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Research Report

The effect of repetition on intersubject synchrony assessed with fMRI

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ABSTRACT

We investigated how repeated exposure to a stimulus affects intersubject synchrony in the brains of young and older adults. We used functional magnetic resonance imaging (fMRI) to measure brain responses to familiar and novel stimuli. Young adults participated in a familiarization paradigm designed to mimic 'natural' exposure while older adults were presented with stimuli they had known for more than 50 years. Intersubject synchrony was calculated to detect common stimulus-driven brain activity across young and older adults as they listened to the novel and familiar stimuli. Contrary to our hypotheses, synchrony was not related to the amount of stimulus exposure; both young and older adults showed more synchrony to novel than to familiar stimuli regardless of whether the stimuli had been heard once, known for a few weeks, or known for more than 50 years. In young adults these synchrony differences were found across the brain in the bilateral temporal lobes, and in the frontal orbital cortex. In older adults the synchrony differences were found only in the bilateral temporal lobes. This reduction may be related to an increase in idiosyncratic responses after exposure to a stimulus but does not seem to be related to how well the stimuli are learned or to differences in attention. Until the effects of repeated exposure on synchrony are fully understood, future studies using intersubject synchrony, where the novelty of the stimuli cannot be guaranteed, may consider exposing all of their participants to the stimuli once before data are collected to mitigate the effects of any systematic differences in stimulus exposure.

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1. Introduction

There is a growing trend in neuroscience to study the human brain using stimuli that contain naturalistic complexity rather than artificially constructed laboratory stimuli. Stimuli such as movies, audiobooks, or music enhance the ecological validity of studies examining brain function. These naturalistic stimuli unfold over time, and therefore require an analysis technique that is sensitive to temporal dynamics. This sensitivity can be gained with neuroimaging analyses (EEG, fMRI, or fNIRS) that use intersubject synchrony to detect common stimulus-driven brain activity across individuals over time. Intersubject synchrony was first introduced by Hasson et al. (2004) to study visual perception during movie viewing using fMRI. Brain areas with similar patterns of activity across participants were identified by calculating voxel-wise correlations over time between pairs of participants. They found that activity in large areas of the occipital and temporal lobes was correlated across participants over the course of the movie. Since this seminal paper, intersubject synchrony has been used to study attention (Ki et al., 2016), memory (Furman et al., 2007; Hasson et al., 2008), emotion (Trost et al., 2015), speech processing (Wilson et al., 2008), music perception (Abrams et al., 2013), consciousness (Naci et al., 2014), and brain function in clinical populations (Anderson et al., 2013; Hasson et al., 2009; Lyons et al., 2020). Intersubject synchrony analyses of naturalistic stimuli provide novel insight into how the brain functions in the world outside of the laboratory, but the way that stimulus characteristics affect synchrony are not fully understood.

The number of times an individual has experienced a stimulus may be an important aspect of the stimuli that should be accounted for in synchrony studies. Synchrony strength is interpreted as being a marker of how similarly individuals experience a stimulus (Hasson et al., 2004) and that experience may be influenced by the number of exposures to the stimulus. For example, an individual's first experience of a song is likely very different from their hundredth experience of that song (e.g., they may be able to sing along with all the words). In support of the idea that experience of a stimulus changes with exposure, there is evidence that intersubject synchrony is reduced with exposure (Aly et al., 2017, 2018). In one fMRI study, synchrony in the posterior medial network decreased from the first to the sixth consecutive viewing of 90 s movie clips. In a similar study using EEG, participants watched three short films twice each (Dmochowski et al., 2012) and synchrony decreased between the first and second viewings. However, neither of these studies fully characterized the timecourse of the synchrony decrease; for example, whether synchrony steadily decreased over multiple viewings or was steeply reduced after a single repetition followed by a plateau. If synchrony steadily decreases with increased exposure and exposure differs systematically with an experimental manipulation, then studies using intersubject synchrony analyses need to take stimulus exposure into account to reduce the possibility of confounds in the results. On the other hand, if synchrony is reduced after a single viewing, then confounds can be avoided by exposing participants to the stimuli before starting the study, or by ensuring that none of the participants have prior experience with the stimuli. In short, characterizing how synchrony is affected by prior exposure is important for understanding how best to design studies that minimize the confound of exposure differences across participants.

Intersubject synchrony may also be a useful method for identifying age-related changes in the temporal patterns of brain activity to naturalistic stimuli such as music or movies. The only two studies of aging and intersubject synchrony to date found an age-related reduction in synchrony, indicating that older adults were more idiosyncratic in their brain activity than young adults (Campbell et al., 2015; Geerligs et al., 2018). Synchrony differences were found across frontal regions (inferior frontal gyrus, middle frontal gyrus and medial prefrontal gyrus) and auditory and visual networks identified using an independent component analysis. The same audio-visual movie stimulus was used in both studies. The authors concluded that this change reflected the fact that behaviourally, older adults experience a movie stimulus in more individualized ways than young adults.

As the prevalence of the intersubject synchrony technique grows and is used in older and clinical populations (Anderson et al., 2013; Hasson et al., 2009; Huntley et al., 2023; Lyons et al., 2020) it is important to take into account that some participants in these groups may have impaired vision. One solution is to examine intersubject synchrony using audio-only stimuli such as music, but the characteristics of the synchrony induced by audio-only stimuli in healthy older adults or clinical populations have not yet been clearly defined.

The current paper presents two studies from a larger series of studies exploring the effects of stimulus repetition on the neural representations of auditory stimuli. The stimuli used across all studies can be found at https://owenlab.uwo.ca/research/research_tools.html. The previously published work explored the effects of stimulus repetition on music and language stimuli using univariate and multivariate pattern analyses (Sternin et al., 2021). The data presented in the current paper were collected from the same participants during the same sessions as the previously published work. The analyses here focus specifically on intersubject synchrony.

The goal of the first study was to systematically examine how exposure to audio-only stimuli influences intersubject synchrony in young adults. A training paradigm was used to objectively control prior experience of a series of auditory stimuli. Participants listened to stimuli in two scanning sessions: before and after a training period. Because the stimuli were novel and not in the public domain, none of the participants had prior experience with them. During training, participants listened to half of the stimuli from the first scanning session through an online audio player that tracked the number of times each stimulus was played. Thus, when they returned for the second scanning session participants were familiar with half of the stimuli. The stimuli presented in the second scanning session were otherwise identical to those presented in the first scanning session. Based on the previous research described above, we expected to see a decrease in synchrony based on stimulus exposure. If synchrony steadily decreases with repeated exposure, we expected less synchrony to the trained stimuli in the second session compared to untrained stimuli. In contrast, if synchrony is reduced after

a single viewing, synchrony should be lower in the second than first session, but synchrony should not differ between the trained half of the stimuli and the half heard only once, during the first scanning session.

The goal of the second study was to capitalize on the way individuals naturally become familiar with musical stimuli over a lifetime to examine how synchrony is affected by listener age and previous knowledge of the stimulus using an even more ecologically valid approach. No studies to our knowledge have investigated changes in synchrony related to long-term knowledge of a stimulus. Older adults were presented with two stimuli that they had been familiar with for more than 50 years. Although each participant may have heard these stimuli a different number of times over their lifetime, presenting participants with well-known stimuli from their past is a method used regularly in studies investigating the neural correlates of musical memory. Previous studies have used widely known movie or TV theme songs, folksongs, children's songs, or popular songs chosen from the period of time when the participants were young (e.g., Agustus et al., 2018; Jacobsen et al., 2015; Sikka et al., 2015). For this study, we chose a familiar song (*Hey Jude* by The Beatles) and a familiar spoken word poem (*'Twas the night before Christmas* by Clement Clarke Moore). For novel stimuli, the same original pieces used in the first study with young adults were used in the second study with the older adults. All the imaging data were collected during a single scanning session to minimize the burden on the older participants. In line with previous results, and in keeping with our hypotheses for Study 1, we expect to find less intersubject synchrony to the long-known stimuli than to the novel stimuli.

2. Ethics and data reporting

Ethics approval for this project was granted by the Health Sciences Research Ethics Board at The University of Western Ontario (#100606, #114263).

We report how we determined our sample size, all data exclusions, all inclusion/exclusion criteria, whether inclusion/exclusion criteria were established prior to data analysis, all manipulations, and all measures in the study.

3. Study 1 methods – young adults

3.1. Participants

Twenty-six neurologically normal, English-speaking participants (14 female) aged 18–39 (mean = 24 years) were recruited at The University of Western Ontario. All participants had completed at least some post-secondary education and nine participants had completed some post-graduate education. According to the Goldsmith's Musical Sophistication Index (Müllensiefen et al., 2014), 17 participants reported having formal musical training (1–10 yrs, mean = 4.5 yrs), but at the time of testing only nine of them played instruments regularly. Seven participants were fluent in a second language. All participants reported listening to music regularly in their daily lives (average 1.5 h per day) via a phone, computer, or car radio.

3.2. Stimuli

Stimuli were similar to those regularly encountered in the real world, and the presence of language and music was manipulated. Stimuli were created from the lyrics and music of eight different songs written and recorded by one of the authors (A.M.O) between 1997 and 2006 for an amateur rock band based in Cambridge, UK. Thus, all stimuli were novel to the Canadian participants. The original songs were written in a similar style and instrumentation included a lead singer, bass, drums, guitar, string instruments, and backing vocals, each recorded on separate tracks. Stimuli from the band's original repertoire were selected based on having male vocals only (over some that included female vocals). All stimuli were recorded using the exact same equipment directly to digital hard drive using the Sonar software (by Cakewalk) and a ShureSM58 microphone. Where the same instruments appear across stimuli (violin, cello, drums, guitar, etc.) the same physical instruments were used.

Four stimulus types were used: (1) whole music (all tracks, with music and sung lyrics), (2) instrumental music without words (all vocal tracks removed, leaving only non-vocal instrument tracks), (3) a capella (all non-vocal instrument tracks removed, leaving only lead and backing vocals) and (4) spoken words (lyrics of each song rerecorded in spoken form by the original lead singer to have a similar length, tempo, and emotional intonation as their original song counterparts). There were two different stimuli of each type, and none of the original songs were used for more than one stimulus type. The full stimuli can be found at https://owenlab.uwo.ca/research/research_tools.html. The scope of the current study was confined to examining the effects of familiarity on intersubject synchrony. Comparisons between the effect of the different stimulus types on intersubject synchrony are included in a different study that is currently in preparation. The effect of repeated exposure on the neural representations of the music and language stimuli using univariate and multivariate pattern analyses have been previously published (Sternin et al., 2021).

The stimuli were modified (e.g., lengthened by adding additional repetitions of the chorus) to each be 5 min long. During the fMRI scan sessions, participants heard the entire 5-min stimulus. Each stimulus was normalized to equate perceived loudness using *Audacity* software (Audacity Team, 2020). During the training period, participants listened to half of the stimuli (4 stimuli, 1 per type) via an online audio player.

There were four learning conditions: 'to be learned' refers to the novel stimuli heard in the first scanning session that the participant subsequently listened to over the training period; 'not to be learned' refers to the novel stimuli heard in the first scanning session that the participant *did not* listen to over the training period; 'learned' refers to the stimuli heard in the second scanning session that the participant had listened to over the training period; and 'not learned' refers to the stimuli in the second scanning session that the participant *did not* listen to over the training period. The 'to be learned' and 'learned' stimuli were identical for each participant, as were the 'not to be learned' and 'not learned' stimuli. The sets of stimuli that were learned were counterbalanced across participants: half the participants familiarized with one half of

the stimuli; the other half of the participants familiarized with the other half of the stimuli (Groups A and B; see Table 1).

3.3. Procedure

Participants completed two functional MRI scans separated by a stimulus training period (14–29 days; mean = 20 days). During both scans, participants passively listened to the stimuli. During the training period, participants listened to the stimuli via an online player (designed in-lab) that tracked the number of times each stimulus was played. Participants were asked to listen to the stimuli at least 5 times per week. To ensure participants were engaged while listening, the player presented a simple question about the stimulus (e.g. "*Were there lyrics present in the previous song?*") at random between stimuli. A response was required to move to the next stimulus. Participants were encouraged to incorporate the music into their everyday lives (i.e. to listen while cooking or driving).

3.3.1. Behavioural familiarity tasks

The behavioural familiarity tasks used to verify whether participants became familiar with the stimuli were collected as part of the larger series of studies. These data have been previously published in detail alongside the study exploring the effect of familiarity on the neural representations of the music and language stimuli using univariate and multivariate pattern analyses (Sternin et al., 2021). An abridged version of the methods and results are included here as the results are relevant for showing that participants became familiar with the trained stimuli as measured by behavioural tasks.

Participants came to the lab every few days to complete four behavioural testing sessions between their two scans. Participants completed two tasks to assess familiarity. The first was a lyric modification task in which participants identified which of two visually presented sentences was a lyric from the training stimuli and which was a modified (incorrect) version of that lyric. The correct and incorrect lyric pairs were piloted prior to the study to ensure that modified lyrics were chosen at least as often as original lyrics in naïve listeners. Because more words repeated in the group A stimuli, more lyric pairs were included for group B to account for the larger number of unique words in the group B stimuli.

Before the first scan session, participants were tested on the full set of lyric pairs, but as they were not yet familiar with any of the stimuli, they were asked to indicate which lyric they believed was *most likely* to come from a real song. During the behavioural sessions, participants were tested on a randomly selected subset of 10 lyric pairs. Participants were tested on the full set of lyric pairs again after the second scan session. Only conditions that contained words (whole music, a capella, and spoken) were tested (see Table 1).

The second familiarity test was melody recognition. After the second scan *only*, participants listened to 23 pairs of 2 s clips taken from the stimuli. Three or four clips were taken from each stimulus and none of the clips contained lyrics. Melodic information was extracted from the a capella stimuli using the *Praat* program (Boersma & Weenink, 2018). During the task, participants were presented with one clip from a trained stimulus and a second clip from an untrained stimulus (in a randomized order). Participants indicated which of the two

Table 1 – Description of how the stimuli were distributed and counterbalanced across Young and Older adult participants and how the behavioural tasks were designed to probe learning of both music and language in the Young Adults.

Young Adults	Eight stimuli	1	2	3	4	5	6	7	8
	Stimulus type	a capella	instrumental music	spoken word	whole music	a capella	instrumental music	spoken word	whole music
	Group A participants (N=11)	learned				not learned			
	Group B participants (N=9)	not learned				learned			
	Lyric modification task	x		x	x	x		x	x
		Group A task				Group B task			
		21 lyric pairs				29 lyric pairs			
		(probing learning of lyrics)				(probing learning of lyrics)			
	Melody recognition task	x	x		x	x	x		x
		Group A task				Group B task			
		(probing learning of music)				(probing learning of music)			
Older Adults	Novel Stimuli			3	4			7	8
				spoken word	whole music			spoken word	whole music
	Familiar Stimuli			*Twas the night before Christmas*	*Hey Jude*				

clips was most familiar. Only conditions with melodies (whole music, a capella, and instrumental) were tested (see Table 1).

To ensure the familiar stimuli were truly familiar, any participant who scored an average of 70% correct or less across the two tasks was excluded from further analyses. For more details on these behavioural familiarity tasks please see (Sternin et al., 2021).

3.4. *fMRI acquisition and analyses*

Imaging was conducted at the Robarts Research Institute on a Siemens Magnetom 7 T scanner with a 32-channel head coil. Functional scans were acquired with 54 slices per volume (TR = 1.25 sec; TE = 20 msec; flip angle = 35°; FOV = 220 × 220 mm; voxel size = 2.5 mm^3). The two scan sessions (before and after the training period) were identical and included eight 5-min functional runs. During each of the runs, participants passively listened to the stimulus in its entirety. Stimulus order was randomized for each participant and in each scan session. Half of the 5-min stimuli were 'to be learned' in the first session, and 'learned' in the second session, while the other half were 'not to be learned' in the first session and 'not learned' in the second session. Between functional runs in the first session only, a whole-head anatomical scan was acquired (TR = 6s; TE = 2.69 msec; FOV = 240 × 240 mm; voxel size = .75 mm^3; 208 slices).

Data from the 5 min runs were processed using automatic analysis (version 4.1; Aly et al., 2017, 2018; Cusack et al., 2015; Dmochowski et al., 2012): a MATLAB based processing and analysis pipeline that integrates with Statistical Parametric mapping (SPM12). Three 'dummy' scans were excluded from the beginning of every run to allow stabilization of the signal. Images were realigned to the first image in the first run using six motion parameters (x,y,z, translation and rotation). Data were normalized to MNI space and smoothing was done with a Gaussian kernel of 10 mm FWHM. Low-frequency noise (e.g., drift) was removed with a high-pass filter of 128s. Data were denoised using cerebrospinal fluid, white matter signals, motion parameters, their lag-3 2nd-order Volterra expansion (Friston et al., 2000), and "spikes" (>3 standard deviations based on mean signal variance across volumes) as nuisance regressors. The data were then further cleaned by running a group ICA (Calhoun et al., 2001) within each stimulus and removing 1–2 components that spatially correlated with a mask of the ventricles to remove non-brain related activity.

3.5. *Intersubject synchrony*

Intersubject synchrony across the whole brain was calculated separately in each session and for each stimulus using a leave-one-out approach. Synchrony was only ever calculated within group A and B to maintain the integrity of the 'learned' and 'not learned' conditions in the second session. For example, stimulus 1 was learned by Group A but not Group B (see Table 1). Synchrony was only ever calculated between identical stimuli. For each stimulus the timecourse of every voxel in each participant was correlated (Pearson and then Fisher z-transformed) with the mean timecourse of every corresponding voxel from the rest of the group's data within that session (that is, the group minus that participant, or $N - 1$ within session 1 or 2). This process created an r-value for each voxel, for each participant, that described the correlation between that participant's voxel and the same voxel in all other participants, for that stimulus in that session. To look for differences in synchrony across sessions, the 'within session' synchrony values for each stimulus in session 1 were then compared to synchrony values for the same stimulus within session 2.

Before comparing synchrony values across sessions, we investigated whether initial synchrony differed between the stimuli that were assigned to be learned in Group A and Group B. The individual correlation values from the first session, calculated as described above, were entered into a second-level flexible factorial model using SPM12 (see Supplementary Figure 1 for a visual depiction of the model). This model labeled learning group (Group A and B) and took subject effects into account. Group A > B and Group B > A t-contrasts were run in SPM to determine whether session 1 synchrony differed between the four Group A and four Group B stimuli. The two stimulus groups were designed to be similar, and indeed, the analysis confirmed no significant clusters. Therefore, in subsequent analyses, the synchrony values from all participants (in Group A and Group B) were labeled based on learning condition, not based on which physical stimulus was heard (i.e. stimulus 1 synchrony values were 'learned' for Group A and 'not learned' for Group B, and stimulus 5 synchrony values were 'learned' for Group B and 'not learned' for Group A, see Table 1).

Individual correlation values for the eight stimuli in session 1 (using the 'within session 1' values) and eight stimuli in session 2 (using the 'within session 2' values) were entered into a second-level flexible-factorial model using SPM12 to probe how learning affected synchrony across the entire group of participants. This model labeled learning condition (4 to be learned and 4 not to be learned stimuli in session 1, 4 learned and 4 not learned stimuli in session 2) and took subject effects into account (see Supplementary Figure 2 for a visual depiction of the model). As a result of the counterbalanced design, all eight stimuli were present in each of the four learning conditions across participants.

To probe changes in synchrony due to learning across the two sessions, a 2 (session 1/session 2) × 2 (trained/not trained stimuli) ANOVA was conducted using the 'within session 1' and 'within session 2' synchrony values. The 'to be learned' stimuli in session 1 and the 'learned' stimuli in session 2 were labeled as part of the 'trained' category. The 'not to be learned' stimuli in session 1 and the 'not learned' stimuli in session 2 were labeled as part of the 'not trained' category. F-contrasts were run in SPM to investigate main effects of stimulus training set, session, and the stimulus training set by session interaction. T-contrasts were then conducted to further investigate the significant main effect of session: session 1 > session 2; session 2 > session 1. For each contrast, the cluster-forming threshold was specified at FWE $p = .0001$ uncorrected (Roiser et al., 2016) to determine the extent threshold. Clusters were defined using the extent threshold and peak coordinates are reported at a corrected cluster level FWE $p < .05$.

If there were significant differences between sessions that were not related to learning, these differences may have emerged rapidly, over the course of session 1 (e.g. becoming familiar with the scanner environment). If so, synchrony should decrease from the first half to the second half of the

scanning session. For this analysis, for each stimulus, the participants were divided into groups based on whether the stimulus had been heard in the first or second half of the session as stimulus order was randomized for each participant. Then, synchrony was calculated within the first half or second half group. We then conducted two *t*-tests to investigate synchrony differences between the two halves of session 1 (session 1 first half/session 1 s half) to understand whether effects seen across the sessions emerged rapidly over the course of the first session.

3.5.1. *Synchrony changes within an individual*

The analysis described above used synchrony values that compared the degree of synchrony between an individual and the rest of the participants to probe whether there were group level changes in synchrony as a result of repeated exposure to the stimuli. However, it was also possible to investigate whether there were changes in synchrony at the individual level. An additional set of synchrony values were calculated for each stimulus within each participant. The 'individual changes' synchrony values were defined by calculating the voxel-wise correlations between session 2 and session 1 for each individual's data within each of the three defined regions (see section 5.3 below). That is, for each stimulus in session 2, the voxel timecourse in each region of interest in every participant was correlated (Pearson and then Fisher *z*-transformed) with the timecourse of every corresponding voxel of that same participant's session 1 data. This process created an *r*-value for each voxel, for each participant, that described the degree to which that participant's voxel during session 2 was correlated with their own data while listening to the same stimulus in session 1. The 'individual changes' synchrony values allowed us to probe how each individual's responses changed with learning in the second session as compared to their own data in the first session. The 'individual changes' synchrony values, averaged across each region's voxels, were extracted from the three significant clusters identified by the 2 (session 1/session 2) × 2 (trained/not trained stimuli) ANOVA using the 'within session 1' and 'within session 2' synchrony values described in the previous section. The values were extracted using MarsBAR (Brett et al., 2002) for further analyses using R (R Core Team, 2013). To investigate the individual changes in synchrony between sessions, we conducted a one-way ANOVA to investigate synchrony differences between the session 2 learned and session 2 not learned stimuli using the 'individual changes' synchrony values.

Finally, to determine whether synchrony to the learned stimuli was related to behavioural scores on the memory tasks, both sets of second session synchrony values ('within session 2' and 'individual changes' synchrony values) for the learned stimuli in session 2 in each ROI were correlated with each individual's average score on the lyric modification and melody memory tasks.

4. Study 2 methods – older adults

4.1. *Participants*

Fifteen neurologically normal, English-speaking participants (nine female) aged 64–74 (mean = 70 years) were recruited in London, Ontario. All participants had completed at least some post-secondary education and four participants had completed some post-graduate education. Using the Goldsmith's Musical Sophistication Index (Müllensiefen et al., 2014), 11 participants reported having formal musical training (1–61 yrs, mean = 20.8 yrs), but at the time of testing only three of them played instruments regularly. Five participants were familiar with a second language but did not rate themselves as fluent in those languages.

4.2. *Long-known stimuli*

Two well-known stimuli were selected: one whole stimulus and one spoken word stimulus. As the target age group was those over the age of 65, we chose 'Hey Jude' by The Beatles as the long-known whole stimulus. This song was popular when the group of participants would have been in their 20s (late 1960s-mid 1970s); 'Hey Jude' was the highest-ranking song on the Canadian billboard charts in 1968 ("The RPM 100 - Top Singles of 1968," 1969). It also maintained similar instrumentation to the novel stimuli (guitar, drums, voice), as well as the accent of the lead singer. The long-known whole stimulus had a length of 3:33. The long-known spoken word stimulus was created in lab by asking the same lead singer of the novel stimuli to record the poem *'Twas the night before Christmas*. The long-known spoken stimulus had a length of 3:46. All participants reported being very familiar with both stimuli (see section 6.2 below).

4.3. *Novel stimuli*

The same four spoken and whole novel stimuli used in the Study 1 with young adults and described above were used here (see Table 1). The instrumental and a capella stimuli were not used to reduce the length of the testing session and the burden of participation for the older adults.

4.4. *Behavioural tasks*

Participants were asked to return to the lab for a behavioural testing session within a week of their fMRI scan session. During the behavioural testing session, participants completed demographic questionnaires, the Goldsmith's Musical Sophistication Index (Müllensiefen et al., 2014), and familiarity questionnaires that asked them to listen to the stimuli they heard in the scanner and rate their level of familiarity on a scale of 1 (not familiar – *I had never heard this stimulus before my scan session*) – 5 (extremely familiar – *I have heard it more than 10 times*).

4.5. *fMRI acquisition and analyses*

Imaging was conducted at the Robarts Research Institute on a Siemens Magnetom 7 T scanner with a 32-channel head coil. Functional scans were acquired with 54 slices per volume (TR = 1.25 sec; TE = 20 msec; flip angle = 35°; FOV = 220 × 220 mm; voxel size = 2.5 mm^3). The scan session included six functional runs: 2 runs for each of the long-known stimuli (each less than 4-min) and four 5-min runs for each of the novel stimuli. During each of the runs,

participants passively listened to each of the stimuli in their entirety. Stimulus order was randomized for each participant. Between functional runs, a whole-head anatomical scan was acquired (TR = 6s; TE = 2.69 msec; FOV = 240 × 240 mm; voxel size = .75 mm^3; 208 slices).

Data from the 5-min runs were preprocessed using the same pipeline described in section 3.4 above.

4.6. *Intersubject synchrony*

The degree of intersubject synchrony across the whole brain during each of the six stimuli (2 long-known and 4 novel stimuli) was calculated using the same leave-one-out approach described in Study 1 (see section 3.5 above). That is, for each stimulus, the time course of every voxel in each participant was correlated (Pearson and then Fisher z-transformed) with the mean time course of every corresponding voxel from the rest of the participants, minus that participant ($N - 1$). This process created an r-value for each voxel, for each participant, that described the degree to which that participant's voxel was correlated with the rest of the participants while listening to that particular stimulus.

Each individual's synchrony values for the six stimuli were entered into a second-level flexible-factorial model using SPM12. This model labeled stimulus type (three stimuli each for spoken and whole music stimuli), familiarity (four novel and two long-known stimuli), and took subject effects into account.

Two t-contrasts were conducted to investigate familiarity: novel > long-known; long-known > novel. Two interaction contrasts were also run to determine where synchrony differed based on familiarity and stimulus type ([novel spoken − novel whole] − [long-known spoken − long-known whole]; ([novel whole − novel spoken] − [long-known whole − long-known spoken]). The cluster-forming threshold in each contrast was specified at FWE $p = .0001$ uncorrected (Roiser et al., 2016). All cluster peaks are reported at a corrected FWE $p = .05$.

5. Study 1 results − young adults

5.1. *Participants*

The final sample size was determined based on the number of complete, useable datasets that were collected. Two individuals withdrew from the study following the first scan session and data from four individuals were not included in the analysis because their average scores on the two behavioural memory tests were lower than 70% correct (a threshold determined prior to data collection). FMRI data from 20 individuals were included in the analysis.

Participants listened to each stimuli an average of 13 times (from 6 to 20 listens) over an average of 20 days (from 14 to 29 days).

5.2. *Behavioural familiarity tasks*

The behavioural data have been published previously in (Sternin et al., 2021) and will be summarized here to facilitate comparisons with the novel imaging data.

Participants significantly improved on the lyric modification task over the training period from 36% correct in the first session to 82% correct in the final session (t (34) = −12.3, $p < .011$, $d = 2.62$; with 3 participants scoring over 90%). There was no difference in average scores between the two learning groups in the final session (A: 80% vs. B: 85%; t (15) = −.66, $p = .52$, $d = .3$). Scores on the lyric modification task did not differ between the three conditions tested (spoken, whole, a capella). For more details on the results of the lyric modification task please see Sternin et al., 2021.

Participants scored an average of 92% ($SD = 6.4$) on the melody memory task completed during the second session, indicating excellent recognition of the melodies heard during the training period.

5.3. *Intersubject synchrony*

The 2 (session 1/session 2) × 2 (trained/not trained stimuli) ANOVA using the 'within session 1' and the 'within session 2' synchrony values revealed a significant main effect of session in three clusters within bilateral temporal areas, and the frontal orbital cortex (see Table 2 and Fig. 1). The threshold was set to the FWEc value ($k = 41$) and clusters were defined at $p < .05$ FWE corrected. The two post-hoc t-contrasts conducted to determine the direction of the synchrony differences between the two sessions (as identified by an F-test) showed significantly more synchrony in the first session than in the second session (see Table 2). No brain areas had more synchrony in the second session than the first. The 2 (session 1/session 2) × 2 (trained/not trained stimuli) also found no significant difference between the set of stimuli that were trained and the set of stimuli that were not trained and no session by stimulus training set interaction.

To further illustrate the session effects and the lack of training effect, Fig. 2 shows the synchrony values for each region in which a significant effect of session was observed.

As synchrony significantly decreased from session 1 to session 2, we analyzed whether this decrease may have occurred over the course of the first session. When comparing the data from the first and second halves of session 1 using two t-tests we found there was significantly more intersubject synchrony in the second half of session 1 than in the first half in the left temporal cluster (1st half mean = .46, 2nd half mean = .56, F (1,158) = 5.94, $p = .02$, $\eta^2 = .04$) and the right temporal cluster (1st half mean = .48, 2nd half mean = .61, F (1,158) = 10.9, $p = .001$, $\eta^2 = .06$). This effect of session 'half' occurred in the opposite direction as the differences between sessions from the 2 (session 1/session 2) × 2 (trained/not trained stimuli) ANOVA, where there was more synchrony to session 1 than to session 2.

To determine whether the synchrony differences were related to session differences in the amount of noise, we compared the signal-to-noise ratio in the data from the two sessions. Separately for each of the 20 participants, for each of the 8 stimuli, in both sessions we calculated the temporal signal-to-noise ratio (tSNR) on a voxel-by-voxel basis by dividing the mean signal by the standard deviation of the signal (Reeder, 2007). We then calculated the average tSNR value separately for each participant, within each stimulus in each session (resulting in 8 tSNR values from each session for

Table 2 – Cluster locations in which there was significantly more synchrony in session 1 than in session 2. Only significant t-values that were also identified by a main effect of session F-test are reported. Reported peaks within each cluster are >4 mm apart. The extent threshold was set for each contrast separately. All p-values <.001 (FWE corrected). STG = superior temporal gyrus.

Harvard–Oxford Atlas labels	(x,y,z) coordinates	Main effect of session extent = 41 F-value	Session 1 > Session 2 extent = 9 t-value
[a]Planum temporale	−52, −20, 0	93.13	13.65
Posterior STG	−62, −34, 8	64.29	11.24
Planum temporale	−58, −34, 10	64.11	11.23
Posterior STG	−68, −22, 2	36.13	–
[a]Planum temporale	60, −16, 4	68.15	11.65
Posterior STG	66, −24, 8	62.70	11.13
Anterior STG	62, 0, −4	31.16	7.89
Heschl's gyrus	38, −26, 10	28.58	7.53
Anterior STG	64, 2, −8	27.31	7.33
Temporal pole	62, 8, −10	25.75	7.11
Temporal pole	60, 12, −10	23.64	6.76
[a] Frontal orbital cortex	−14, 8, −24	24.26	–
Frontal orbital cortex	−12, 4, −28	22.39	6.69
Frontal orbital cortex	−12, 18, −20	19.76	6.16
Frontal orbital cortex	−16, 12, −24	19.40	6.19

[a] Denotes the three clusters extracted and used as regions of interest in further analyses.

each of the 20 participants). A t-test comparing all participants' tSNR values from the two sessions found there were no differences in tSNR between the two sessions (t (159) = 1.5, p = .13). This result indicates that the reduction in synchrony in the second session cannot be attributed to differences in the data signal between the two scanning sessions.

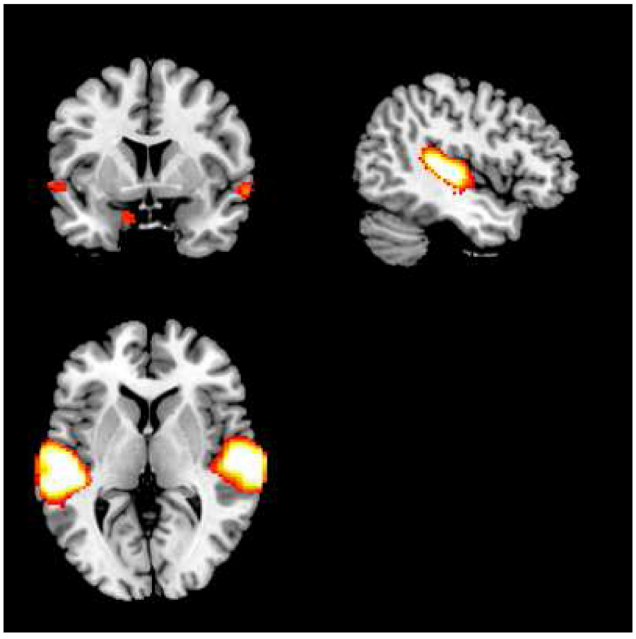

Fig. 1 – Brain regions in which intersubject synchrony differed between session 1 and session 2. These areas were identified using an F-contrast describing a main effect of session from a 2 (session) x 2 (stimulus training set) ANOVA. The three regions depicted (and described in Table 2) were extracted for use as regions of interest in further analyses. Extent threshold = 41. Displayed slices are at x = −45, y = 5, z = 4.

To further investigate the synchrony reduction across the sessions, we calculated intersubject synchrony between non-identical stimuli within the same three regions of interest identified above (See Supplementary Materials). The non-identical stimuli were chosen so that each combination was distinct and that identical stimuli were not used (i.e., 'true' synchrony was never calculated). Synchrony was calculated by correlating the data from one stimulus in each individual to the data from another stimulus in the rest of their training group in session 1 and in session 2. Once synchrony was calculated we ran a t- test within each of the three ROIs comparing the session 1 and session 2 data. In each of the three regions, there was significantly more synchrony in the first session than the second session (p < .001). We then ran a t-test within each of the three ROIs to determine whether the decrease in synchrony from session 1 to session 2 calculated when using non-identical stimuli was similar to the decrease in synchrony from session 1 to session 2 when using identical stimuli. In the bilateral temporal lobe ROIs there was a significantly larger decrease from session 1 to session 2 in the synchrony calculated using identical stimuli than when calculated using non-identical stimuli (p < .001).

Finally, we computed a correlation between the 'within session 2' synchrony values for all learned stimuli in each cluster with each individual's average score on the lyric modification and melody memory tasks. The p-values were FWE corrected across all clusters. There were no significant correlations between the synchrony values and the behavioural scores.

5.3.1. *Individual changes in synchrony*

The one-way ANOVA using the 'individual changes' synchrony data to investigate synchrony differences between the

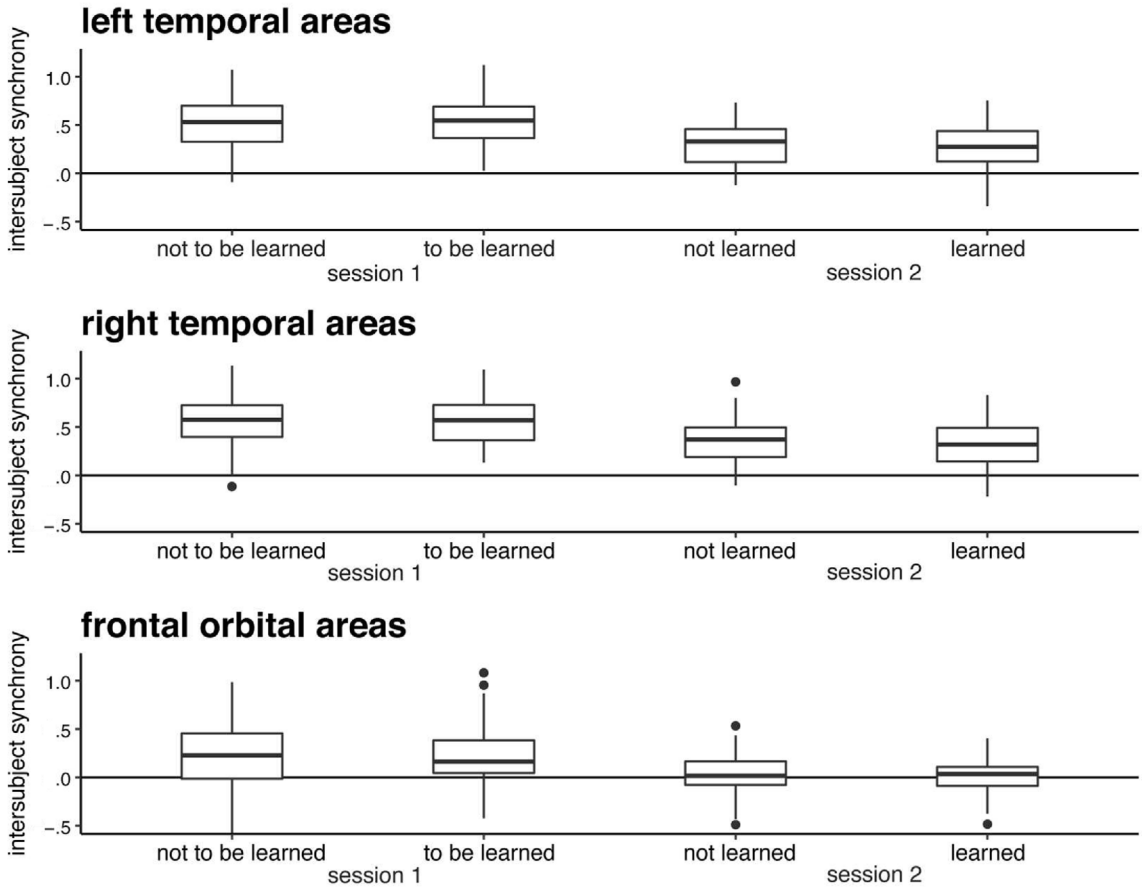

Fig. 2 – Synchrony values plotted for each of the three clusters for each of the learning conditions. The 'within session 1' and 'within session 2' synchrony values are shown here. Boxplots show the median value and contain values from the 25th to 75th percentile within each box. Whiskers represent 95% confidence intervals with outliers depicted as individual points.

session 2 learned and the session 2 not learned stimuli found no significant differences in synchrony in any of the clusters. Thus, there was no evidence that training altered synchrony within an individual.

We computed a correlation between the 'individual changes' synchrony values and each individual's average score on the lyric modification and melody memory tasks. The *p*-values were FWE corrected across all clusters. There were no significant correlations between the synchrony values from the familiar stimuli and the behavioural scores.

6. Study 2 results – older adults

6.1. *Participants*

The final sample size was determined based on the number of complete, useable datasets that were collected given the constraints placed on testing older adults during the COVID-19 pandemic. One participant did not complete the scan session due to technical difficulties and data from the long-known stimuli were not collected. A second participant withdrew from the study. A third participant was excluded because of excessive movement in the scanner (>2 mm displacement in *z*). Therefore, fMRI data from 12 individuals were included in the analysis.

6.2. *Stimulus familiarity*

Participants reported being much more familiar with the 'familiar stimuli' than the novel stimuli ($p < .001$). The average familiarity score for the two long-known stimuli was 4.9 ($SD = .06$) and the average familiarity score for the four novel stimuli was 1.3 ($SD = .13$). Participants also estimated having heard the long-known whole stimulus (*Hey Jude* by The Beatles) for the first time when they were an average age of 18.5 years ($SD = 2.9$) and having heard the long-known spoken stimulus ('*Twas the Night Before Christmas*) for the first time when they were an average age of 6 years ($SD = 2.2$). Therefore, all participants had known each of the long-known stimuli for more than 50 years.

6.3. *fMRI results*

The two *t*-contrasts investigating the differences in synchrony induced by the novel and long-known stimuli showed that there was significantly more synchrony to novel than long-known stimuli in bilateral temporal areas (clusters at FWE

Fig. 3 – The brain regions in which intersubject synchrony differed based on familiarity in the older and young adult data. All clusters were defined at $p < .05$ FWE. Green: Older adult novel > long-known t-contrast. The extent threshold was set to the FWEc value = 64. Magenta: Young adult session 1 to be learned > session 2 learned t-contrast. The extent threshold was set to the FWEc value = 128. Displayed slices are at $x = 47$, $y = -26$, $z = -2$.

$p < .05$; see Fig. 3). There were no regions with more synchrony to long-known than novel stimuli. Fig. 3 presents the overlap in the brain areas in which synchrony differed based on familiarity, as identified by the novel > long-known t-contrast in the older adult data and by a session 1 to be learned > session 2 learned t-contrast in young adults. The peak values from the older adult clusters for novel > long-known can be found in Table 3. The two familiarity by stimulus type interaction t-contrasts in the older adult data also found no significant differences in synchrony in any areas of the brain.

Table 3 – The coordinates of peak values from the significant clusters identified in the Older Adult novel > long-known t-contrast. The clusters were defined at $p < .05$ FWE. Peak values > 4 mm apart are listed.

Older Adults novel > long-known t-contrast extent = 64	
Posterior STG	−66, −18, 8
Posterior STG	−60, −22, 2
Anterior STG	−66, −8, 0
Posterior MTG	44, −26, −4
Planum polare	54, −4, −6
Planum polare	42, −22, −4
Planum polare	40, −18, −8
Planum polare	44, −14, −8
Planum polare	48, −14, −6
Heschl's gyrus	40, −28, 0
Anterior STG	64, −4, 0
Posterior STG	56, −22, −4
Posterior STG	50, −22, −4
Posterior STG	60, −20, −2
Posterior STG	56, −16, −4
Posterior MTG	42, −32, −2
Posterior MTG	46, −22, −6

7. Discussion

The current paper presents two studies exploring the effect of stimulus familiarity on intersubject synchrony in young and older adults. We investigated whether intersubject synchrony to auditory stimuli was affected by previous exposure to the stimulus in two ways: in the first study, young adults trained on novel stimuli using a controlled paradigm while in the second study, older adults listened to both novel and well-known stimuli. Behavioural measures in both age groups indicated that the trained or well-known stimuli were known significantly better than the novel stimuli. In young adults, the scores on the lyric modification task and the melodic memory task improved during the training period between the two fMRI scans, confirming that participants learned the stimuli over time. Moreover, an online follow-up study verified that the improvement in scores required training and was not simply a result of repeated exposure to the task itself (Sternin et al., 2021).

The intersubject synchrony in young adults was reduced between the two scanning sessions, but this exposure effect was not related to training. When synchrony within session one was compared to synchrony within session two, three clusters showed more synchrony in session 1 than 2: the bilateral temporal lobes, and a frontal orbital area. There was no interaction between session and training, and contrary to our hypothesis, synchrony decreased between the two sessions regardless of whether the stimuli had been learned or not. Thus, even for untrained stimuli, synchrony reduces after a single session, despite a three-week gap between sessions. Moreover, this synchrony change does not appear to be caused by substantial learning during a single session, as a previous study found participants did not improve in any behavioural learning measures when they did not train on the stimuli (Sternin et al., 2021). Some evidence of prolonged neural changes after exposure to auditory stimuli exists in the electroencephalography (EEG) and magnetoencephalography (MEG) literature (Tremblay et al., 2001, 2009). Early evoked responses, specifically the P200 event-related potential, increases in amplitude with repeated exposure to auditory stimuli and this increase is thought to reflect enhanced auditory representations of the stimuli (Tremblay et al., 2001, 2009). When participants heard a stimulus four times (baseline, 24 h later, one week later, up to one year later) the enhanced P200 persisted across the four sessions even when participants had not heard the stimuli for many months (Tremblay et al., 2010). The increased P200 amplitude occurred as a result of repeated exposure, regardless of behavioural evidence of learning (Tremblay et al., 2014). Temporal lobe areas, such as those that, in the current study, showed synchrony differences between session, have been implicated as the cortical sources of the increased P200 amplitude. Although these previous studies were not in fMRI, the results suggest that persistent neural changes can be induced in similar bilateral temporal areas that showed synchrony decreases across sessions without behavioural evidence of learning in

the current study. However, changes in ERP amplitudes are not directly related to synchrony measures. In fact, changes in the amplitude of neural activity that do not affect the pattern of fluctuation will have little effect on synchrony across individuals. However, intersubject synchrony is a fairly new analysis technique and little has been done to characterize synchrony changes and how they relate to other measures of neural activation to auditory stimulation. Therefore, the current results support the idea that a single exposure to a stimulus may be enough to cause neural changes that are reflected in synchrony analyses.

Given that there was more synchrony in session 1 than in session 2 to stimuli that had been heard once, heard multiple times, and even non-identical stimulus pairs it is likely that any number of additional factors beyond stimulus familiarity may be driving the synchrony reduction across sessions. We did not scan participants after each stimulus exposure. If synchrony steadily decreased in relation to the number of exposures to a stimulus, we would have expected synchrony differences between the learned (heard many times) and not learned (heard once before) stimuli in the second session. We did not find learned vs. not learned differences, indicating that the number of times participants had heard the stimuli was likely not related to the changes in synchrony. This is in contrast to the research presented above regarding EEG and MEG measures of neural changes induced by repeated exposure to auditory stimuli that show *progressive* increases in P200 amplitudes with increased stimulus exposure. However, the P200 amplitudes are a very fast neural response to auditory stimuli and may be a more sensitive measure of identifying neural changes as a result of stimulus exposure than intersubject synchrony.

If participants processed the stimuli equally differently in the second session in comparison to the first, it would be possible for synchrony, calculated 'within session 2', to not differ from the synchrony calculated 'within session 1' while the synchrony calculated by comparing an individual's second session data with their own first session data would be reduced. In other words, all participants could deviate from their first session 'baseline' synchrony by the same amount in the same direction resulting in individual changes across sessions but similar levels of synchrony within session 1 and session 2. Therefore, we calculated the 'individual changes' synchrony values to determine whether there were changes in how an individual processed the stimuli that may have been missed when synchrony was calculated using the average participant data within session 2. This analysis indicated that there was no difference in synchrony based on learning at the individual level; participants processed the stimuli in the second session differently than the way those same stimuli were processed in the first session regardless of whether the stimuli were learned or not.

In the second study, we found a similar effect of familiarity on synchrony in the older adults as was seen in young adults: greater synchrony to novel than to long-known stimuli. In older adults, these differences were present in bilateral temporal regions. Although the regions in the older adults were spatially smaller than the areas that differed between learned and not learned stimuli in young adults, there was overlap in the posterior STG on the left and Heschl's gyrus and posterior STG on the right. As was the case in young adults, the older adults did not synchronize more to the familiar than the novel stimuli in any brain regions. The results from both the older and young adult studies investigating the effects of familiarity on synchrony indicate that novel stimuli induce greater intersubject synchrony than stimuli that have been previously encountered over a short (3 weeks) or very long (50 years) period of time.

Strong intersubject synchrony is driven by similar neural responses across a group of individuals; higher similarity results in stronger synchrony. As individuals deviate from the group average and become less similar, the strength of the correlations is reduced. If participants each learned the stimuli to a different level of expertise or developed personal associations when listening to the stimuli over time, then they may have developed idiosyncratic responses to each learned stimulus. Such idiosyncrasies could have reduced the degree of synchrony across participants in the second session. For example, in the young adult study all stimuli in the first session were equally unfamiliar and synchrony was likely driven by the experience of hearing the stimulus for the first time (e.g. participants may be more attentive to the lyrics or melodic changes the very first time the stimulus is heard). In the second session, each participant's experience of the learned stimuli will have been slightly different. For example, one participant may have learned 100% of the lyrics after just a few exposures while another may only have known 75% of the lyrics by the end of training. Although we did not collect data regarding the percentage of the lyrics each participant learned, there is literature that speaks to differences in how individuals memorize music (Korenman & Peynircioglu, 2007; Mishra, 2011). This research suggests that the ease with which music is memorized depends greatly on participants' preferred learning style, learning strategies, and musical abilities. Although it is possible that individual differences in level of knowledge contributed to the idiosyncrasies in the second scanning session, there was a lack of correlation between the behavioural memory scores and the second session synchrony scores. This null result indicates, either that the reduction in synchrony was unrelated to differing levels of knowledge with the stimuli, or that our behavioural tasks were not sensitive enough to detect the subtle differences in familiarity across participants. The participants may also have listened to the songs while doing different activities, developing different associations that were recalled during scanning. Data regarding personal associations that participants may have made with each of the stimuli by the end of the training period were not collected and therefore we cannot speak to whether this was indeed a factor at play within this dataset. The differing levels of knowledge and personal associations created unique listening experiences in the second session for each participant and likely contributed to the reduction in synchrony across sessions.

As synchrony is affected by attention (Regev et al., 2019), it is possible that attentional differences between sessions reduced synchrony in the second session. For example, if participants attended more to the novel stimuli, this may have resulted in more synchrony within the first session. However, it is unlikely that the decreased second session synchrony is due solely to less attention to the stimuli themselves, as

synchrony decreased similarly to both the 'learned' and 'not learned' stimuli as well as to synchrony calculated between non-identical stimuli. Considering that participants did not train on the 'not learned' stimuli, and some participants reported not recognizing the 'not learned' stimuli in the second session, these stimuli may reasonably be considered as novel as they were in the first session. This result disputes the idea that the differences in synchrony across sessions were due solely to participants paying more attention to novel stimuli.

Changes in attention could also have resulted from familiarization with the scanner environment. To investigate this possibility, we compared synchrony in the first and second halves of session 1 (using the 'within session 1' synchrony values). If the reduction in synchrony across sessions was related to the time spent in the scanner, then there should have been less synchrony in the second than the first half of the session. However, only the left and right temporal clusters showed an effect of 'half' and in both clusters this difference was in the opposite direction: more synchrony in the second than the first half. Therefore, the synchrony reduction across sessions does not appear to be related to familiarity with the scanner environment.

Additionally, the reduction in synchrony across sessions was not due to any systematic changes in the testing environments between the two sessions as the data were collected serially over a 12-month period; many participants completed both of their scanning sessions before others had completed their first session. Given that attention was likely not different as a result of familiarity with the stimuli or familiarity with the scanner environment, we can rule out attention differences as the driving force behind the decrease in synchrony across the two scanning sessions.

Finally, although we did see a reduction in synchrony across sessions even when synchrony was calculated between non-identical stimuli, the decrease was significantly less than when synchrony was calculated between identical stimuli. Therefore, even if some of the synchrony reduction can be attributed to the environment or other factors as discussed above, the larger decrease is likely to be driven by participants' neural responses to the stimuli.

We do acknowledge that although the young adults trained on only half of the stimuli over the course of the experiment, no stimuli they experienced in the second session were entirely novel (although anecdotally, after having completed the second session, participants did not remember having ever heard the stimuli they did not train on). This arguably creates a confound of familiarity and session. However, the data collected from the older adult participants may shed light on understanding this confound in the young adults. The data collected in the older adults showed the same pattern of increased synchrony to novel stimuli even though the novel and the familiar stimuli were heard in the same scanning session. This suggests that the synchrony results in the young adult data are related to stimulus familiarity despite the familiarity/scanning session confound. However, a complete understanding of the synchrony reduction between session 1 and 2 in the young adult data should be investigated further.

The current paper presents data in young and older adults to understand how previous exposure to a stimulus influences intersubject synchrony. We expected that synchrony would decrease as exposure to the stimuli increased. Rather than an effect of stimulus training in young adults, we found a session effect where there was reduced synchrony in the second session compared to the first regardless of whether the stimuli had been learned or not. We also found that older adults, like young adults, show a reduction in synchrony to familiar stimuli. However, given the design of the experiment, we cannot say whether the reduction to long-known stimuli seen in older adults is greater than the reduction in stimuli in recently learned stimuli in young adults. This reduction may be related to an increase in idiosyncratic responses after exposure to a stimulus but does not seem to be related to how well the stimuli are learned or differences in attention. To further characterize how synchrony changes with repeated exposure, this result should be replicated in future studies using different types of stimuli (e.g. movies and stories) and measures of attention, engagement, and personal associations should be collected. The consistent reduction in synchrony after previous exposure has implications for studies using intersubject synchrony measures. If, for example, participants' degree of exposure to a stimulus systematically varies with the experimental conditions, this could complicate interpretation of the results. It will be important to further investigate this effect by collecting synchrony data after each stimulus exposure to further characterize the reduction in synchrony. Until the effects of repeated exposure on synchrony are fully understood, future studies using intersubject synchrony, where the novelty of the stimuli cannot be guaranteed, may consider exposing all of their participants to the stimuli once before data are collected to mitigate the effects of any systematic differences in stimulus exposure.

CRediT author statement

Avital Sternin: conceptualization, methodology, software, formal analysis, investigation, data curation, writing – original draft, writing – review & editing.

Lucy M. McGarry: conceptualization, writing – review & editing.

Bobby Stojanoski: methodology, software.

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Adrian M. Owen: conceptualization, methodology, writing – review & editing, supervision, funding acquisition.

Data availability

No parts of this study procedures or analyses were preregistered prior to the research being conducted.

All stimuli, analysis scripts, raw fMRI data, and behavioural data can be accessed at: https://osf.io/467ae/?view_only=ec5b37b8955c47d2bd03f673875c03c0.

Open Practices

The study in this article earned Open Data and Open Material badges for transparent practices. The data and materials used

in this study are available at: https://osf.io/467ae/?view_only=ec5b37b8955c47d2bd03f673875c03c0.

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Supplementary data

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