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Authors

Zanto, Theodore P
Johnson, Vinith
Ostrand, Avery
et al.

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How musical rhythm training improves short-term memory for faces

Theodore P. Zanto^{a,b,1} , Vinith Johnson^{a,b}, Avery Ostrand^{a,b}, and Adam Gazzaley^{a,b,c,d}

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Playing a musical instrument engages numerous cognitive abilities, including sensory perception, selective attention, and short-term memory. Mounting evidence indicates that engaging these cognitive functions during musical training will improve performance of these same functions. Yet, it remains unclear the extent these benefits may extend to nonmusical tasks, and what neural mechanisms may enable such transfer. Here, we conducted a preregistered randomized clinical trial where nonmusicians underwent 8 wk of either digital musical rhythm training or word search as control. Only musical rhythm training placed demands on short-term memory, as well as demands on visual perception and selective attention, which are known to facilitate short-term memory. As hypothesized, only the rhythm training group exhibited improved short-term memory on a face recognition task, thereby providing important evidence that musical rhythm training can benefit performance on a nonmusical task. Analysis of electroencephalography data showed that neural activity associated with sensory processing and selective attention were unchanged by training. Rather, rhythm training facilitated neural activity associated with short-term memory encoding, as indexed by an increased P3 of the event-related potential to face stimuli. Moreover, short-term memory maintenance was enhanced, as evidenced by increased two-class (face/scene) decoding accuracy. Activity from both the encoding and maintenance periods each highlight the right superior parietal lobule (SPL) as a source for training-related changes. Together, these results suggest musical rhythm training may improve memory for faces by facilitating activity within the SPL to promote how memories are encoded and maintained, which can be used in a domain-general manner to enhance performance on a nonmusical task.

musical rhythm training | short-term memory | electroencephalography | superior parietal lobule

Playing a musical instrument engages numerous cognitive abilities (1–3). Notably, sensory perception is critical to receiving feedback, temporal attention (selective attention to time) is required to track the beat and adjust timing, and short-term/working memory is needed to maintain the intended musical template by which movements are produced and errors are judged. While this is a simplified view into a much more complicated behavior, the point is that in order to successfully produce music, multiple cognitive functions are needed and they must work together in concert. It is therefore not surprising that by engaging different cognitive functions during musical performance, those same cognitive functions may become improved following musical training, which include temporal attention, sensory processing, and short-term memory (4–10). Yet, the extent to which these trained cognitive abilities may benefit performance on other (nonmusical) tasks remains controversial (11–14). Compounding the issue is a paucity of data identifying the mechanism by which such transfer of benefit may occur (15), if transfer were to occur at all. Therefore, the goal of this research was to employ a randomized clinical trial to directly assess whether musical training may facilitate performance on a nonmusical task, and, if observed, assess neural mechanisms underlying the transfer of benefit.

One of the most commonly reported benefits of musical training is improved short-term/working memory. Due to domain-specific expertise, it is easy to understand why memory for tonal structures would be enhanced in musicians (16–18). It is less clear why musicians would also exhibit greater verbal (18–23) or visual (18, 22–29) short-term memory, although improvements in these domains may be more modest than domain-specific improvements or not present at all (9, 18, 27, 28). It is generally accepted that a transfer of benefit to verbal or visual short-term memory, if indeed present, stems from shared processes that were engaged during training (30–32). Given the numerous cognitive functions engaged during musical performance, here we consider three possible mechanisms by which short-term memory may be enhanced via musical training.

One possibility is that musical training may facilitate sensory processes that would increase the fidelity of information encoded into short-term memory. Indeed,

Significance

Musical training can improve numerous cognitive functions associated with musical performance. Yet, there is limited evidence that musical training may benefit nonmusical tasks and it is unclear how the brain may enable such a transfer of benefit. To address this, nonmusicians were randomized to receive 8 wk of either musical rhythm training or word search training. Memory for faces was assessed pre- and post-training while electroencephalography data were recorded to assess changes in brain activity. Results showed that only musical rhythm training improved face memory, which was associated with increased activity in the superior parietal region of the brain when encoding and maintaining faces. Thus, musical rhythm training can improve face memory by facilitating how the brain encodes and maintains memories.

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Competing interest statement: A.G. is co-founder, shareholder, BOD member, and advisor for Akili Interactive Labs, a company that produces therapeutic video games.

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¹To whom correspondence may be addressed. Email: theodore.zanto@ucsf.edu.

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musicians exhibit sharpened auditory perceptual processes (7, 33–36) and greater gray matter within auditory cortex (37, 38). This, in turn, may lead to enhanced phonemic discrimination ability and subsequent verbal short-term memory (39, 40). Although it is unclear whether similar sensory improvements may occur in the visual domain, dynamic visual acuity is known to improve following engagement with tasks that place demands on dynamic visual acuity (41, 42). Thus, musical training that taxes dynamic visual acuity, such as moving the eyes and head to rapidly identify a piano key or drum pad to hit, may improve visual perception and subsequently enhance the fidelity of items encoded into visual short-term memory.

A second possibility is that music related improvements in sensory processing may stem from changes in selective attention (43, 44), as selective attention is known to bias sensory processes and subsequently affect short-term memory (45, 46). In support of this, research has shown a relationship between selective attention ability and musical aptitude (44, 47), and that musical training facilitates neural mechanisms of selective attention (20, 48, 49). Of note, this musicianship advantage is not specific to when selective attention is oriented to auditory or visual stimuli, but also when attention is oriented to time (i.e., temporal attention) (50–53). This is important because orienting attention to when a relevant stimulus is expected can facilitate short-term memory performance (54–56).

A third and more straightforward possibility is that musical training engages neural regions that are utilized by short-term memory in nonmusical tasks. Some research has supported the possibility that musical structures and language both share neural regions involved in short-term/working memory function (23), which encompasses frontoparietal regions (57–59). Similar results are observed in the visual domain. Specifically, when musicians sight-read a musical score, this engages short-term/working memory processes (among others), and is known to involve increased activity within Broca's area, the superior parietal lobule, and motor regions (60). Moreover, musicians exhibit increased gray matter in both Broca's area and the superior parietal lobule (37, 61). As such, Broca's area and the superior parietal lobule are neural regions engaged by musical training and may serve as candidate frontoparietal regions that may enable improved short-term memory on a nonmusical task.

Despite these three reasonable hypotheses on the mechanistic basis for how musical training may facilitate short-term memory (i.e., sensory, selective attention, or shared resources), evidence supporting one over the other remains lacking. Here, we addressed these three possibilities by randomizing older adult nonmusicians to receive either digital musical rhythm training or word search training as control. Older adults were assessed because of known age-related declines in short-term memory (62, 63), sensory processing (64–66), and selective attention abilities (67–70), which will avoid ceiling effects that may otherwise hinder the detection of training-related changes. Whereas the rhythm training paradigm placed specific demands on visual tracking (sensory processing), temporal attention, and short-term memory, the control training had little-to-no such demands on these cognitive functions. Therefore, it was hypothesized that only the rhythm training group would exhibit enhanced short-term memory ability.

Visual short-term memory was assessed pre- and post-training through a categorically cued delayed match to sample task. We have previously used this task to demonstrate an age-related decline in visual short-term memory for faces (68). While participants were engaged in the short-term memory task, electroencephalography (EEG) data were recorded. To assess potential

training-related changes in sensory processing, analysis focused on the P1 and N1 amplitudes of the event-related potential (ERP) to face stimuli that were to be encoded. These ERP components are known to reflect perceptual processing in sensory-selective regions (71–74). Moreover, we have previously shown that visual perceptual training can alter this index of sensory processing and subsequently improve visual short-term memory performance in older adults (65). To assess potential changes in selective attention, we evaluated whether these ERP components were modulated based on cue type (i.e., valid or neutral cues). Indeed, we have previously used this task, and other similar short-term memory tasks, to demonstrate that age-related declines in short-term memory may be attributed to deficient selective attention processes (67, 68, 75, 76). Furthermore, temporal attention was characterized based on anticipatory (prestimulus) activity as indexed by the contingent negative variation and alpha (8 to 12 Hz) activity, which we have also shown to be deficient in older adults (70). Finally, to test the possibility that musical rhythm training enhanced short-term memory via shared short-term memory processes, analysis focused on the P3 amplitude of the ERP. The P3 has been associated with short-term memory encoding (77, 78) and age-related declines in short-term memory ability (75, 79). Additionally, to assess potential training-related changes in short-term memory maintenance, delay period activity was assessed using a two-class (face/scene) machine learning algorithm, as prior work has demonstrated that short-term memory contents may be stored in hidden states that may be decoded (80–82). Together, analysis of the EEG data during the short-term memory task provides important evidence as to whether training-related improvements in short-term memory may be attributed to alterations in sensory processing, selective attention, or short-term memory function.

Results

Effects of Musical Rhythm Training on Short-Term Memory Performance. Short-term memory accuracy and response times were each submitted to an ANOVA with group (Rhythmicity, control), cue (cued, neutral), and session (pre, post) as factors. Results from the accuracy data indicated no main effects for cue ($F_{1,35} = 1.89$, $P = 0.18$, partial eta squared [η_p^2] = 0.05), session ($F_{1,35} = 0.92$, $P = 0.34$, $\eta_p^2 = 0.03$), or group ($F_{1,35} = 0.15$, $P = 0.70$, $\eta_p^2 = 0.004$). Importantly, a group \times session interaction was observed ($F_{1,35} = 5.46$, $P = 0.025$, $\eta_p^2 = 0.13$). Assessment of this interaction showed that only the rhythmicity group exhibited a significant improvement in short-term memory accuracy post-training ($t_{17} = 2.18$, $P = 0.044$, $d = 0.52$; Fig. 1 and *SI Appendix, Fig. S1*), not the control group ($t_{18} = -1.02$, $P = 0.32$, $d = 0.22$). Of note, this improvement in short-term memory within the rhythmicity group cannot be attributed to a change in response bias (see *SI Appendix, Supplementary Results*). Furthermore, results are slightly more significant when the participant associated with the outlying data point (lowest accuracy in Fig. 1) is removed from analysis. Direct comparisons between groups indicate no differences pretraining ($t_{35} = 1.36$, $P = 0.18$) or post-training ($t_{35} = 0.87$, $P = 0.39$). No other interactions were observed (group \times cue: $F_{1,35} = 0.74$, $P = 0.40$, $\eta_p^2 = 0.02$; session \times cue: $F_{1,35} = 0.74$, $P = 0.40$, $\eta_p^2 = 0.02$; group \times session \times cue: $F_{1,35} = 1.82$, $P = 0.19$, $\eta_p^2 = 0.05$).

Results from the response time data indicated no main effects for cue ($F_{1,35} = 0.34$, $P = 0.56$, $\eta_p^2 = 0.01$), session ($F_{1,35} = 0.84$, $P = 0.37$, $\eta_p^2 = 0.02$), or group ($F_{1,35} = 0.28$, $P = 0.60$, $\eta_p^2 = 0.008$). Moreover, no interactions were observed

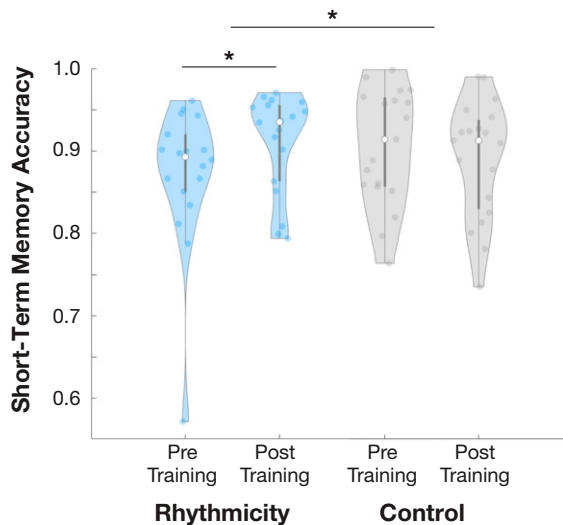


Fig. 1. Short-term memory accuracy for the Rhythmicity (blue) and control (gray) groups. * $P < 0.05$.

(group \times session: $F_{1,35} = 0.02$, $P = 0.88$, $\eta_p^2 = 0.001$; group \times cue: $F_{1,35} = 1.11$, $P = 0.30$, $\eta_p^2 = 0.03$; session \times cue: $F_{1,35} = 3.15$, $P = 0.085$, $\eta_p^2 = 0.08$; group \times session \times cue: $F_{1,35} = 1.07$, $P = 0.31$, $\eta_p^2 = 0.03$). Together, these results demonstrate musical rhythm training specifically improves short-term memory accuracy on a nonmusical task.

Neuroplastic Changes following Musical Rhythm Training. To assess whether rhythm training-related improvements in short-term memory may have resulted from enhanced cognitive processes, neural indices associated with anticipatory processes (selective [temporal] attention), early encoding (sensory processes), and late encoding (short-term memory) were submitted to ANOVAs with group (Rhythmicity, control), cue (cued, neutral), and session (pre, post) as factors. Analysis of the anticipatory (contingent negative variation [CNV], alpha band) activity as well as the early encoding activity (P1, N1) exhibited no effects based on musical rhythm training (see *SI Appendix, Supplementary Results and Fig. S2*), indicating temporal attention and sensory processes were unaffected by training, respectively.

Analysis of the late encoding stages associated with short-term memory processes were indexed by the P3 global field power (GFP) (Fig. 2*A* and *SI Appendix, Fig. S3*). Results indicated no main effects for cue ($F_{1,35} = 0.28$, $P = 0.60$, $\eta_p^2 = 0.008$), session ($F_{1,35} = 0.25$, $P = 0.62$, $\eta_p^2 = 0.007$), or group ($F_{1,35} = 0.00$, $P = 0.96$, $\eta_p^2 = 0.000$). However, a group \times session interaction was observed ($F_{1,35} = 8.87$, $P = 0.005$, $\eta_p^2 = 0.20$). Assessment of this interaction was conducted by using an independent samples t test comparing the change in the P3 (pre versus post) within each group. Results showed that musical rhythm training increased the P3 GFP (Fig. 2*B*; $t_{17} = 2.66$, $P = 0.017$), unlike for the control group ($t_{20} = -1.62$, $P = 0.12$). Comparisons between groups indicate no differences pretraining ($t_{35} = 0.87$, $P = 0.39$) or post-training ($t_{35} = 0.87$, $P = 0.39$). No other interactions were observed (group \times cue: $F_{1,35} = 0.18$, $P = 0.67$, $\eta_p^2 = 0.005$; session \times cue: $F_{1,35} = 0.59$, $P = 0.45$, $\eta_p^2 = 0.02$; group \times session \times cue: $F_{1,35} = 2.23$, $P = 0.14$, $\eta_p^2 = 0.06$).

To characterize the neural regions that gave rise to this change in the P3, source localization was conducted. Permutation tests were used to compare within groups pre/post-training. Results from the rhythmicity group exhibited a significant increase in P3 activity post training within the right postcentral gyrus and superior parietal lobule (Fig. 2*C*; maximal difference Montreal Neurological Institute (MNI) template: X = 10, Y = -45, Z = 70). Smaller, albeit significant, increases were also observed in the right lateral occipital cortex and left frontal pole. No significant increases in activity were observed in the control group pre- to post-training. Together, these results indicate that musical rhythm training facilitates late stages of short-term memory encoding, which involves increased activity largely within the postcentral gyrus and superior parietal lobule.

Alterations in Decoding Short-Term Memory. It was hypothesized that if musical rhythm training facilitated short-term memory maintenance, this should be reflected by changes in classification accuracy during the maintenance period. Results from the two-class (face/scene) decision tree classification analysis on the maintenance period singular vector (see *Materials and Methods; SI Appendix, Fig. S4*) demonstrated a significant

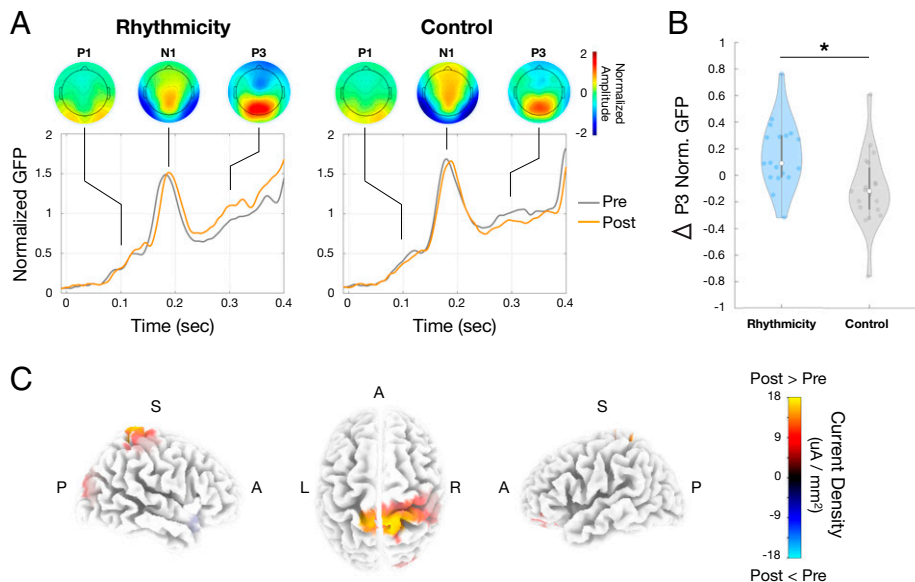


Fig. 2. ERPs to the encoded stimuli. (A) GFP time series and topographies for each group. Topographies are averaged across sessions for display purposes. (B) Change in P3 GFP (post/pre-training). * $P < 0.05$. (C) Differences (post/pre-training) from the Rhythmicity group in the P3 source localization. Only significant differences are shown. A, anterior; P, posterior; R, right; L, left; S, superior.

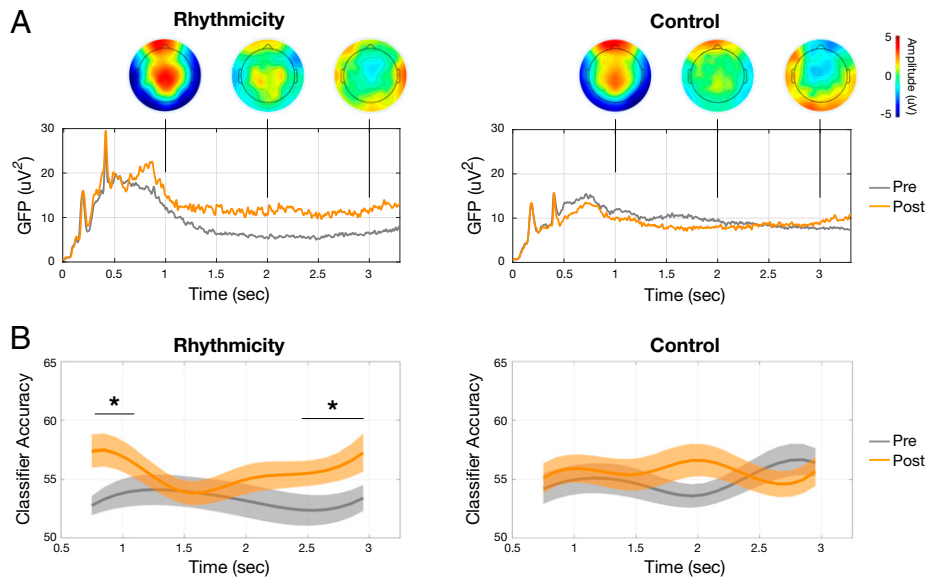


Fig. 3. Neural activity during short-term memory maintenance. (A) GFP time series and topographies for each group. Topographies are averaged across sessions for display purposes. (B) Classification accuracy for each group. Shaded area represents SEM. * $P < 0.05$.

increase in classification accuracy following musical rhythm training (Fig. 3B; $P < 0.05$). This increase in face/scene decoding was only observed at the beginning and end of the maintenance period. No such changes in the classification accuracy was observed in the control group. No differences were observed between groups pre- or post-training (all $P > 0.09$). Assessment of the confusion matrices (SI Appendix, Fig. S5), as well as sensitivity and specificity performance of the classifier (SI Appendix, Table S1), demonstrated that the highest accuracies achieved was in the rhythmicity group post-training, specifically for face stimuli (i.e., true positive: actual face/predicted face).

To characterize the neural regions that gave rise to the enhanced memory decoding after rhythm training, source localization was conducted and permutation tests were used to compare pre/post-training within each group. Results from the rhythmicity group demonstrated a significant ($P < 0.05$) post-training increase in activity within the right superior parietal lobule (Fig. 4; MNI: X = 25, Y = -50, Z = 70). Comparing pre/post-training in the control group showed no significant increases. Together, these results indicate that musical rhythm training facilitates short-term memory maintenance as evidenced by enhanced decoding, which involves increased activity within the right superior parietal lobule.

Relationship between Training and Transfer. An exploratory analysis was conducted in the rhythmicity training group by correlating training performance with changes (post-/pre-training) in our

outcome (transfer) measures (i.e., memory accuracy, P3 GFP, classification accuracy). Training performance focused on the mean level achieved during the final week of training and the change in the performance variability across the 8 wk of training. Performance variability was calculated as the SD of the tap asynchrony (difference between when a tap occurred and when it should have occurred), then this was averaged across each week. The change in performance variability was then characterized as the slope of a line fitting the performance variability across the 8 wk of training.

Results from a Spearman's correlation with the mean final rhythmicity level exhibited a significant correlation with the change in short-term memory accuracy ($r = 0.50$, $P = 0.043$; SI Appendix, Fig. S6A), such that participants who achieved the highest levels of performance at the end of training were those who exhibited the greatest improvements in short-term memory accuracy. No such relationship was observed with the P3 GFP ($r = 0.20$, $P = 0.44$) or classifier accuracy ($r = -0.09$, $P = 0.74$). Results from a Spearman's correlation with the change in performance variability demonstrated a significant correlation with the change in the classifier accuracy ($r = 0.53$, $P = 0.031$; SI Appendix, Fig. S6B). The positive correlation indicates that those participants who were most challenged by the memory component of the training (i.e., higher variability during weeks 5 to 8 when the cues disappeared) were the ones who exhibited the largest increase in classification accuracy. No such relationship was observed with short-term memory accuracy ($r = -0.12$, $P = 0.66$) or P3 GFP ($r = 0.25$, $P = 0.34$).

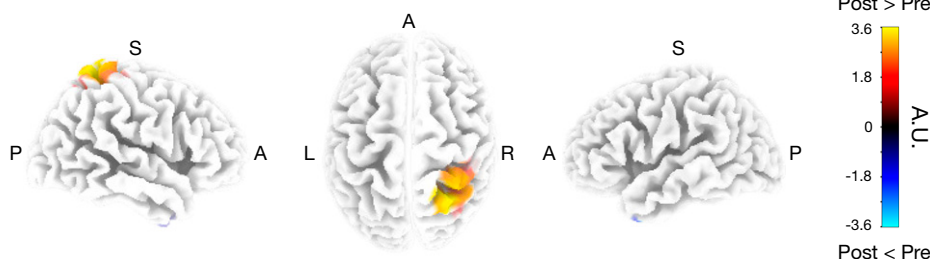


Fig. 4. Differences (post-/pre-training) in the source localization of the spatial coefficients from the maintenance period in the Rhythmicity group. Only significant differences are shown. A, anterior; P, posterior; R, right; L, left; S, superior.

Discussion

In this study, we assessed whether musical rhythm training would yield improved performance on a visual short-term memory task, and what neuroplastic changes may underlie such transfer of benefit. Results showed an improvement in visual short-term memory specifically in the rhythm training group, and not in the control group. Interestingly, participants who achieved higher levels of training were the ones who exhibited the greatest improvements in short-term memory for faces. This provides important evidence that musical rhythm training can indeed transfer benefit to non-musical tasks. To assess whether this improvement arose from neuroplastic changes associated with sensory processing, selective attention, or short-term memory, EEG data were assessed. Results indicated no change in neural activity associated with sensory processing, as indexed by the P1 and N1 of the ERP. Similarly, no change in neural activity associated with selective attention was observed, as indexed by a lack of change in cue-based modulation of the P1, N1, CNV, or anticipatory alpha band activity. However, the rhythm training group, but not controls, exhibited enhanced short-term memory encoding, as indexed by the P3 of the ERP to face stimuli. Similarly, only the rhythm training group exhibited enhanced short-term memory maintenance, as evidenced by increased decoding accuracy of the short-term memory contents. Changes in both short-term memory encoding and maintenance were localized to alterations within the right superior parietal lobule. Although the musical rhythm training placed demands on sensory processing, selective attention, and short-term memory, we provide intriguing evidence that musical rhythm training selectively taxes short-term memory resources within the superior parietal lobule to facilitate the encoding and maintenance of visual short-term memory in a nonmusical task.

Transfer of Benefit. The fact that musical rhythm training generalized to improve short-term memory for faces is noteworthy in its own right. It is known that cognitive interventions typically improve the trained cognitive domain (31, 83). However, the musical rhythm training paradigm did not place any demands on short-term memory for face stimuli. It is recognized that the visual cues (aliens) had faces, but it is a stretch of the imagination to think this feature may have played a role in facilitating short-term memory function. Rather, data suggest this transfer of benefit occurred via shared short-term memory resources between the training and outcome tasks.

In an exploratory analysis assessing the relationship between training and transfer, we showed that those participants who reached the highest levels of rhythm training were the ones who showed the largest improvements in transfer (short-term memory accuracy). This relationship highlights the importance of acquired musical skill in facilitating nonmusical cognitive abilities and supports prior work demonstrating that short-term/working memory performance is related to musical sophistication (84) and the duration of musical training (85). We also observed a relationship between the change in performance variability across the training period and the change in classification decoding accuracy. Specifically, those participants who were most challenged by the memory component of the training (i.e., higher variability during weeks 5 to 8 when the cues disappeared compared to weeks 1 to 4 when cues were ever-present) were the ones who exhibited the largest increase in decoding accuracy. Conversely, participants who were not challenged by the memory task (i.e., less impacted when the cues disappeared) were the ones who did not exhibit much (if any) improvement in decoding accuracy. This finding supports the

notion that transfer is best facilitated by challenging the same cognitive function between the training and transfer tasks (86). Thus, musical training, and cognitive training more broadly, will likely be most beneficial when the training is hard enough to deeply engage the target cognitive ability.

Together, these results provide important insight as to why prior research has repeatedly demonstrated differences in cognitive performance and neural activity between musicians and nonmusicians. Yet, it needs to be recognized that 2 mo of musical rhythm training, as conducted here, does not make these participants musicians. Indeed, no participant was able to achieve performance at the highest levels of the rhythmicity game, where participants are required to tap at the rate of 16th notes. Through pilot testing, we observed that typically only musicians (10 or more years of experience) were able to achieve such performance in rhythmicity. It is therefore not surprising that 2 mo of rhythm training was insufficient to reach musician-level drumming performance. Importantly, this can help explain why these groups did not statistically differentiate from each other when assessed at isolated time points. Rather, each group differentially altered their performance and neural activity following their respective intervention as hypothesized. In order to observe larger group effects, a longer duration of musical rhythm training will likely be required. Indeed, participants who reached higher levels of training were the ones who exhibited greater benefits in short-term memory performance. Thus, group differences in short-term memory will likely be most prominent when sufficient training has been done so that one group may be considered a “musician.” Future longitudinal research should track the progression from nonmusician to musician and how that may gradually alter nonmusical cognitive abilities over time.

The implications for this research extend to real-world practical benefits of engaging musical training, as deficient memory for faces can create an awkward social situation when forgetting someone you just met. Here we demonstrated that 2 mo of musical rhythm training was sufficient for a within-group improvement of 4% in short-term memory for faces, resulting in a moderate ($d = 0.52$) effect size. While it is unclear whether such a modest improvement would be noticeable in everyday life, we expect many years of musical training (as required to be considered a musician) would yield larger effects on short-term memory performance. Indeed, years of musical training has been associated with preserved cognitive abilities in aging (87), lowered risk of dementia (88), and delayed onset of dementia (89). Importantly, we demonstrate that the cognitive benefits from musical rhythm training are not relegated to those who can afford an instrument and professional in-person instruction. Through the use of a digital training paradigm conducted at-home without professional instruction, short-term memory was improved, which highlights the success of closed-loop adaptive algorithms in facilitating cognitive function (86, 90–92).

It remains to be seen whether improvements in short-term memory may be observed in a healthy young adult population in such a short amount of time, as their short-term memory ability typically has less room for improvement. Prior research has indicated that the benefits of behavioral interventions may be most pronounced in populations with the greatest need (93, 94). It is possible that longer durations of training may be needed as ability approaches ceiling. Yet, it is unclear how much musical training is sufficient to promote cognitive function. Paradoxically, some research has shown that amateur musicians exhibit metrics of more youthful brains compared to professional musicians (95). This begs the question as to whether there is an optimal amount

of time to spend on musical training for cognitive benefits, where professional-level training may take away time from other cognitively enriching activities.

Mechanisms of Transfer. These results provide novel mechanistic insight as to how such a transfer of benefit may occur. Specifically, musical rhythm training was associated with an increased P3 amplitude and enhanced short-term memory classification (decoding) accuracy, which serves to index improvements in short-term memory encoding and maintenance, respectively. These changes in encoding and maintenance were localized to alterations within the right superior parietal lobule. We interpret these findings as evidence for short-term memory processes that are shared between the rhythm training paradigm and the visual short-term memory task. In support of this interpretation, the superior parietal lobule is known to be involved in visual aspects of musical performance (e.g., sight-reading sheet music) (60), as well as involved in visual short-term/working memory in nonmusical tasks (96, 97). Moreover, compared to nonmusicians, musicians engage the superior parietal lobule to a greater extent during short-term/working memory (16, 17, 59) and have larger gray matter volume in this region (37, 61). Therefore, we suggest that the superior parietal lobule was utilized not just in short-term memory for faces as observed in our outcome measure, but also it was likely utilized during training to encode rhythmic patterns, which include both spatial and temporal information. This interpretation supports prior behavioral research indicating that musical training improves domain-general, or shared, short-term memory resources (98).

It is recognized that additional research will be required to assess neural activity during the musical training sessions to provide stronger evidence that the superior parietal lobule is engaged during both the training and short-term memory outcome task. However, it is unclear what the alternative case may be if a shared resource is not the source of transfer. How else would transfer occur if training did not engage the same (or related) process? This is why it is generally acknowledged that cognitive interventions will commonly exhibit a near-transfer of benefit (31, 83), where training facilitates performance on different tasks that use the same cognitive ability that was trained.

Role of the Superior Parietal Lobule. An important question remains regarding the precise role of the superior parietal lobule in supporting short-term memory function. The current results along with prior research indicate the superior parietal lobule is involved in numerous forms of short-term memory content, including musical sound, auditory verbal, visual verbal, visual objects (e.g., faces, shapes), visuospatial, and musical notation (16, 60, 74, 99–102). As such, it seems unlikely that the superior parietal lobule would be involved in encoding or maintaining specific content of the stimuli. Whereas the observed change in classification accuracy following musical training could suggest content-specific decoding, it is more probable that this reflects an abstract process that systematically varies based on content. Indeed, research has shown that the superior parietal lobule is more involved in the manipulation, rather than maintenance, of short-term memory contents (103) and that its role in short-term/working memory may be that of attentional control (102, 104). In this framework, we speculate that the superior parietal lobule during the short-term memory task manipulated the face/scene neural representations in a way that would enable the efficient storage and later retrieval of the contents. This would help explain why the results from our classification analysis only exhibited a significant change at the

beginning and end of the maintenance period. Perhaps this was indicative of a process that helps encode and retrieve information, such as the allocation of attention toward the memory content, which would bias neural activity in regions that maintain the stimuli (74, 99, 105).

Although this interpretation is speculative, it is not unwarranted. It is well established that short-term memory contents may be stored in hidden states (80–82). Importantly, refreshing the contents of short-term memory (i.e., orienting attention to specific memory content) relies on a network of frontoparietal regions, including the superior parietal lobule (106), which results in enhanced classification accuracy (107). In addition to refreshing, the superior parietal lobule has been associated with encoding the contents of short-term memory (16, 108) as well as episodic memory (105, 109), and is thought to play a role in a frontoparietal network guiding the top-down allocation of attention in the service of memory encoding (74, 99, 105). Yet, the interpretation of the superior parietal lobule having an attentional role is not in conflict with our results, indicating changes in short-term memory were not attributed to selective attention processes. It is known that attention can operate during both perceptual and post perceptual processing stages (110). The current results showed that selective attention (including temporal attention) did not bias neural activity in anticipation of a stimulus or during early visual (perceptual) processing stages. Rather, the superior parietal lobule exhibited training-related changes during post perceptual processing stages. Therefore, it is reasonable to presume that changes in the superior parietal lobule resulted in enhanced attentional allocation to the internal representation of the stimuli. It is this attentional process that may bias neural activity in regions that maintain the stimulus content to facilitate the encoding and retrieval of said content.

Results demonstrated that training-related alterations within the superior parietal lobule occurred specifically within the right hemisphere. This is interesting given research suggesting rhythm processing may be left lateralized (111–113). However, others have shown that nonmetrical auditory stimuli that do not follow a steady repeating pattern evoke more right lateralized activity (114, 115), which may help explain the right lateralized activity observed here, as the short-term memory task did not utilize metrical rhythms. This would also support our interpretation that the metrical rhythm performance aspect of the training did not underlie the improved short-term memory for faces, but rather, encoding rhythms into memory during the training facilitated the transfer effects. Yet, lateralized rhythmic processing is generally attributed to auditory sensory processing regions within the temporal lobe, not superior parietal lobule. Prior research has demonstrated that the right superior parietal lobule, compared to the left, mediates visuospatial attention and has stronger anatomical connections with the frontal lobe and contralateral parietal cortex (116). Furthermore, the right superior parietal lobule in older adults has been associated with short-term memory, whereas the left superior parietal lobule was associated with executive function/working memory (100). Together, these studies support our interpretation that the right superior parietal lobule played a role in allocating attention to facilitate short-term memory.

Controlling Previous Confounds. These results support mounting evidence that musical training can facilitate visual short-term memory on nonmusical tasks (18, 22–29). Yet, much of this research to date has been through cross-sectional research that compares musicians to nonmusicians. As such, there is the possibility that preexisting differences between these groups

may underlie both their pursuit of musical training and short-term memory ability (13, 14). Through the use of a randomized clinical trial design, we directly addressed this potential confound and show that preexisting differences that may bias someone toward musical training do not account for training-related changes in short-term memory. This is evidenced through the recruitment of older adult nonmusicians who have had a lifetime of opportunity to learn music, but did not. Moreover, participants were recruited for this study without their knowledge of the specific music/word search interventions used in the study. It is safe to say that these participants were not predisposed toward learning music.

Another common potential confound of cognitive interventions (not just musical training) is a lack of control for how the expectation of training may affect performance on the outcome measures (83). Here, we conducted an experiment prior to conducting this interventional study and showed that both training paradigms (musical training, word search training) resulted in comparable expectation of benefit on the visual short-term memory (outcome) task. Thus, our results not only support prior research indicating a benefit from musical training on short-term memory ability, but extend these findings to show that such benefit is not attributable to group differences in predispositions or expectations.

Summary. Overall, these results contribute to a growing literature indicating musical training yields cognitive benefits on nonmusical short-term memory tasks. Importantly, it was shown that these benefits in short-term memory were not attributable to group differences in their predisposition for musical training or an expectation of benefit from training. Analysis of neural activity indicated that training-based benefits in short-term memory were not due to alterations in sensory or selective attention processes. Rather, neural activity during the short-term memory encoding and maintenance periods indicated a training-related change in activity in the right superior parietal lobule. Engagement of this region was interpreted as evidence for increased attentional control that facilitated the encoding and retrieval, but not storage, of the short-term memory contents. Thus, musical training that places demands on short-term memory for rhythmic patterns in space and time facilitates domain-general, or shared, attentional processes that enable enhanced short-term memory for face stimuli.

Materials and Methods

Procedure. In this preregistered study (Open Science Framework; <https://osf.io/fynpd>), participants were randomized to either a musical rhythm training (Rhythmicity) group or a word search training (control) group. Each group engaged with the training paradigm for 8 wk (5 d per week, ~20 min per day) in their own home. At pre- and post-training, participants were assessed in-laboratory on their short-term memory ability, which serves as the primary outcome measure for this study. Temporal attention, sensorimotor synchronization, and target detection data were collected but not reported here, as they are outside the scope of the short-term memory hypotheses. While engaged in the outcome assessments, EEG data were recorded.

Participants. Forty-seven older adult nonmusicians aged between 60 and 79 y were recruited for this study (24 females). Nonmusicians were defined as having less than 3 y of formal instrument, song, or dance instruction and have not engaged in playing an instrument within the last year. The full study protocol was approved by the University of California, San Francisco (UCSF) Institutional Review Board, and all participants gave informed consent prior to participation. Participants were randomized into one of two groups: a musical rhythm training group (Rhythmicity) or a word search training group (control). Both participants

and researchers collecting outcome measures were blinded to the group assignments. Participants had no history of neurological or psychiatric disease, no history of brain tumors, were not taking medications that modulate brain excitability (e.g., neuroleptic, anti-depressant, stimulant, hypnotic), had no amblyopia, strabismus, or color blindness, and had normal or corrected to normal vision and hearing. To ensure participants were cognitively healthy, all participants scored within 2 SD of standardized scores on 12 tests of neuropsychological and physical function: California Verbal Learning Test-II, animal fluency, digit symbol, Patient Health Questionnaire, Delis-Kaplan Executive Functioning System Trails, Number and Number-Letter, Stroop, Measurement of Everyday Cognition, Ishihara Color Deficiency test, physical assessments (chair sitting and standing speed), hearing, and visual acuity. Five Rhythmicity participants were dropped from the study (3 for noncompliance, 2 for device malfunctions that prevented training/schedule adherence), resulting in 18 participants used for data analysis in the Rhythmicity group ($M = 67.7$ y, $SEM = 1.2$, range = 60 to 79 y, 7 females). Five control participants were dropped from the study (4 for noncompliance, 1 for technical problems during data collection), resulting in 19 participants used for data analysis in the control group ($M = 68.8$ y, $SEM = 1.4$, range = 62 to 78, 11 females). Noncompliance was defined as falling more than 2 wk behind the schedule or lost to follow-up. Participants received \$15 per hour for participation and a \$50 bonus for completion of the study.

Training Paradigms. Musical rhythm training was conducted using a custom-designed video game, Rhythmicity (Fig. 5A). Rhythmicity was created at Neuroscape and incorporates closed-loop adaptive algorithms to consistently challenge cognitive function, which is thought to optimize training benefits (86) and can be used to improve multiple cognitive abilities (90–92). It was played on a Microsoft Surface 3 tablet that permits tapping on a screen akin to certain types of drumming. Participants tapped the screen of the tablet in synchrony with the musical “beat,” which was also visually cued by moving targets (aliens). The visual cues moved from the bottom to the top of the screen (toward a mothership). Cues for the left hand were in a red-shaded area on the left side of the screen, while cues for the right hand were in a blue-shaded area on the right side of the screen. When the cues reached the top of the shaded area, this indicated when the participant was to tap on the screen. Each tap produced a novel drum sound and by following the visual timing cues, participants were able to contribute a new rhythmic structure to the song, just as a percussionist would do while playing in a band. While the use of these visual timing cues is uncommon to traditional music instruction, they serve a dual purpose—that of sheet music indicating which “drum” to hit and that of an instructor/conductor providing the

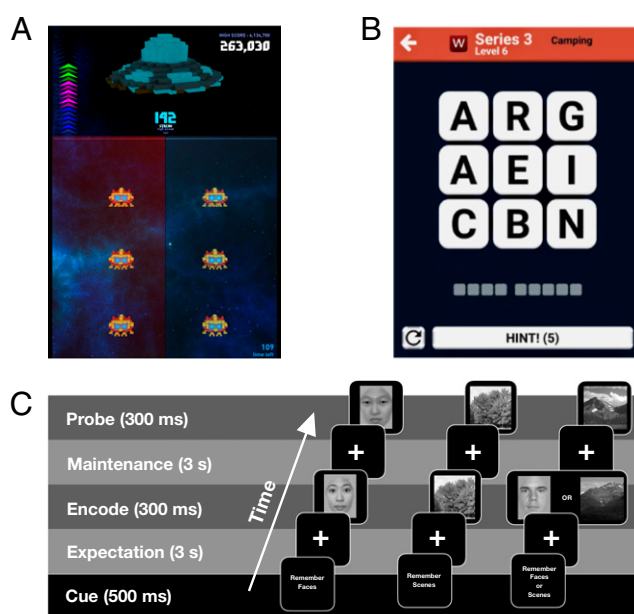


Fig. 5. Training and experimental paradigms. Screenshots from (A) Rhythmicity and (B) Worder training paradigms. (C) Overview of the short-term memory task.

timing cues. The game is designed to challenge rhythm and timing abilities, such that a nonmusician may learn to tap a steady rhythm. Rhythm training was selected because rhythm is a core feature of most forms of musical instrument training. Indeed, it is important to learn how to maintain a steady beat before one can create more complex rhythms or introduce new notes that would complicate the production of a rhythm or create a melody. As such, Rhythmicity was designed to be an easy way for nonmusicians to learn a fundamental aspect of musical performance.

Adaptivity was built into Rhythmicity so that with practice, the rhythms become increasingly difficult, but if performance falters, the rhythmic demands become easier. As difficulty increases, participants subsequently accumulate more points. Difficulty of rhythms increased along three dimensions: tempo, complexity, and precision. Tempo refers to the speed of the rhythm, complexity refers to the number of taps required before the rhythm repeats (two, four, or eight taps), and precision refers to the amount of temporal offset allowed for a tap to be considered "on-beat." During weeks 5 to 8 of training, the visual cues were presented so that participants may encode the rhythmic pattern into memory, then the cues disappeared, and participants continued tapping the previously cued rhythmic pattern. In doing so, participants relied more on their short-term memory to produce the rhythmic pattern.

The control group trained on a word search game, Worder (Fig. 5B), which was played on an iPad. Worder is a word search game that gets more difficult as the training progresses by expanding the field of letters to search. For example, Worder starts with a 3×3 grid of letters and advances to a 4×4 grid upon sufficient progress. To play Worder, participants were presented gray boxes at the bottom of the screen, which indicated how many words and how many letters per word were hidden within the grid of letters. Participants were to use their finger to trace a line connecting adjacent letters (horizontally, vertically, or diagonally) to complete the target words. All letters were to be used and no letter could be used more than once. For example, the answer to Fig. 5B is "Gear" and "Cabin." Hints were offered in case a participant got stuck, but the number of daily hints was limited to maintain a challenging environment. Importantly, Worder places no demands on timing or short-term memory abilities, and so it was hypothesized that only Rhythmicity would result in enhanced short-term memory ability. For both Rhythmicity and Worder, data were uploaded automatically to UCSF servers, which enabled the monitoring of participation adherence.

Short-Term Memory Task. A categorically cued delayed match-to-sample task was implemented pre- and post-training to assess training-related changes in short-term memory (Fig. 5C). At the beginning of each trial, participants were given a 500-ms cue that says either "Remember Face," "Remember Scene," or "Remember Face or Scene," which indicated that the impending to-be-encoded (target) stimulus would be either a face, a scene, or either (50% likelihood), respectively. After the categorical cue, a 3-s expectation period was presented containing a fixation cross, which allowed participants to prepare to encode the target stimulus into short-term memory. Target stimuli were presented at central fixation for 300 ms. A 50-ms checkerboard mask was then presented to remove any afterimage. A 3-s maintenance period was then presented, containing a fixation cross until a 300-ms probe image was displayed. Participants indicated with a button press whether the probe stimulus matched the target.

Probe stimuli matched target stimuli on 50% trials (randomly distributed). No stimuli were repeated across trials. Each participant was given 240 trials, divided evenly across the four task conditions (60 trials per condition): cued faces (CF), cued scenes (CS), neutral-cue faces (NF), and neutral-cue scenes (NS). Conditions were blocked into three block types: CF, CS, and NF/NS. Each block contained 20 trials and 12 blocks were randomly presented (3 CF, 3 CS, and 6 NF/NS). Short-term memory accuracy and response times to face stimuli (CF, NF) were assessed. Face stimuli were selectively analyzed because our previous research using this task exhibited a selective age-related decline in short-term memory for faces (68). Moreover, this prior research demonstrated high memory accuracy to scene stimuli, which would preclude the use of these stimuli as an outcome measure due to ceiling effects. Notably, expectations for improvement on this task were assessed and results of this analysis indicated that short-term memory performance was not biased by a priori expectations of training (see [SI Appendix](#)).

EEG. EEG data were recorded from a BioSemi ActiveTwo system with 64 Ag/AgCl active electrodes (Cortech Solutions). Signals were amplified and digitized at

2,048 Hz with a 24-bit resolution and no online filter. All electrode offsets were maintained at ± 20 mV. EEG analysis was conducted in MATLAB 2020b (MathWorks). Raw EEG data were down-sampled to 512 Hz and bandpass filtered between 0.1 and 50 Hz with a zero-phase shift finite impulse response filter. Data were epoched into segments beginning 0.1 s prior to cue and ending 0.8 s after probe stimuli. Eye artifacts were removed through an independent component analysis (ICA) by excluding components consistent with topographies for blinks, eye movements, and the electrooculogram time series. Noisy (or bad) electrodes were excluded from ICA, then recreated using spherical interpolation. EEGLAB functions (117) were used for ICA (binica), spherical interpolation (pop_interp), and plotting topographies (topoplot). Data were rereferenced to the average and epochs containing artifacts greater than ± 75 μ V were excluded.

For analysis of the ERP to target stimuli, epochs were baseline corrected to the 0.1-s pretarget period prior to averaging for the ERP. ERP amplitudes were assessed based on normalized GFP, which was calculated by first normalizing the ERP data through a Z score across all time points, electrodes, conditions, and sessions per participant. The normalized amplitudes were then squared and averaged over all electrodes. Peak P1 values were chosen as the largest local peak GFP between 50- and 150-ms post stimulus onset, the N1 was identified as the largest local peak GFP between 150 and 250 ms, and the P3 values were chosen as the largest local peak amplitude between 250- and 350-ms post stimulus onset. These temporal windows do not reflect the range of observed peak latencies, but rather serve to guide selection of ERP measures. Mean GFP was measured by averaging over a temporal window (10 ms for P1 and N1; 40 ms for P3) centered around each individual participant's peak before statistical analysis. Source localization was conducted using the LORETA-KEY software (118). P3 data to target stimuli were submitted to standardized low-resolution electromagnetic tomography (sLORETA).

For analysis of the CNV, epochs were baseline corrected to the 0.1-s pre-cue period prior to averaging across trials. Statistical analysis of the CNV utilized electrodes from central parietal-occipital regions (CPZ, POZ, PZ, P1, P2), in line with previous research on the use of this neural metric as an index of temporal attention (70). Mean amplitudes were calculated within a window of 0.3 to 0.1 s prior to target onset.

Spectral data (4 to 50 Hz) was extracted via complex Morlet wavelets (family ratio: $f_0/\sigma_f = 7$) applied to the epoched data. Spectral power was calculated from the wavelet coefficients by averaging the magnitude of the wavelet coefficients over trials. Spectral power was then normalized for each participant by calculating the Z score over time from data that were concatenated across all conditions and cue types. This normalization was done independently for each session (pre/post-training). Analysis focused on alpha band (8 to 12 Hz) activity during the end of the expectation period by averaging data 0.3 to 0.1 s prior to target onset. Analysis of alpha activity utilized electrodes from lateralized parietal-occipital regions by averaging over electrodes from the left (P7, P9, PO3, PO7, O1) and right (P8, P10, PO4, PO8, O2) hemispheres, in line with previous research on the use of this neural metric as an index of temporal attention (70).

Statistical Analysis. Statistical analysis of behavioral performance, ERP, CNV, and spectral activity utilized an ANOVA with group (Rhythmicity, control), cue (cued, neutral), and session (pre, post) as factors. A Greenhouse-Geisser correction was applied when appropriate, and η_p^2 was used to assess effect sizes. Statistical analysis of source-localized activity used nonparametric permutation tests to assess differences between sessions. A cluster correction based on a Monte Carlo simulation was used to account for multiple comparisons. A cluster corrected *P* value < 0.001 was retained as significant to discount potential small spurious clusters of activity.

Classification Analysis. A centralized circular topographical distribution across the duration of the maintenance period was observed to be consistent between groups and sessions (Fig. 3A). For classification analysis, we used a singular value decomposition to identify single trial activity with a topographical distribution that is similar to the mean topography. To achieve this, data from each participant and session were analyzed separately. Individual trials from face and scene epochs were concatenated together over time and a singular value decomposition was applied. A principal component of interest was identified by the singular vector (spatial principal direction) that best matched the mean

topography (for examples, see *SI Appendix, Fig. S4*). Trial-wise maintenance period activity was then reconstructed from that principal component of interest. Mean maintenance period activity was then calculated within 500-ms nonoverlapping windows, spanning 0.75 to 3 s after target onset. These data were then submitted to a two-class (face/scene) decision tree classifier to decode neural activity associated with the maintenance of face or scene stimuli.

Decision tree classification was conducted through the fitctree MATLAB function with four decision splits, automatic hyperparameter optimization, and the 64 electrodes serving as features. Classification accuracy was then derived from 10-fold cross validation. To ensure the classifier was not biased, equal numbers of face and scene epochs were always used. Although equal numbers of face and scene epochs were not always present after artifact rejection, whichever set of stimuli (face or scene) that had more epochs remaining, trials were randomly sampled to match the smaller stimulus set. This entire process was iterated 10 times and the mean accuracy was then submitted to statistical analysis via nonparametric permutation tests and a cluster correction for multiple comparisons over time.

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Data, Materials, and Software Availability. Anonymized behavior and EEG data have been deposited in Mendeley Data ([10.17632/bf49k2822m.2](https://doi.org/10.17632/bf49k2822m.2)) (119). All other study data are included in the article and/or *SI Appendix*.

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Author affiliations: ^aDepartment of Neurology, University of California San Francisco, San Francisco CA 94158; ^bNeuroscape, University of California San Francisco, San Francisco CA 94158; ^cDepartment of Physiology, University of California San Francisco, San Francisco, CA 94158; and ^dDepartment of Psychiatry, University of California San Francisco, San Francisco, CA 94158

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