of the observations such that neither group nor condition main effect affects the corresponding F-ratio, would leave no possible permutations of the data. An approximate test can be constructed by restricting permutations of condition levels to occur within participant and subsequently permuting whole participants across groups (Anderson and Ter Braak, 2003; Rivolta et al., 2014; Suckling and Bullmore, 2004). Though variability due to the main effects is not held constant under such a permutation scheme, their variability impinges on all terms of the model, giving a reasonable approximate test. Additional post-hoc comparisons were calculated by two-tailed dependent t-tests (2000 permutations, cluster-alpha = 0.05).

In order to test whether the training effect on beta band activity was driven by one of the intervals, we conducted 2×2 ANOVAs with the factors 'interval' and 'training' on 12–30 Hz activity in all SOA conditions. In addition, a $2 \times 2 \times 2$ repeated-measures ANOVA was conducted to investigate possible interactions between the factors Training (pre-vs. post-training), SOA (0 ms vs. IWpre vs. 300 ms), and Interval (1st vs. 2nd).

3. Results

3.1. Behavioural assessments

Fig. 2a depicts the accuracy rates for each SOA produced in the behavioural assessments by one individual. A 2×6 repeated-measures ANOVA with the factors training (pre-vs. post-training) and SOA (50 ms, 100 ms, 150 ms, 200 ms, 250 ms, and 300 ms) revealed main effects of Training [$F(1,13) = 1463.62$, $p < 0.0001$, $\mu^2 = 0.99$] and SOA [$F(5,65) = 57.62$ $p < 0.0001$, $\mu^2 = 0.82$], and a significant interaction [$F(5,65) = 2.46$, $p = 0.042$, $\mu^2 = 0.16$] for accuracy. The main effect of Training indicates higher accuracy rates following training compared to pre-training (pre-training: 68.70%; post-training: 83.47%). Participants were significantly more accurate as the SOA between the auditory and visual stimuli increased (50 ms: 54.45%; 100 ms: 65.30%; 150 ms: 76.80%; 200 ms: 81.40%; 250 ms: 86.60%; 300 ms: 91.95%). A Tukey honest-significant-difference (HSD)-corrected post-hoc tests on the interaction showed that the increase in accuracy following training was significantly different for the 100 ms, 150 ms ($ps < 0.001$), and 200 ms ($p < 0.05$) SOAs, compared to the pre-training SOAs (Fig. 2b). See Suppl. Fig. S1 for similar behavioural performance in the MEG. It can be difficult to interpret the results from the ANOVA given the non-linear relationship between the factors of Training and SOA (Garcia-Marques et al., 2014). Thus, an additional non-linear regression was performed to compare the slopes from the SOAs between the pre- and post-training sessions. There was a significant difference between the two slopes [$R^2 = 0.664$, $p = 0.0001$] (Fig. 2b). This further demonstrates that there was a significant behavioural difference between the pre-training and post-training sessions.

The previous analyses did not specifically examine whether each participant's individual temporal binding window was reduced following training. To determine if there was a significant difference in mean individual window size between the pre- and post-training session, a paired-samples *t*-test was conducted. The mean IW size of all 16 participants decreased significantly from 153 ms to 85 ms following training ($t(15) = 6.45$, $p < 0.0001$, Cohen's d = 1.6). This reduction in IW size of 44% (SD = 29%) is in line with previous psychophysical findings (Powers et al., 2012). All participants exhibited a reduction in IW size (Fig. 2d). The extent of the reduction can be predicted by the initial IW size at baseline ($r(15) = 0.71$, $p = 0.001$; Fig. 2e). The subset of 14 participants who underwent MEG measurements significantly improved in the IWpre (t (13) = −8.31, $p < 0.0001$, Cohen's d = 4.6) and the 300 ms SOA conditions ($t(13) = -2.75$, $p = 0.016$, Cohen's d = −1.5; Fig. 2f).

To determine whether accuracy depended on the interval at which the asynchronous stimuli were presented, a $2 \times 2 \times 6$ repeated measures ANOVA was conducted with training (pre- and post-training), Interval (1st and 2nd), and SOA (50 ms, 100 ms, 150 ms, 200 ms 250 ms, and 300 ms) as factors. Once again, there was a significant main effect of Training [$F(1,13) = 53.41$, $p < 0.0001$, $\mu^2 = 0.80$], with increased accuracy post-training compared to pre-training. There was a trend for a main effect of Interval [$F(1,13) = 3.94$, $p = 0.069$, $\mu^2 = 0.23$], with better performance when the asynchrony was presented in interval 1 (84.75%) compared to interval 2 (81.62%). Finally, there was a main effect of SOA

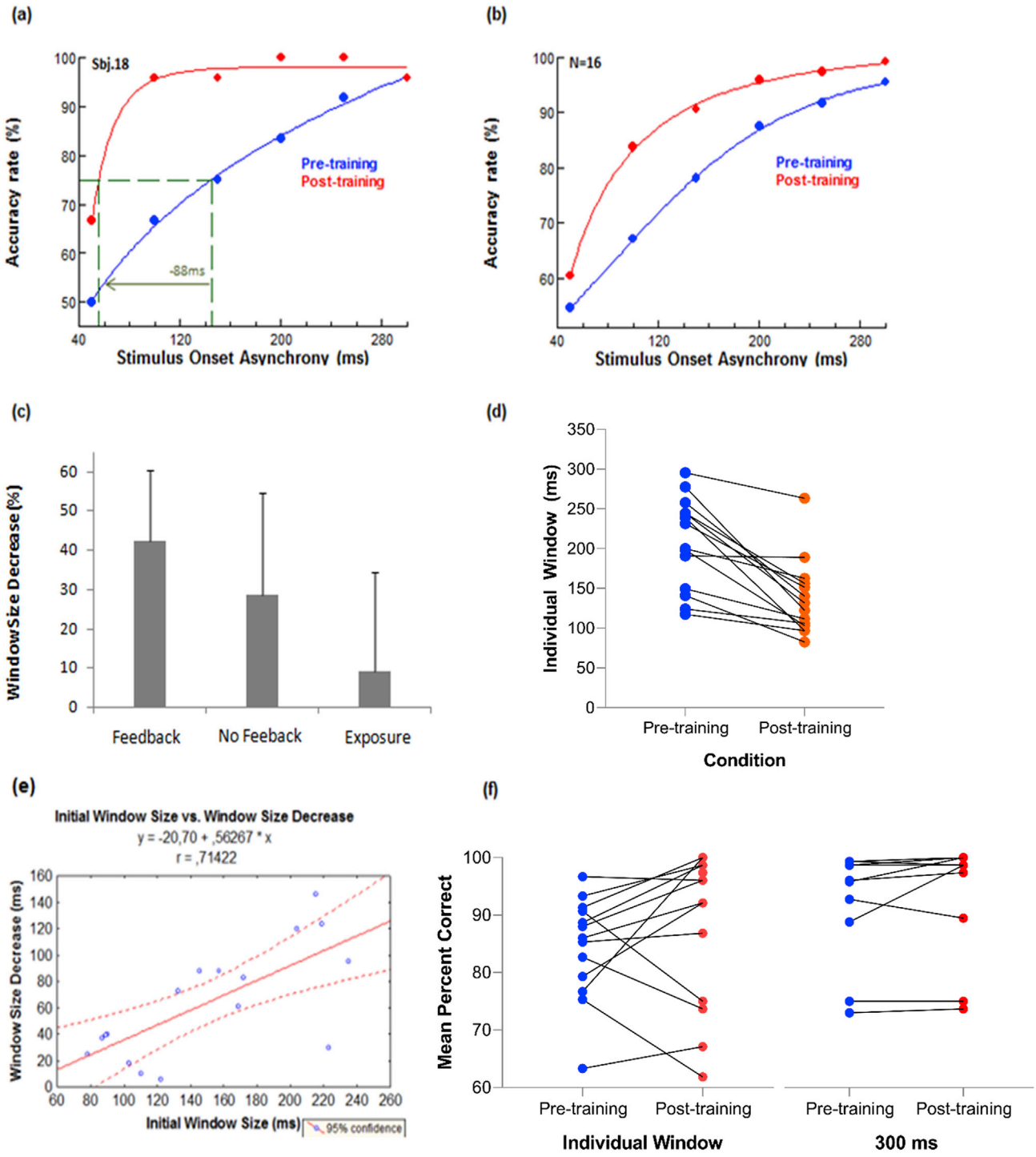


Fig. 2. Training on the 2-IFC SJ task significantly altered the size of the TBW. (a) Results from a single participant, fitted with a sigmoid curve from which a measure of the Individual Window (IW) was derived (criterion: ~76%). For this subject the IW decreased by 88 ms following training. Please note that the accuracies for pre- and post-training were identical (95.8%) at the 300-ms SOA. (b) Following training, mean accuracy rose significantly for the 100, 150 and 200 ms SOAs. (c) Decrease in Individual Window size following training for the three training groups. Error bars indicate standard deviations. (d) IW sizes for each subject. All subjects exhibited a decrease in IW size. (e) Correlation of initial IW size and IW size decrease over all 16 participants. Large initial IWs predicted success in training. (f) Accuracy rates for the IWpre and 300 ms conditions, for subjects with MEG recordings. These data are taken from the behavioural assessments. Accuracy increased significantly following training in the IWpre and in the 300 ms condition (*$p < 0.05$, **$p < 0.001$). Accuracy rates for the 0 ms condition were not calculated because in both intervals the audiovisual stimuli were presented simultaneously, thus errors could not be calculated.

[$F(5,65) = 92.64$, $p < 0.0001$, $\mu^2 = 0.88$], with accuracy improving as the SOA increases (50 ms = 57.21%; 100 ms = 75.34; 150 ms = 84.25; 200 ms = 91.64; 250 ms = 93.98%; 300 ms = 96.68%). Again, there was an interaction between Training and SOA [$F(5, 65) = 3.85$, $p = 0.004$, $\mu^2 = 0.23$]. Finally, there was a significant interaction between Interval and SOA [$F(5,65) = 15.97$, $p < 0.0001$, $\mu^2 = 0.55$]. In the 50 ms SOA condition, participants were more accurate when the simultaneous condition was presented in Interval 1 ($p = 0.0001$). In all other SOAs, there was no significant difference between intervals. There were no other significant interactions.

The effect of the Training Regime (Feedback, No Feedback, or Exposure) on behavioural performance was analyzed using a between-subjects ANOVA. There was a main effect of Training Regime on window size decrease [$F(2,45) = 8.18$, $p = 0.0009$]. Tukey HSD-corrected post-hoc tests revealed that informative feedback significantly reduced the individual window compared to the exposure-only group (Feedback = 42.4%, Exposure = 9.2%; $p = 0.0007$; Fig. 2c).

A 2 × 3 repeated measures ANOVA with the factors of Training (pre- and post-training) and SOA (0 ms, IWpre, 300 ms) on reaction times of correct responses revealed no main effect of Training [$F(1,13) = 3.29$, $p = 0.09$]. There was a significant main effect of SOA [$F(2,26) = 29.86$, $p < 0.0001$, $\mu^2 = 0.70$], with significantly longer reaction times for the simultaneous condition (mean = 522.11 ms) compared to the 300 ms (mean = 417 ms) and IWpre conditions (mean = 431.35 ms; all $ps < 0.0005$). Finally, there was a significant interaction between these two factors [$F(2,26) = 4.10$, $p = 0.03$, $\mu^2 = 0.24$] (Fig. S1). A Tukey HSD post-hoc test revealed that participants were significantly slower in the pre-training simultaneous condition compared to all other conditions ($p = 0.0001$).

3.2. Induced spectral power changes

A 2 × 3 repeated-measures non-parametric ANOVA with the factors Training (pre-vs. post-training) and SOA (0 ms, IWpre, 300 ms) was conducted. There was a main effect of Training on 12–30 Hz activity between 80 ms and 410 ms (after auditory onset) at left and right central, parietal, frontal and temporal sensors ($p = 0.016$; see Fig. 3a). Post-hoc *t*-test revealed that beta-band (12–30 Hz) activity was higher in the post- compared to the pre-training sessions ($p < 0.001$).

There was also a main effect of SOA ($p < 0.0001$) in the beta-band, between −400 ms and 410 ms at parietal and occipital sensors (see Fig. 3b and c). Post-hoc tests revealed increased beta-band activity in the 0 ms condition compared to the IWpre ($p < 0.0001$) and 300 ms ($p < 0.0001$) conditions (see Suppl. Fig. S3). Beta-band activity was also significantly higher in the IWpre compared to the 300 ms condition ($p < 0.0001$). There was a trend for an interaction between Training and SOA ($p = 0.06$; see Fig. S2). Exploratory post-hoc *t*-tests between the pre- and post-training SOAs within each condition indicated that the increase in beta-band activity occurred only in the asynchronous IWpre ($p = 0.001$) and the 300 ms conditions ($p = 0.0005$), but not in the simultaneous 0 ms condition ($p = 0.35$). We did not find any significant effects of Training or SOA in the other frequency bands. It is important to recognize that there is a possible non-linear relationship between changes in beta-band power and the effects of training and SOA. Thus, we cannot exclude that there is a monotonic relationship between these factors without explicit testing (Garcia-Marques et al., 2014).

To analyse whether the training effect on beta band activity was driven by one of the intervals, we ran separate 2 × 2 ANOVAs with the factors Interval (1st vs. 2nd) and Training (pre-vs. post-training) on the beta-band power in the 300 ms and the IWpre condition. In the analysis of the IWpre conditions, there was a main effect of Interval ($p < 0.0005$) with greater beta-band activity in interval 1 compared to interval 2, for the time period of: −0.400 ms – 0.400 ms (Fig. 4a). In the 300 ms SOA conditions, once again there was a main effect of Interval ($p < 0.0005$), with greater beta-band activity in interval 1 compared to interval 2, between the time period of −0.350 ms – 0.400 ms (Fig. 4b). There was no significant interaction between these two factors. The increase in beta-band activity in Interval 1 compared to Interval 2 could represent participants 'preparing' their template models of what should be perceived, before each trial began.

To investigate whether brain activity for each interval was affected by SOA, an additional 2 × 2 × 2 repeated measures ANOVA with Training (pre-vs. post-training), SOA (0 ms vs. IWpre vs. 300 ms), and Interval (1st vs. 2nd) as factors was conducted to determine if there were significant differential effects when considering Interval. Once again, we found significant main effects of Interval, SOA, and Training; however, we did not find a three-way interaction. Thus while there was greater beta band activity in Interval 1 compared to 2, this was independent of SOA.

In order to compare the effect of the IWpost condition to the IWpre condition *within* the post-training block, a *t*-test was conducted between these two conditions. There was a significant difference between the post-training IWpre and IWpost conditions, with significantly greater beta-band activity in the IWpre condition compared to the IWpost condition ($p < 0.05$). Significant channels were located over occipital and parietal cortex from −0.01s or 0.13s (Fig. 5).

4. Discussion

The present study was set out to identify the electrophysiological signature of improved cross-modal temporal acuity following perceptual training on an audio-visual SJ task. We measured the individual TBWs of subjects prior to, and one day following training on the 2-IFC SJ task and additionally recorded their neural activity during the task on both days using MEG. In line with previous research by Powers et al. (2009, 2012) we found that training with feedback on the 2-IFC SJ task elicited a significant narrowing of the TBW by 44%. In our experiment, we assessed the TBW only for visual-leading stimulus pairs, because this is the environmentally more prevalent condition as light reaches the observer faster than sound. Furthermore, perceptual training was reported to have a much smaller effect on the TBW for auditory-leading events (Powers et al., 2009, 2012). We also found that training without feedback exhibited significant albeit smaller decreases in the size of the binding window while the mere exposure to the stimuli, without practice, left performance unaffected. This is in line with previous studies which demonstrated the importance of an instructive signal, such as feedback, for sensory reorganization in the adult (Pleger et al., 2009).

The increase in temporal acuity was accompanied by elevated beta-band activity following training. The main effect of Training on beta-band activity emerged over central and parietal sensors at 80–410 ms. Exploratory t-tests between the pre- and post-training session within each SOA-condition showed that the increase in beta-band activity (albeit not significant at the $p = 0.05$ level) occurred predominantly in the asynchronous 'Individual Window' and the 300-ms condition, which were accompanied by improved behavioral performance. This suggests that the increase in beta-band activity might reflect the improved perception of asynchronies rather than a general unspecific activity change after training (e.g. due to adaptation to the stimuli or the task). Additionally, beta-band activity was greater in the individual window condition compared to the 300 ms condition. We also believe that this is due to the increased perceptual acuity (e.g., more precise template information) compared to the 300 ms condition. It could also be argued that this difference in SOA performance was caused by a difference in baseline activity. However, this is unlikely as the same baseline window was taken for each condition. Furthermore, there is no difference in pre-stimulus activity when comparing each SOA, averaged across training conditions (Suppl. Fig. S3).

As asynchronous pairs from both intervals of a trial were pooled for analysis, the question could arise whether the effect was carried by one of the intervals. We did find a significant increase in beta-band activity during the time of Interval 1. This could be due to participants building their template information before the trials begins. It is also possible that participants devoted more attention in Interval 1 compared to Interval 2. Participants could have employed the strategy of attending to only Interval 1 and determining if they detected the asychronous trial. If not, they could have automatically defaulted their response to Interval 2. Conversely, it is also possible that the decrease in beta-band amplitude in Interval 2 compared to Interval 1 represents pre-motor preparation if participants already knew their response (Barutchu et al., 2013). We did not find an interaction between interval and training on beta band activity, suggesting that the training effect was not driven by only one interval. It is also important to point out that there was no significant difference in behavioural performance between the two intervals.

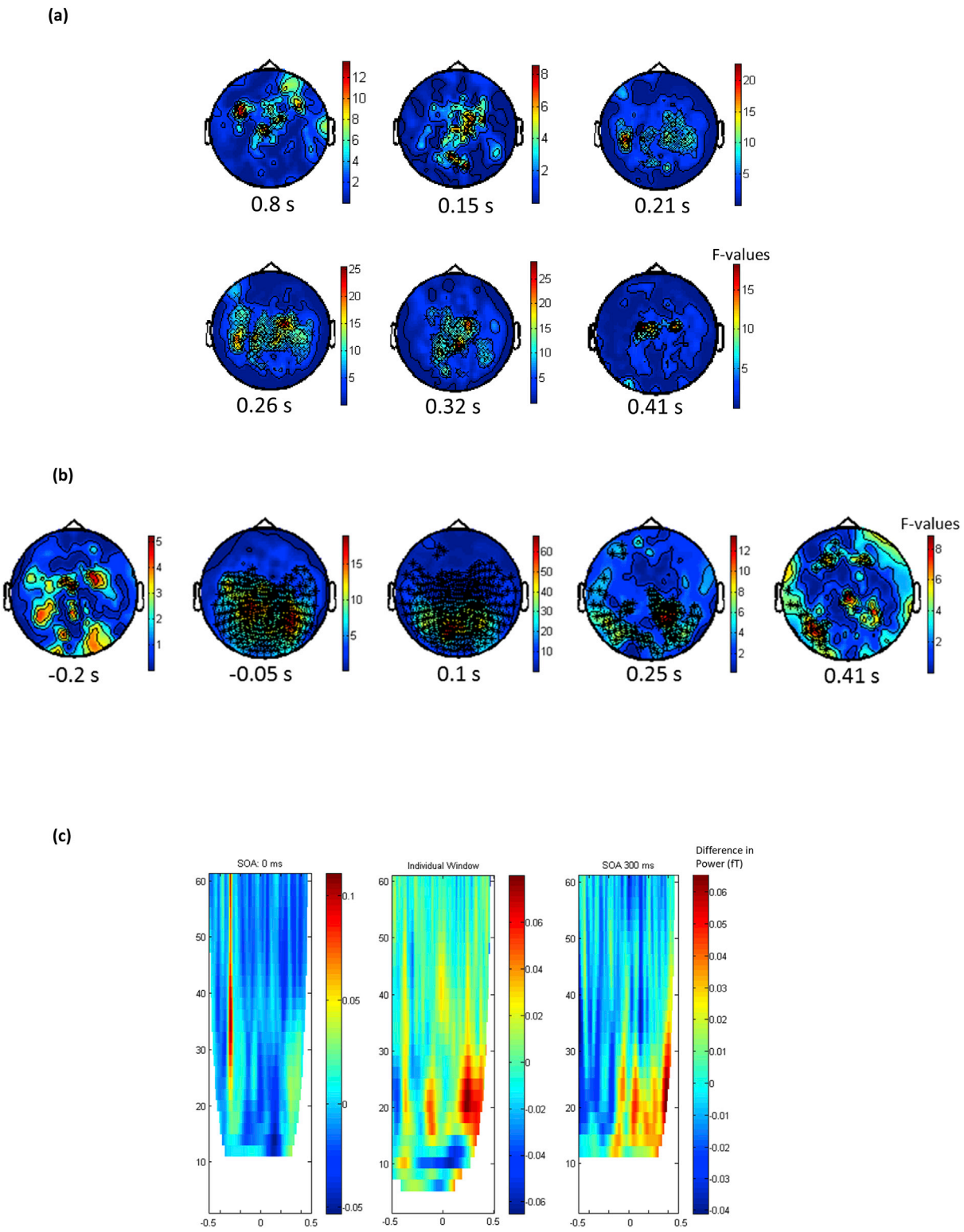


Fig. 3. A) Topography of the significant cluster associated with the main effect of Training on 12–30 Hz activity. Beta-band power was increased at left and right central, parietal, frontal and temporal sensors in the post-training session compared to the pre-training session. B) Topography of the significant clusters associated with the main effect of SOA on 12–30 Hz activity. Markers represent significant channels. The color bar represents the F-values of the ANOVA for each topographical plot. C) Spectral power differences between the training conditions (post-training – pre-training). The color bar represents the difference in power between pre- and post-training, and the time point of zero represents the onset of the auditory stimulus. Beta power was enhanced in the post-training session compared to pre-training. Please note that what appears to be an evoked response in the 0 ms condition is an artefact of the baseline correction method: To have a common baseline for intervals 1 and 2, the time-of-interest was cut for interval 2 and concatenated with the baseline window before interval 1. This created the impression of a phase reset.

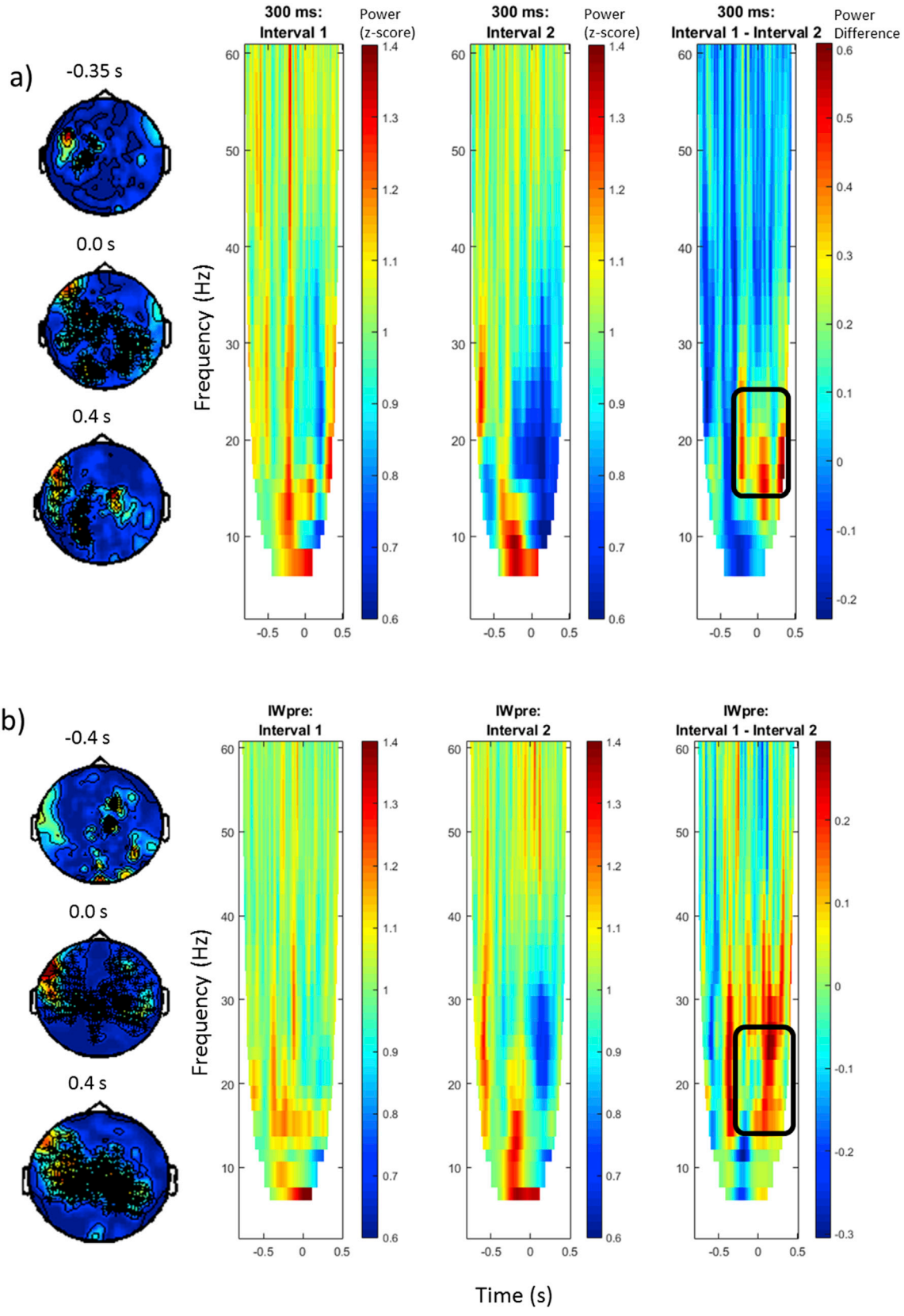


Fig. 4. A) Topographical plots of sensors showing a significant main effect of Interval in the 300 ms condition. The time-frequency plots on the right represent the power spectrum for each Interval and the difference between intervals. B) Topographical plots of sensors showing a significant main effect of Interval in the pre-training Individual Window condition. The time-frequency plots on the right represent the power spectrum for each Interval and the difference between intervals.

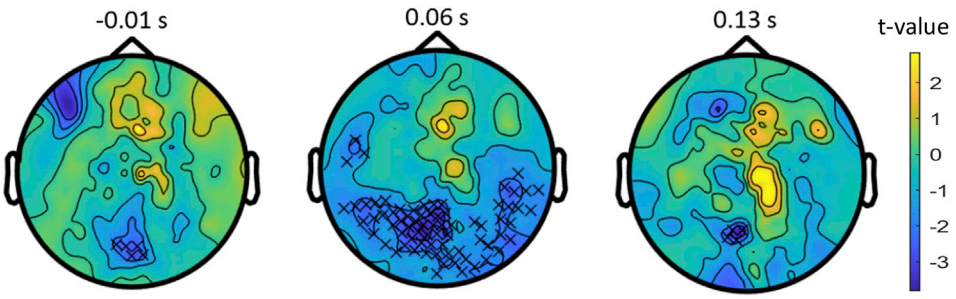


Fig. 5. Topography of the significant cluster associated increased beta-band activity in the post-training IWpre condition, compared to the IWpost condition (IWpost > IWpre). The color represents the t-values. For all topographical plots, symbols represent the different p-values: p < [0.01 (*), 0.05 (x), 0.1 (+), 0.2 (o) 0.3 (.)]. Each topological plot at any given timepoint represents the center of a 20 ms time window.

Functionally, beta oscillations have been associated with the propagation of descending information from higher to lower areas in the cortical hierarchy, often in the form of top-down signals (see Arnal and Giraud, 2012 for a review; Engel et al., 2001; Wang, 2010). This could occur by preselecting cell populations coding for 'asynchrony' in order to enhance their chances to dominate over competitive cell populations (e.g. coding for 'synchrony') at the time when ambiguous sensory information arrives. Similarly, predictive coding theory (see Arnal and Giraud, 2012; Bastos et al., 2012, for reviews) suggests that the brain actively predicts forthcoming sensory events by sending 'templates' of the expected events down the descending pathway via beta oscillations to match them with the incoming sensory information. If the prediction and sensory input do not match, a prediction error is assumed to be propagated forward the cortical hierarchy via gamma oscillations to update the inappropriate templates. Accordingly, the present increase in beta-band activity from pre- to post-training measurement could indicate that during training participants developed a stronger expectation of 'asynchrony' that resulted in a corresponding template that was activated in the post-training test. Changes in gamma-band power were not detected in these data, presumably because the template updating occurred during the training, which was not recorded in the MEG. It is a limitation of the study that brain activity was not recorded during the training session.

Unfortunately, not all participants agreed to an anatomical MRI scan, therefore source reconstructions could not be performed. However, it is notable that the training effect on beta-band activity persisted until 410 ms after the onset of the auditory stimulus and moved across frontal, central, parietal, and temporal sensors, suggesting that a distributed network of areas was modulated following training. As shown by previous work, both the encoding of audio-visual asynchronies and training on unimodal interval perception recruit a large-scale network of sensory-motor areas, including the insula, cerebellum, posterior parietal (Bueti et al., 2012;Bushara et al., 2001; Powers et al., 2012), prefrontal (Bushara et al., 2001; Powers et al., 2012) and superior temporal cortices (Powers et al., 2012). Modulations of the processing within such a large-scale network would also be expected to emerge in the beta-band, since beta oscillations are specifically suited for synchronization over long conduction delays (Bibbig et al., 2002; Donner and Siegel, 2011; Kopell et al., 2000; Siegel et al., 2012). Taken together, this indicates that multisensory temporal learning does not only take place at the level of primary sensory cortices, but rather in the large-scale network that was shown to be involved in the encoding of asynchronies. One limitation of this study is that the analyses were restricted to the sensor level.

The main effect of SOA found beta-band activity increases as SOA decreased (i.e., 0 ms > IWpre > 300 ms). It cannot be ruled out that the main effect simply represents the delay between the two stimuli, particularly since the analyses were locked to the auditory stimulus. It is also possible that since the 0 ms condition and Individual Window conditions were the most difficult conditions for template updating, the increase in beta-band activity represents this updating.

Interestingly, when comparing the IWpre and IWpost conditions *within* the post-training block, there was increased beta-band activity in the IWpre condition compared to the IWpost condition. This could be because after training, the participant's perceptual template for binding information now included the SOA which was at their prior pre-training threshold. However, the IWpost SOA was at the participant's threshold, and thus exceeded their template information, providing further evidence for the predictive coding model.

As an alternative to the hypothesis of enhanced top-down control, the neuronal dynamics leading to the button press might be considered the cause of the beta band effect. Beta oscillations over sensorimotor cortex have been associated with motor preparation in response to sensory input (Sanes and Donoghue, 1993; MacKay and Mendonca, 1995). Specifically, beta *desynchronization* over central areas has been linked to motor preparation (Tzagarakis et al., 2015). In fact, the present TFR landscapes of pre- and post-training SOA conditions at the significant channels (main effect of training) reveal lower beta band activity during the time of the effect as compared to baseline. This decrease was weaker in the post- than in the pre-training session, resulting in the overall effect of higher beta-band activity following training. In other words, there was an overall decrease in beta-band activity that is likely related to motor preparation. However, given that motor preparation is associated with a *decrease* in beta-band activity (Tzagarakis et al., 2010, 2015; Zaepffel et al., 2013) it is unlikely that the relative *increase* in beta-band activity in the post-training session, compared to pre-training, is related to motor preparation.

How exactly training on the SJ task induces these changes remains to be investigated. In the somatosensory domain, response feedback was shown to promote somatosensory perceptual learning by reactivating the cortical representation of the preceding choice (Pleger et al., 2009) and the strength of reactivation was mediated by dopamine. In order to evaluate if a similar mechanism is involved in temporal perceptual learning on the SJ task, further research may modulate dopamine levels during training and monitor the training session as well. Finally, it might be of clinical interest if the present training paradigm could be successfully transferred to mental pathologies that exhibit an enlargement of the TBW, such as schizophrenia or autism spectrum disorder (ASD; de Gelder et al., 2005; Foss-Feig et al., 2010). Given that ASD and schizophrenia have been linked to impaired long-range synchronization in the beta band (Uhlhaas et al., 2006; Uhlhaas and Singer, 2006 for review), it may be possible to use perceptual training to improve their cortical connectivity.

5. Conclusion

This study provides first insights into the electrophysiological correlates of multisensory temporal learning by showing that improved temporal acuity following perceptual feedback training is accompanied by enhanced beta band activity. A more simplistic explanation for that data could be, as a task becomes easier, there are increases in beta-band power. While this cannot be completely ruled out, the ease of the task

is likely due to this refinement of the template information.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.neuroimage.2019.116312.

For all topographical plots, symbols represent the different p-values: $p < [0.01$ (*), 0.05 (x), 0.1 (+), 0.2 (o) 0.3 (.)]. Each topological plot at any given timepoint represents the center of a 20 ms time window.

For all time-frequency representations the spectral power are changes relative to baseline averaged across the sensors forming the cluster depicted. For all topographical plots, symbols represent the different p-values: $p < [0.01$ (*), 0.05 (x), 0.1 (+), 0.2 (o) 0.3 (.)]. Each topological plot at any given timepoint represents the center of a 20 ms time window.

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