

The structure and acquisition of sensorimotor maps

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Conflict of Interest: The authors declare that they have no competing interests.

Acknowledgements:

This work was supported by National Institute of Child Health and Human Development R01 HD075740 and Les Fonds Québécois de la Recherche sur la Nature et les Technologies, Québec (FQRNT) and a Banting Fellowship BPF-NSERC-01098.

We are indebted to Bilal Alchalabi and Eric di Tomasso for assistance in data collection and Paul Gribble and Mark Tiede and members of the Motor Control Lab at McGill for valuable discussions.

Abstract

One of the puzzles of learning to talk or play a musical instrument is how we learn which movement produces a particular sound: an audiomotor map. Existing research has used mappings that are already well-learned such as controlling a cursor using a computer mouse. By contrast, the acquisition of novel sensorimotor maps was studied by having participants learn arm movements to auditory targets. These sounds did not come from different directions but like speech were only distinguished by their frequencies. It is shown that learning involves forming not one but two maps: a point map connecting sensory targets with motor commands and an error map linking sensory errors to motor corrections. Learning a point map is possible even when targets never repeat. Thus, while subjects make errors, there is no opportunity to correct them because the target is different on every trial, and therefore learning cannot be driven by error correction. Further, when the opportunity for error correction is provided, it is seen that acquiring error correction is itself a learning process that changes over time and results in an error map. In principle the error map could be derived from the point map but instead these two maps are independently acquired and jointly enable sensorimotor control and learning. A computational model shows that this dual encoding is optimal and simulations based on this architecture predict that learning the two maps results in performance improvements comparable to those observed empirically.

Introduction

When first learning to talk or to play a musical instrument, a fundamental challenge is to learn which movement to use to produce a particular sound, i.e. a sensorimotor map. There is a substantial understanding of how existing sensorimotor maps are adjusted in situations in which these maps are already well-learned at the outset, such as when subjects respond to visual rotations during reaching or auditory perturbations during speech (Huberdeau et al., 2015; Krakauer, 2009; Houde and Jordan, 1998). These perturbations require subjects to make relatively minor adjustments to previously acquired mappings (Telgen et al., 2014), which is reflected in the fact that performance reaches asymptote rapidly. However, such perturbation responses may not provide insight into the process by which maps are acquired in the first place. Here a paradigm is presented in which participants acquire an entirely novel audiomotor map. This is a challenging task in which performance improvements are seen over several days of training. Previous work has shown that learning is possible under these conditions (Mosier et al., 2005; Liu et al., 2011; Radhakrishnan et al., 2008; Mussa-Ivaldi et al., 2011) but it remains unclear what is the structure of the acquired maps. Initially, participants face two problems: given a target sound they do not know where to move to, and when they make an error, they have no basis on which to correct it. Monitoring participants during learning allows insight into how sensorimotor maps are structured to solve these two problems.

In order to learn a motor skill it is necessary to learn the sensory effects of one's movements. It is also necessary to be able to correct errors when they occur, and this requires different type of knowledge, namely of a mapping between sensory errors and motor corrections. In the present paradigm, both of these have to be learned. The former map is essentially a function from sensory output s to motor commands m (i.e. $f(s) = m$), which here is referred to as a *point map*, whereas the latter is a mapping between sensory errors Δs and motor corrections Δm (i.e. $f'(\Delta s) = \Delta m$), which is called an *error map*. Knowledge of this latter type is what is required to compute a proportionate correction of an error as is done in error correction models (Ghahramani et al., 1997; Herzfeld et al., 2014; Thoroughman and Shadmehr, 2000; Shadmehr et al., 2010). In principle, the error map could be computed from the point map, since it is its mathematical derivative. That is, there could be one single map on which both movement selection and

error correction depend. However, a computational architecture in which limited informational units are allocated to either a point map or an error map (Fig. 1) suggests that reaching would be most accurate when informational units are divided (equally) between the two maps, instead of one. This architecture motivates a set of predictions, in particular that two separate maps should exist: a point and error map. Simulations based on this architecture which assume that learning involves the addition of units to the maps (see Model Simulations) predict that point map learning should be observable as reduced error when subjects make reaching movements to random targets, even if these targets never repeat. Further, the simulations predict that error map learning should result in improved convergence onto targets that are presented repeatedly; in particular, both the rate of convergence and asymptotic performance should improve.

The present study tested the hypothesis that participants acquire two separate maps, a point and error map, by monitoring reaching movements to auditory targets. Auditory feedback was presented at the end of each movement. Conditions were created in which participants either could apply error correction or could not. In a random presentation condition, which assessed the acquisition of a point map, targets were different on each trial, thus precluding error correction. In order to probe learning of the error map, the same target was presented on multiple subsequent trials, thus allowing engagement of error corrective processes. It was hypothesised that this error corrective process itself has to be learned: the formation of an error map is a learning process. Moreover, error map learning was hypothesised to be independent from the acquisition of a point map.

Experimental Procedures

Subjects and experimental tasks

A total of 88 participants were recruited. All participants were right-handed (as verified by the Edinburgh handedness inventory) and had no or only minimal musical training. Participants reported no neurological or hearing impairments. Each session lasted approximately 1.5 hours. Participants provided written consent and all procedures were approved by the McGill University Institutional Review Board.

Participants made reaching movements to auditory targets while holding a robot handle. A 2-degree of freedom (DOF) planar robotic arm (InMotion2; Interactive Motion Technologies) was used (Fig. 2a) that sampled the position of the handle at 400 Hz. First, in a calibration phase, participants were asked to hold the robot handle in front of their body midline. The lateral coordinate of this position was captured and used as the movement start point throughout the experiment. A *target circle* was then defined as a half-circle around this midpoint, and during the experiment participants made movements from the start point to points on this circle (Fig. 2b). This circle was never shown visually but participants were shown a schematic drawing of it before the experiment and the robot demonstrated points on this circle (at 0, 90 and 180 degrees CCW from the right) by moving the participants hand to them. Vision of the circle and of the arm was blocked. All experiments followed the same schedule on a testing day and differed only in number of days and the way the auditory targets were chosen.

Auditory stimuli

The sounds (target and feedback) consisted of three sine wave oscillators: one with fixed frequency (F_0 , 165 Hz); the frequency of the other two signals (F_1 , F_2) linearly decreased or increased, respectively with the angle of the movement endpoint (Fig. 2c). The frequency range of the F_1 and F_2 oscillators correspond to the first and second formant frequencies of vowel sounds (Remez et al., 1981). These particular signals were chosen because they provide a rich yet learnable stimulus that participants are already familiar with by virtue of its structural similarity to vowels. These more complex stimuli limit the benefit to performance that might arise due to prior expectations which could readily have occurred had auditory stimuli been used that varied monotonically over the workspace. In order to normalise the space-to-frequency mapping, angles were mapped linearly to frequencies in mel-space, which is an interval-scale encoding of frequency differences (Stevens, 1937). In order to correct for perceived loudness differences, the amplitude of each oscillator was adjusted using equal loudness curves (Robinson and Dadson, 1956) to 75 phon (so that each sound would be perceived to be as loud as a 1kHz tone of 75 dB). In this way, equal displacements in the motor space cause perceptually equal change in sound frequency and little or no change in sound intensity. Sounds were presented over Beyerdynamic DT770M

headphones. This mapping between positions and sounds remained the same throughout all experiments. Since the mapping is one-to-one, without ambiguity the sounds will be referred to by the angle they were mapped to on the interval of angles $[0, \pi]$ radians. The sounds themselves were not localised in space: the same sound was presented to both ears, hence there were no acoustic location cues and only their frequency content contained information about the position they were mapped to.

Audiomotor training

In audiomotor training trials, participants received a target sound and were instructed to move to the location that corresponded to the sound. At the start of each trial, the robot returned the handle to the starting point using a minimum-jerk trajectory and held it there for 500 ms. Then the target sound was presented for 1000 ms during which time the forces holding the participants' hand in place were gradually decreased, leaving the participant free to move when the sound ended. Movement onset was defined as the moment when handle was more than 5 cm away from the starting position, and movement end was when the velocity fell below 5% of peak velocity for 50 ms. At movement end, the robot held the participant hand at its current position using an attractor controller. The sound corresponding to the angle between the starting point and the end position was presented for 1000 ms. The amplitude of participants' movement was inconsequential to the sound. Other than the sound no feedback was provided.

Movement-copy

Movement-copy trials served to familiarise the participant with the size of the target circle (since it was not shown visually) and to measure baseline motor accuracy in reaching towards particular directions. During each trial, the robot first brought the handle back to the starting position. Then the hand was moved out to a target position on the target circle in a minimum-jerk trajectory of 900 ms, held there for 500 ms, and then moved back. A visual icon *MOVE* appeared that signaled participants to move to the indicated target location in a single, straight, swift movement. No forces were applied by the robot during the participant's movement. Movement onset and end were detected as in the audiomotor trials

above. Target directions were equally spaced at 10% of the half circle, including the endpoints, yielding a total of 11 target locations presented in random order.

Audiomotor no-feedback trials

Audiomotor no-feedback trials were obtained before and after the audiomotor training sequence. These trials were identical to training trials except that no feedback sound was presented. Ten trials were administered before and after the training phase (Fig. 2d).

Auditory psychophysical testing

Auditory psychophysical testing was completed away from the robot with the participant seated in front of a computer. On every trial, a train of four sounds of 200 ms duration each was presented with a 75 ms pause between sounds. Three of the sounds were identical and one (either the second or third) was different. Participants' task was to respond by pressing a button whether the mismatched sound was the second or third in the sequence. The three identical sounds were those that were mapped to the $.5\pi$ angle in our auditory-motor mapping and the mismatched sound corresponded to the angle $.5\pi + \delta x$ where δx was one of ten logarithmically spaced values between 0.0015π and $.09\pi$. Participants completed a total of 200 trials (10 stimulus levels in each direction x 10 repetitions) in blocks of 20 with a short break in between. No feedback was given about the accuracy of the participants' response.

In order to obtain auditory thresholds psychophysical curves were fitted to the data offline using maximum likelihood. The psychophysical curves were sigmoid functions defined by the formula $p(x) = .5 + (.5 - \lambda) * \frac{1}{2} [1 + \text{erf}(\frac{x-m}{s\sqrt{2}})]$ where p is the probability of giving the correct response, x is the stimulus level (angle that defines the sound) and erf is the mathematical error function. The fit parameters are m (curve midpoint), s (parameter controlling the slope) and λ (lapse rate). Psychometric curves were discarded when their fit was poor ($R^2 < .5$).

Experiments

Random continuous targets (continuous-1day)

Auditory targets were chosen from a continuous uniform random distribution on the interval $[0, \pi]$ (in radians) with the constraint that the angular distance between the target on trial $n + 1$ and the movement endpoint of trial n was at least $.3\pi$ radians. The rationale for this constraint originated from a pilot study observation that participants were more accurate on trials whose target was close to their previous movement endpoint, which allowed them to achieve better-than-chance performance without knowledge of the audiomotor mapping. The minimum distance requirements prevented participants from using such a strategy. Eighteen participants (10 female) participated aged $21.4 (\pm 3.6)$ years. Participants were tested for one session.

Discrete targets (5-targets-1day)

For each participant a set of five unique targets was selected and on each trial one of these five was presented, with the constraints that (1) the same target could not be repeated on consecutive trials and (2) the angular distance between the target on trial $n + 1$ and the movement endpoint of trial n was at least $.3\pi$. The set of targets was determined randomly as follows: five angles were placed equidistant on the interval $[\ .05\pi, .95\pi]$ (including endpoints) and then jittered with zero-centered normal noise with SD $.02\pi$. When the absolute value of the jitter for any of the targets exceeded $.1\pi$ in magnitude then the noise vector was recomputed. Eighteen participants (12 female) participated aged $22.4 (\pm 2.5)$ years. Participants were tested for one session.

Discrete targets (5-targets-3day)

Target placement was identical to experiment 5-targets-1d except that the minimum angular distance between endpoints and subsequent targets was set to $.05\pi$ to achieve greater uniformity of the target distribution. The set of targets were determined as during the *5-targets-1d* experiment. Sixteen participants

(10 female) participated aged $22.1 (\pm 3.5)$ years. Participants were tested on 3 days with 2-4 day intervals in between.

Repeated targets (1day)

Trials were divided into batches of 16 trials on which the same target sound was presented repeatedly. Every 16 trials a new target was selected from a continuous uniform distribution on the interval $[0, \pi]$ with the constraint that the target had to be a minimum distance $.2\pi$ radians away from the last trial (previous batch) movement endpoint. Twenty-one participants (14 female) participated aged $23.6 (\pm 4.2)$ years. Participants were tested on one day. For analysis included data from the first day of the 3-day experiment was included since the design was identical.

Repeated targets (3day)

Target selection was identical to that of the 1-day experiment. Fifteen participants (10 female) participated aged $23.9 (\pm 3.4)$ years. Participants were tested on 3 days with 2-4 day intervals in between.

Repeated targets analysis

In the experiments involving repeated target presentation, learning curves were fitted to individual subjects. For a group of trials with the same target, we averaged the absolute angular error as a function of trial within batch, and fitted a learning curve defined by the equation $e(t) = (a - b) \exp(-t/t_c) + b$ where $e(t)$ represents the angular error on within-batch trial t and a is the intercept of the learning curve, b is the asymptote, and t_c is the time constant. In order to enforce a and b to be non-negative, we transform them into pseudo-parameters using the exponential function.

Lag-1 autocorrelation (ACF1) was calculated as the Pearson correlation between the vector of movement endpoints and the vector of movements shifted by one in chronological order. We skipped the 4 initial movements to each target since these generally had larger errors than later trials and might have disproportionate effects on the correlation.

Statistics

Unless otherwise specified, we computed linear mixed models (LMM) statistics with subject as random factor and maximal random structure.

Results

Participants made reaching movements to auditory targets that were presented over headphones (Fig. 2). The same signal was presented to both ears and therefore no acoustic location cues were given; however, the frequency content of the sounds depended on the angle of the movement. This situation is directly analogous to learning to speak, where the position of articulators (e.g. tongue) changes the frequencies of the produced sound, not the perceived physical location of the sound itself. As in learning to speak, the subjects have to learn the appropriate movement direction to produce a particular combination of frequencies.

Model simulations

Simulations were run based on the architecture introduced previously (Fig. 1) in order to find predicted indices of the acquisition of point and error maps, respectively. Maps were modeled as lookup tables, which encode input-output pairs without making assumptions about the overall structure of the maps. The simulations assume that the learning process comprises the addition of units to the point and/or error maps. Learning is assessed in terms of changes in predicted reaching accuracy. Alternative model frameworks (Jordan and Rumelhart, 1992; Pouget and Snyder, 2000) may be used to account for the data here but here a simple model was opted for that could account for the data with only minimal assumptions.

We simulated "participants" with various numbers of units in point and error maps, respectively, and investigated the effects of map density on performance. In a random target condition (Fig. 3a) on each trial a new target was selected at random and then its nearest neighbour looked up in the model's point

map. Gaussian noise ($\sigma = .05\pi$) was added to both auditory input and motor output. As point map resolution increases (larger number of entries in a look-up table) the simulations predict a reduction in error (Fig. 3a). The model presented here is not a model of learning, since it does not specify in what locations in the map units are added, but it can be used to extract predicted changes in performance as a result of increases in map density. For simplicity, the simulations assumed that units are added incrementally in random locations (Fig. 3a green trace). For reference, we also performed separate simulations for each point map density in isolation, where map units were put in optimal locations (Fig. 3a purple trace). Note that in these latter simulations units were not added to the map incrementally in any one simulation, but separate simulations were run for each map density.

In order to investigate the effect of error map learning, the point map was held constant (one unit) while error map density was varied. Error correction was enabled in these simulations by presenting the same target repeatedly for 16 trials. On the first trial of a batch, since the target is novel, the model performs a lookup in its point map. On a subsequent trial n in a batch ($n > 1$) the model aims to correct a proportion ($\eta = .3$) of the (signed) error experienced on the previous trial, e_{n-1} by looking up the closest entry to ηe_{n-1} in its error map (look-up table) and applying that correction to the previous movement u_{n-1} . Gaussian noise ($\sigma = .05\pi$) is added to movement output and auditory inputs. To the average absolute error within batches we fit the learning function $e(t) = (a - b)\exp(\frac{-t}{t_c}) + b$, where $e(t)$ is the error on trial t within the batch, b is the asymptotic performance (at the end of the batch), a represents the intercept and t_c is the time constant. We varied the number of entries in the error map and observed that with increasing error map resolution, convergence to the target is more rapid and asymptotic performance is improved (Fig. 3b). Absolute errors are reported for the model as they are for the human subjects so that both datasets are processed identically.

In sum, as units are added to the point map (point map learning) there should be a reduction in error when reaching to random targets (Fig. 3a). As units are added to the error map (error map learning) there should be improved convergence when the same target is repeated for a number of consecutive trials, in particular a faster rate of convergence and lower asymptotic error (Fig. 3b). Why would the time constant of learning curves change? The reason is that even though on a given trial the model always aimed to correct a given proportion of the error, it would be less succesful in generating exactly that

correction when error map density is low, and more successful when error map density is high. Similarly, the asymptote of the learning curve decreased with increasing error map density because a more dense error map would allow the encoding of smaller errors and hence enable the model to correct for them.

Learning a point map

Continuous targets

In order to study point map acquisition empirically, a different target was presented on each trial. When targets are different on subsequent trials, the correction appropriate for an error on one trial cannot be applied directly to the next trial because it is a movement to a different target. Participants made reaching movements towards auditory targets, corresponding to angular positions chosen uniformly from the half-circle workspace (since the audiomotor mapping is one-to-one we will refer to the movement angles and corresponding sound positions as points on the workspace $[0, \pi]$ without ambiguity). A decrease in absolute angular error was observed (angular distance between the auditory target location and the movement endpoint) over the course of audiomotor training (Fig. 4a). Before and after learning participants completed trials where no auditory feedback was presented. These trials probed the point map exclusively because error correction could not operate in the absence of feedback. Performance on no-feedback trials after training was significantly improved relative to before training ($F(1,15)=58.39$, $p<.00001$).

In order to assess whether this improvement was attributable to the mapping instead of perceptual or motor learning in isolation, measures of auditory perceptual and motor learning performance were added as covariates to the above analysis, specifically (1) the auditory psychophysical threshold (curve midpoint) before vs. after learning, and (2) the motor-copy error (trials in which we measured absolute angular error when participants reproduced movements indicated by the robot) (Fig. 4a). Performance on these tests was not significant as predictors of the audiomotor error ($F(1,57.9)=1.00$, $p=.32$ for auditory thresholds and $F(1,218.19)=2.63$, $p=.11$ for motor-copy trials; see also supplementary Fig. S1). Furthermore, motor-copy angular absolute error was not different after training relative to before ($F(1,15)=.64$, $p=.43$) nor were auditory psychophysical thresholds ($F(1,15)=3.18$, $p=.09$). That is, evidence for learning was

obtained in the audiomotor task that cannot be explained by motor learning or auditory perceptual learning in isolation and therefore can be attributed to learning of the mapping between movements and sound. The same was true for the other experiments reported below (see supplementary materials A.2).

Did participants really learn the mapping from scratch? For individual subjects, the (Spearman) correlation between target angle and movement angle was computed for the no-feedback trials before and after audiomotor training. The r-to-z-transformed correlation coefficients were not significantly different from zero before training ($t(15)=-1.23$, $p=.24$), indicating that participants initial reaching was at chance level and they had no knowledge of the mapping. Correlation coefficients were significantly higher after the audiomotor training relative to before ($F(1,15)=43.03$, $p<.0001$) (Fig. 4b) confirming that participants learned the mapping. In order to gain insight into the earliest stages of learning of the audiomotor mapping, initial segments of audiomotor training trials were compared statistically with the before-training no-feedback trials using t-tests, finding that after as few as 8 trials the error on audiomotor trials were better than the no-feedback chance levels ($p<.05$ Bonferroni-corrected) (Fig. 4c). This indicated that rudimentary knowledge of the mapping was acquired rapidly by participants. Investigating how participants' errors varied across the workspace, the targets were divided into bins and the pattern of errors as a function of target bin was found to be different from those that would be expected if subjects had no knowledge of the audiomotor mapping (Fig. 4d).

In sum, although the exact same target was never repeated, participants remarkably showed the capacity to learn the mapping and the learning was already evident within a handful of trials.

Five targets random presentation

It is unclear how much detail subjects acquired about the audiomotor mapping. Here, the acquired point map was probed by having participants reach to a set of five targets, spaced equally across the workspace with a small jitter and presented in random order. The no-feedback trials showed a significant decrease in error after audiomotor training relative to before ($F(1,322)=64.33$, $p<.0001$) (Fig. 5a). The error for the initial audiomotor training trials was significantly lower than the preceding no-feedback trials after 9 movements ($p<.05$, Bonferroni-corrected t-tests) and onwards. During the later trials (trial 150 and

onwards) the endpoints of movements towards the five individual targets were significantly segregated ($F(3.18,50.82)=105.23$, $p<.0001$ main effect of target) (Fig. 5b). Planned contrasts using Bonferroni-corrected t-tests with pooled SD revealed that for all pairs of targets the movement endpoints were significantly different from one another (Fig. 5c). This shows that the point map acquired by subjects in a single day contained sufficient information to encode multiple (at least five) distinct targets.

Five targets 3-day

In order to study whether learning was retained and could continue to improve across days, participants were measured on three testing days with 2-4 intervening non-testing days. Within-day reaching accuracy improvements on no-feedback trials differed over the three testing days ($F(2,866.00)=4.52$, $p=.01$). Planned contrasts revealed a reduction in error after training relative to before on the first day of training ($p<.001$) but not on day 2 ($p=.27$) or day 3 ($p=.24$) (Fig. 6a). There was also a reduction in before-training errors from day 1 to 2 ($p<.001$) but not from day 2 to 3 ($p=1$). In line with the results of the 5-targets-1d experiment, reaches towards individual targets were significantly different for the first day and continued to be so for the subsequent days as evidenced by a tighter clustering of movements around actual target locations (Fig. 6b). In support of this observation, the angular absolute error did not differ between targets ($F(4,14.09)=1.2$, $p=.35$) but decreased over days ($F(2,18.10)=37.85$, $p<.0001$) (Fig. 6c). Planned contrasts showed a reduction in error between day 1 and 2 ($p<.0001$) and between day 2 and 3 ($p=.03$). In sum, learning is retained across days and improvements continue to occur into the third day of training, revealing that the audiomotor map that is learned is persistent.

Learning an error map

In the next series of experiments, the same target was repeated multiple times in a row (16 trials). This allowed participants to correct an error experienced on a given trial. Each new target sound was selected randomly and was different from all prior targets. In this process, it was hypothesised that participants would collect this error corrective information and form an error map. We specifically test the hypothesis

that error map formation is itself a learning process. Evidence for learning an error map would not simply be convergence to the target, but rather an improved capacity to correct errors across multiple targets. This improved convergence should be seen as a faster rate of learning, and a better asymptotic performance.

Targets presented repeatedly (1-day)

Reaching behaviour was markedly different (Fig. 7a) from the random presentation experiments (cf. Figs. 4,5) with errors large in the beginning of a batch which decreased rapidly until reaching an asymptote (Fig. 7c). Error levels reached towards the end of a batch were much lower than those achieved during random presentation (cf. Figs. 5a, 4a). Based on simulations it was hypothesised that error map learning should be accompanied by a reduction in asymptotic performance, which is tested here below. However, point map learning may also have occurred in parallel, with the addition of each new target, and this point map learning could potentially have resulted in improvements in asymptotic performance. In order to verify that the improvements observed here are due to error map learning and not point map learning, we test for improvements in asymptotic performance whilst taking the first trial in each batch as a covariate. To quantify asymptotic performance the absolute angular error was averaged for the last five repetitions of a target and it was found that this error decreased in later batches ($F(1,446.47)=11.19$, $p=.0009$), as predicted by error map learning. This was true even when accounting for the reduction of error on the first trial to each new target as covariate ($F(1,470.96)=1.07$, $p=.30$). Hence the data indicate error map learning that could not be accounted for by improvements in performance due to point map learning.

Point map information was acquired as well during this condition, but to a lesser extent than seen in the random condition. The first trial for each new target was essentially a random trial comparable to the random experiments where subjects only performed such trials. A statistical trend for a reduction in error of this first trial over time was observed ($F(1,25.95)=3.70$, $p=.07$). The no-feedback trials, another measure of point map learning, before and after training showed significant improvement ($F(1,605.27)=12.22$, $p=.0005$) (Fig. 7a) but this reduction in error in the no-feedback trials was significantly smaller than that observed in the continuous-1d experiment ($F(1,930)=25.28$, $p<.0001$). The difference in improvement

in no-feedback trials in repeated and random presentation provides evidence against the possibility that participants learn a single map which gathers all sensorimotor information, because participants in both conditions made the same number of movements and received the same number of auditory feedback trials (Fig. 7b).

In sum, performance improvements obtained during repeated presentations of the same target were not carried over to the point map as probed in no-feedback trials which, to the contrary, revealed less learning than in the random experiments. Crucially improvements in convergence were observed, i.e. improvements in error-corrective behaviour that could not be explained by an improvement in the point map, suggesting the existence of a separate error map that is independent of the point map.

Targets presented repeatedly (3-day)

Another set of participants performed the repeated target experiment on each of three days. In support of the idea that there is error map learning, it was observed that the error decreased more rapidly on later days, reaching lower asymptotes (Fig. 8b). Learning curves were fitted to the error as a function of trial within each group of five batches (in order to obtain a sufficient signal-to-noise ratio). The intercept of the learning curves showed a reduction over time ($F(1,15.41)=5.79$, $p=.029$), indicative of point map learning. Importantly, convergence on to the target was improved, as reflected in a lower asymptote ($F(2,87.70)=3.94$, $p=.02$) and decreased time constant of the learning curve (the slope) ($F(2,25.62)=9.23$, $p=.001$); both of these were computed taking into account changes in curve intercept (Fig. 8b). This improvement (from day 1 to day 3) could not be explained as a change in motor-copy error ($t=1.09$, $p=.31$) or auditory threshold ($t=1.49$, $p=.17$) (Fig. S1). The improvements in performance observed here empirically with repeated targets across days are consistent with those observed during simulations with increasing error map density.

Again, point map information was also acquired as shown by performance on no-feedback trials. Performance in the no-feedback trials improved on all three days after audiomotor training (all $p<.02$) relative to before. In addition, the error on the first trial for each new target was reduced over time ($F(1,295.69)=10.52$, $p=.001$).

The improvement in learning curve time constant (and asymptote) reflected an increased ability for convergence within the auditory-motor workspace. This was hypothesised to be due to the formation of an error map that enabled more accurate error correction. In order to test this idea trial-by-trial correlations of the movements (lag-1 autocorrelation, ACF1) were investigated, which are typically observed in error-based learning models as well as in the simulations reported here (Fig. 3b). As shown in Figure 8c, the autocorrelation increased during the first day and then remained at non-zero levels during day 2 and day 3. The absence of autocorrelation at the beginning of the first day suggests that there was little systematic use of error information to converge to the target. The autocorrelation then increased over the course of the first day ($t=1.87$, $p=.06$), suggesting more gradual adjustment of movements based on errors. This nonzero autocorrelation was then maintained during the second and third day ($p<.001$ and $p=.025$ resp.). For comparison, we extracted, for each target separately, the chronological series of movements in the 5-targets-3d experiment (ignoring intervening reaches towards different targets). ACF1 was calculated in windows of 16 movements and then averaged in order to ensure compatibility with the repeated target 3-day data by equating biases in short time series autocorrelation (Marriott and Pope, 1954). If the same learning process would operate in these experiments, one would expect to see similar autocorrelations. Contrary to this, a zero lag-1 autocorrelation was found in the five-targets 3-day experiment (Fig. 8c).

Learning a point map and an error map are independent

The preceding section showed that error map acquisition cannot be explained by point map learning (Fig. 8b). But could error map learning contribute to point map acquisition? If error map learning contributed to point map learning then repeated trials to the same target should contribute towards the acquisition of the point map. To test this idea, the error on the first trial ("random" trial) of every new target was tracked in the repeated-targets experiment (a total of 45 trials) and compared with subjects in the continuous target experiment who were tested with random trials only (Fig. 9a). If only the first trial in each batch contributes to point map formation, then both groups should show similar learning. Indeed, it was found that both groups improve ($F(1,29.03)=9.96$, $p=.004$) but there was no difference between the groups or between the slopes ($F(1,29.03)=.01$, $p=.94$) in spite of the fact that participants in repeated targets

experiment performed 15 times more movements (and therefore received substantially more exposure to the auditory-motor workspace). This argues against the idea that subjects learn a single mapping and instead shows that repeated movements to the same targets do not contribute to point map learning, but rather that subjects are engaged in a different type of learning contributing to an error map.

One alternative explanation could be that if participants in the repeated targets 3-day experiment would move to roughly the same direction for each presentation of the same target, then they would obtain little additional information about the mapping beyond the first movement to that target. In order to test whether this could explain the above finding the spatial coverage of the set of movements (including the repeated-targets trials >2) was computed, where more negative values indicate greater spatial coverage (for details about spatial coverage see supplementary section S6). It is seen that the repeated-targets participants' movements achieved greater spatial coverage than the random participants' movements, thus invalidating this potential confound (Fig. 9b).

Separate acquisition of point and error maps

Point map acquisition was shown by improved reaching towards random targets. Error map formation was shown by improved convergence across days when targets were presented repeatedly. In neither version of the task could improved performance be reduced to motor or perceptual learning in isolation, since these remained stable, and therefore learning was attributable to the formation of a mapping between them. In principle, the error map could be computed as the spatial derivative of the point map. In other words, participants would learn only a single map. However, below are summarised the observations that suggest that this is not the case here.

First, repeated movements to the same targets did not contribute to map learning over and above the first movement to each new target. That is, performance on the first movements to each new target in the repeated-targets experiment is indistinguishable from performance on the first 45 trials in the random experiment in spite of the fact that repeated-target participants performed fifteen times more trials than random target participants. This shows that error corrections made in the course of repeated movements to the same target did not contribute to point map formation.

Second, learning error correction in the course of repeated movements to one target improves error corrective behaviour to novel targets, that is, learning the error corrective process is not tied to particular locations in space. Specifically, error map acquisition is shown by improvements in time constant and asymptotic error when the same target was presented repeatedly and these improvements cannot be explained by improvements in performance on the first trial of each new target (indicative of point map acquisition).

Third, in the repeated targets experiments trial-to-trial correlations of reaching movements were observed that would be expected in error-corrective learning, and indeed were seen in simulations of error map learning, whereas these correlations were absent in the series of reaches towards the same target in the random target presentation condition.

These observations taken together suggest that two distinct sensorimotor maps are formed. Random target presentation favours formation of a point map and in that condition error map formation is negligible because there is no direct opportunity for error corrections to be applied. Repeated presentation of the same target involves formation of both maps. A point map is formed, but it receives the equivalent of one new data point for every new target. The repeated movements to the same target do not feed information to the point map but instead contribute to the formation of an error map which in turn allows, over the course of many new targets, improved convergence.

Discussion

A paradigm is introduced here to study how participants initially acquire sensorimotor maps. Participants make arm movements to auditory targets. The sounds do not come from different physical locations but like speech sounds are distinguished only by their frequency content. Participants are in much the same situation as an infant learning to talk: they have to learn from scratch which movements to make to produce particular sounds and to learn how to correct errors when they occur.

One principal observation is that learning is possible even when targets never repeat. This learning is not directly driven by error correction, because when targets were selected randomly there was no opportunity

to move to the same target again and hence no opportunity to correct an error. Instead, simulations (Fig. 3) indicate that the learning observed here could be accounted for by the acquisition of a mapping whose structure could be as simple as a look-up table in which information about movements and their sensory consequences is progressively accumulated.

A second observation is that when participants are given the opportunity to correct errors by moving repeatedly to the same target, the error correction process itself has to be learned. This is because when participants first come to this task, even if they experience an error on a given trial, they are unable to use error correction because by design the mapping from sensory errors to motor corrections is initially unknown. In the course of the experiment, across many batches, each to a novel target, participants learn to better correct their errors, indicating the acquisition of a mapping between sensory errors and motor corrections (an error map). It is seen that this learning of the error corrective process is not linked to particular targets because for each novel target the learning rate and asymptotic performance improves.

A final observation is that the point and error maps are learned independently. Learning a point map does not contribute to learning an error map nor vice versa.

Relation to previous work on sensorimotor adaptation

The point map is a function from sensory output s to motor commands m (i.e. $f(s) = m$) and the error map a mapping between sensory errors Δs and motor corrections Δm (i.e. $f'(\Delta s) = \Delta m$). While sensory information is needed for the formation of both maps, learning in the present context proceeds on a trial-to-trial basis, and both kinds of maps contribute to feedforward control, in one case to produce movements to novel targets (point map), and in the other to produce movements that are appropriate adjustments to previous movements to correct for sensory errors (error map). The error map enables trial-to-trial corrections. It may also contribute to online control of movements but in the present paradigm such control was not investigated and in other work online control of movement was found to be partially independent of trial-to-trial control (Yousif and Diedrichsen, 2012).

In adaptation learning, trial-to-trial errors are thought to contribute to updating the feedforward controller

(Wolpert and Ghahramani, 2000; Nakanishi and Schaal, 2004; Kawato, 1999). However, the error corrective process itself is fully formed and is not updated during the learning process. The present studies tap into an earlier stage of learning in which by design the needed mappings are initially unknown. This revealed properties of learning that differ from those involved in adaptation.

First, in this early stage of learning, the error corrective process itself has to be learned, that is, that the mapping between sensory errors and motor corrections is initially unknown and then learned. The notion that error correction is learned and not a static process is consistent with previous data. Braun et al (2009) train subjects using random visuomotor rotations in batches of 8 trials and find that the error corrective process is not static because learning a subsequent, novel rotation is accelerated. Herzfield and colleagues (2014) show that the error corrective process that allows adaptation to alternating perturbations (such as visuomotor rotations or force fields) is influenced by the history of errors which could give rise to faster learning similar to the present observation of accelerated convergence to novel targets.

A second property of this early stage of learning is that error correction is not needed to build a feed-forward controller. Specifically error correction does not produce improvements in performance when moving to novel random targets (Figure 9). Moreover, the point map can be learned in the absence of the opportunity for error correction as is the case when the target changes on each trial. The present work is thus part of a growing literature documenting motor learning in the absence of error correction. In reinforcement-based learning success or failure drives learning without the need to know either the direction or magnitude of error (Sutton and Barto, 1998; Izawa and Shadmehr, 2011). In use-dependent learning performance improvements are observed in the context of repetition of movement alone (Diedrichsen et al., 2010; Nudo et al., 1996). However, there is little opportunity for use-dependent learning when the target, and therefore the movement, is different on every trial (see below for a discussion of the potential role of reinforcement in the present learning).

Error corrective trials do not feed into the point map, but instead contribute to forming an error map, which is learned independently. Using two maps may allow a more efficient encoding of space than a single map as shown by a computational architecture (Fig. 1). In the context of that architecture adding a third map (or more) would seem to yield a yet more efficient coding of space, but for the sensorimotor

apparatus to use such third map (a derivative-error map) it would have to be able to compute a trial-to-trial change in error, a capability for which to our knowledge there is no empirical support. The closest operation the sensorimotor apparatus has been shown to be capable of is to compute the sign of the change of errors (Herzfeld et al., 2014). The present study in principle does not rule out the existence of additional maps (in addition to the point and error map) but is concerned with showing that there are at least two maps.

When targets never repeat, learning could in principle be driven by sensory prediction error: after each movement, the predicted sensory effect of that movement (the forward model) is updated based on the actual feedback. The updated sensory prediction is the previous prediction plus a fraction of the prediction error (difference between prediction and actual feedback) (Synofzik et al., 2008, 2006; Tseng et al., 2007). However, this account relies on the assumption that prediction errors update a forward model, and this assumption entails that all information is gathered in a single sensorimotor map. If only one map is learned that all movements are fed in to, then repeated movements to the same target should yield better learning than making only one movement to each target, which is contradicted by the present data (Fig. 9). Furthermore, learning dependent on sensory prediction error requires that subjects generate sensory predictions, but the present data suggests that at least initially they do not, as demonstrated by the absence of a correlation between targets and movements.

Both point and error map learning display characteristics of generalisation. Specifically, in point map learning the target on every trial is different, yet subjects' performance improves over the course of training. In error map learning, each set of movements involves a unique target, yet the convergence onto novel targets improves with training. Simulations (Fig. 3) indicate that such generalisation behaviour would be expected, even if the map is as simple as a lookup table. This is because as units are added with learning and hence map density is increased, the nearest neighbour to any given target will be closer and therefore reaching error will be smaller. Note that the look-up table account assumes the presence of a distance metric. The returned value is then used to probe the look-up table. Whether maps indeed represent instance-based learning (a lookup table) or instead encode the structure of the space remains a question for future research.

The question whether reinforcement could drive the learning observed here merits consideration. In a restricted sense where subjects repeat previously rewarded movements, reinforcement could not account for the learning here. On a given trial, when a subject produces a movement that is similar to the target sound, although they could experience it as rewarding, if they would in future trials attempt to repeat this movement, it will not necessarily be beneficial because the target may be different. However, in a more general sense, reinforcement paired with a map approximation function could drive learning. The question is what this map approximation function would be. One option proposed here is that it could be as simple as a lookup table.

Adapting existing sensorimotor maps

The acquisition of sensorimotor mappings has been studied previously, but often in cases where participants either already had fully formed sensorimotor maps or prior expectations about the structure of the sensory-to-motor relationships. For example in visuomotor adaptation vision of the arm is experimentally displaced as participants make reaching movements (Krakauer, 2009). The newly acquired sensorimotor map can be represented as the existing sensorimotor mapping plus a correction term that pertains to the particular experimental perturbation (Telgen et al., 2014). Indeed, this is typically how sensorimotor adaptation is computationally modeled (Cheng and Sabes, 2006; Ghahramani et al., 1997). The novelty of the work here is not simply that it pertains to the auditory (instead of visual) modality. Indeed, during speaking people are known to compensate for altered auditory feedback (Houde and Jordan, 1998). The novelty of the paradigm is that there is no pre-existing sensorimotor map that gets adjusted. Apart from work on babbling in early infancy little is known about how these maps are initially formed.

Acquisition of sensorimotor mappings closer to that investigated here is reported in studies in which participants controlled a screen cursor using physical movements with the fingers or hands (Sailer et al., 2005; Mosier et al., 2005; Yamamoto et al., 2006) but through a nontrivial transformation. The present work builds on these studies by elucidating the structure of the acquired maps.

Learning musical instruments

Learning a musical instrument (Herholz and Zatorre, 2012; Bangert and Altenmüller, 2003) also requires forming an audiomotor map and therefore its neural underpinnings may be similar to the neural structures that enable sensorimotor map learning observed here (Zatorre et al., 2007). A large body of research documents differences between musicians and non-musicians in brain morphology (Gaser and Schlaug, 2003; Vaquero et al., 2016) or brain networks documented using resting state scans (Luo et al., 2012; Palomar-García et al., 2016; Feinberg and Setsompop, 2013). These differences occur in a distributed network of areas including auditory cortices, and primary motor cortex, premotor areas, superior temporal gyrus, somatosensory cortex and the basal ganglia. However, it is unclear whether the observed differences are specifically due to musical training or to neuroanatomical factors that predispose one to become a musician.

A number of studies monitor participants directly as they learn to play a musical instrument and these studies implicate a number of brain areas. Activity in dorsal premotor cortex (dPMC) was found to be reduced late vs. early in learning to play a musical melody on a keyboard (Chen et al., 2012); another study found increased activity in dPMC after non-musicians had been trained to associate musical chords with keystrokes (Bermudez and Zatorre, 2005). Lega and colleagues applied transcranial magnetic stimulation during a task in which participants learned associations between keystrokes and sounds, and found that dorsal premotor cortex (dPMC) is causally involved in this learning (Lega et al., 2016) (for a related paradigm see Wise and Murray 2000; Säfström and Edin 2006). Other areas associated with musical training are the posterior superior temporal gyrus (pSTG) which following drum training showed increased connectivity with the rest of the brain (Amad et al., 2016).

There are differences between learning to play a musical instrument and the audiomotor task employed in the present studies that bear on the interpretation of reported patterns of neural activity. First, the acquisition documented in studies of learning to play musical instruments presumably relies on prior information, because even non-musicians have structural expectations about the mappings between space and pitch (Rusconi et al., 2006). Second, learning to play a musical instrument not only involves the formation of an audiomotor map but also entails changes to motor and perceptual function as well (Kraus

and Chandrasekaran, 2010). Accordingly, it is not possible based on current studies of musical instrument learning to dissociate areas whose activation specifically reflects map learning.

Summary

Participants acquired novel sensorimotor maps by making reaching movements to auditory targets and in this process form two independent mappings: a point map connecting sensory targets to motor commands and an error map that links motor corrections to sensory errors. The present study identifies the structure of these maps and the future challenge is to determine the learning rules by which their content is acquired.

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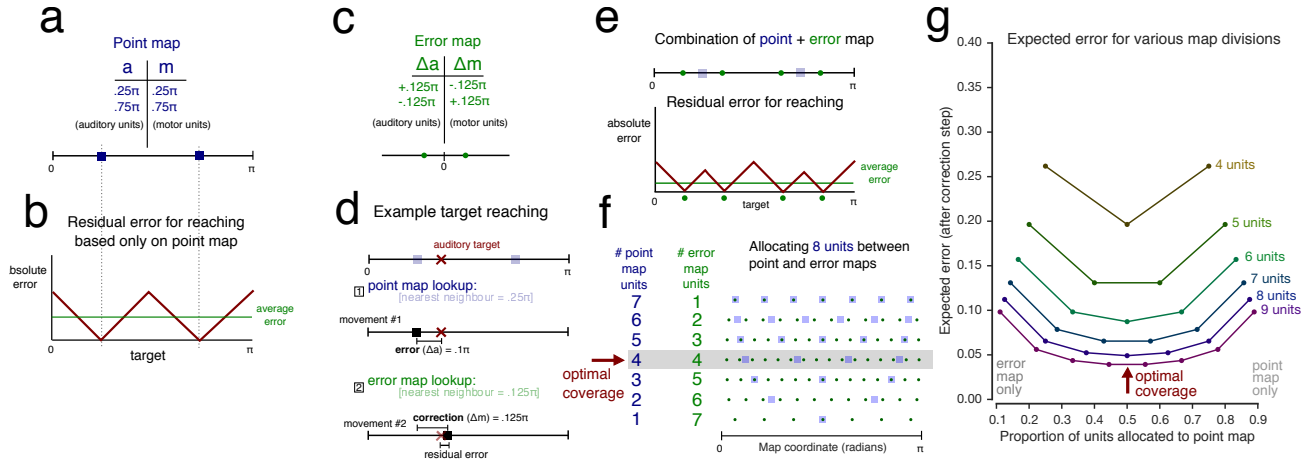


Figure 1: A computational architecture that demonstrates the optimal design of a sensory-motor controller includes both a point and error map instead of only one of the two. **a**, Consider a controller that has access to a point map which is a look-up table of units connecting a particular movement with a sensory effect, and an error map which connects sensory errors with motor corrections (**c**). Since we assume that the mapping between movements and sounds is one-on-one, we can without loss of generality represent these lookup tables as points on a motor/sensory space, here for simplicity a one-dimensional interval of movement angles $[0, \pi]$ which corresponds to those used in the present empirical study. **b**, When a target is presented, the point map is queried and returns the nearest neighbour entry. For the point map example above this leads to a pattern of errors (red line) and, if the targets are equiprobable, an expected absolute error (green line). Note that the error varies with the distance between the target and the nearest neighbour. **d**, On a given trial, first an auditory target is presented. The controller selects the point map entry (out of 2 in this example, marked in blue) closest to the target and performs the corresponding movement (movement #1). If the movement is not exactly on target a nonzero error occurs, which is a difference vector that is then looked up in the error map (units not shown) resulting in a corrective movement (movement #2). Even though by way of simplification the controller aims to correct an error completely (gain=1), due to the limited resolution of the error map, a residual error exists when the trial ends. **e**, Example of a combined map that has two point map entries and a two-entry error map reproduced at each point map location. Note that there is a single error map which is not linked to particular targets but can be applied at any position in the workspace when error correction is possible. The red trace indicates the residual error for each target location given the above two-movement scheme (a point map movement and a corrective movement). **f**, Adding more elements to either the point or error map increases performance as measured by a reduction in expected residual error, but if resources are limited, how can available units be best divided between these two maps? In the example case of 8 units, assuming the units are placed optimally on the maps, the best coverage of the space is achieved when the 8 units are divided equally between the point and error maps. **g**, This is indeed true in general: the lowest cost (optimal division) is achieved for an equal split of units between a point and error map. This leads to the prediction that two maps encode information more efficiently than one. Although this is a simplified architecture, relaxing its assumptions to make it more realistic (such as the addition of noise in reaching or map lookup) will not alter the computational argument that dual encoding provides optimal spatial coverage.

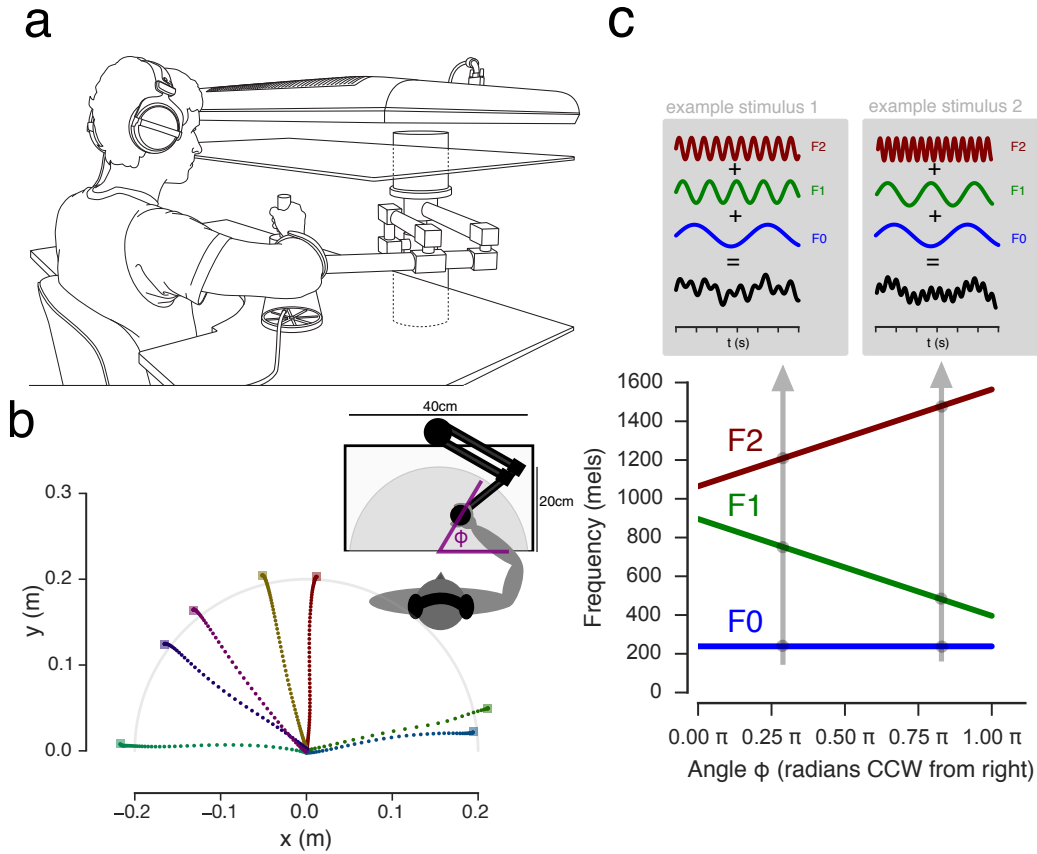
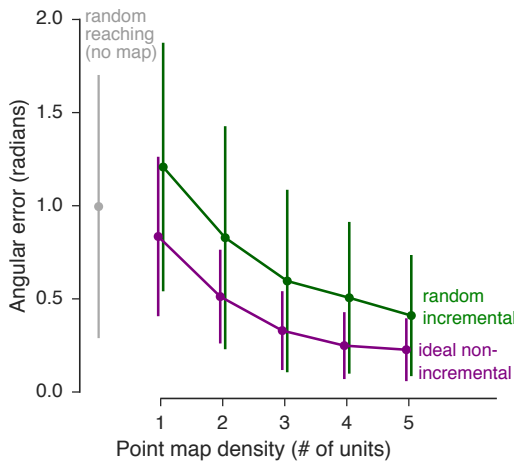


Figure 2: Participants make movements to auditory targets. Prior to each trial, a target sound is presented. Participants then make a reaching movement to the presumed location of the sound. **a**, Side view of the workspace. Participants made reaching movements from the center of the workspace to points on a semi-circle (not visible to participants). When participants had stopped moving auditory feedback was presented that depended on the angle between the starting point and the end of the movement. The amplitude of the movement was inconsequential to the sound. No acoustic location cues were present in the sounds since the same signal was presented to both ears. **b**, Example movements for one subject. Square markers indicate the final hand position, whose angle relative to the starting point (ϕ) determines the feedback sound. For reference, the target circle is indicated in gray but not seen by the subject. **c**, The sounds that were played to participants at the end of each movement consisted of three oscillators whose frequencies depended linearly on the angle at movement end ϕ (see grey inlays for a decomposition of two example stimuli that correspond to the movement angles indicated by the arrows). In order to ensure perceptual uniformity of the auditory space, we used the mel scale for sound frequency.

a Simulations for varying point map densities



b Simulations for varying error map densities

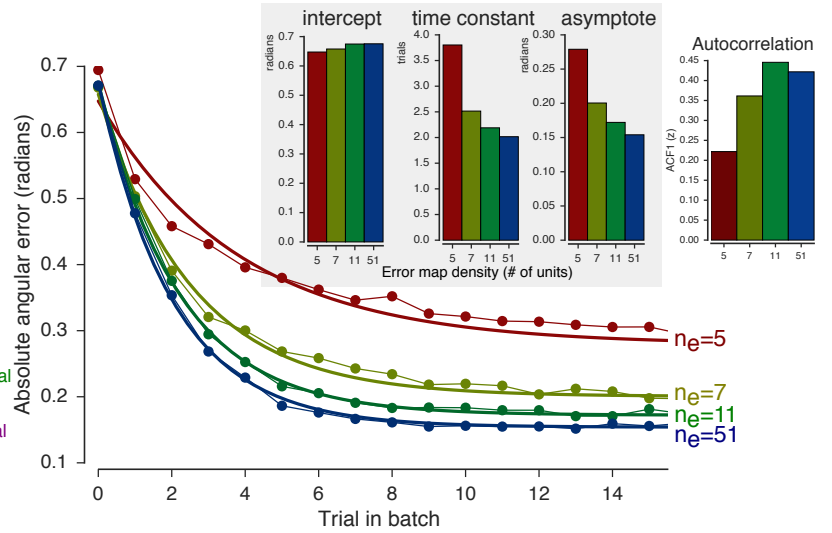


Figure 3: Model simulations show that adding units to the point map (n_p) results in reduced error in reaching to random targets and adding units to the error map (n_e) results in improved convergence to repeating targets. **a, Random target simulations reveal that increasing point map resolution (adding units to the point map) yields decreased angular error in reaching to random targets. Simulations were performed by incrementally adding units to the point map in random locations (green trace). For reference, the purple trace indicates model performance when the same number of units are placed in optimal locations (which are different for different numbers of map units) and random reaching performance is shown in grey. Error bars indicate SD. **b**, Increased error map resolution (adding units to the error map) results in improved convergence to the target, as measured by a smaller time constant and lower asymptotic performance while the intercept of the learning curve did not decrease (see inlay barplots). In addition, as error map density increases the trial-to-trial autocorrelation of movements to the same target increases. Dots represent the data points and lines represent the fitted learning curves.**

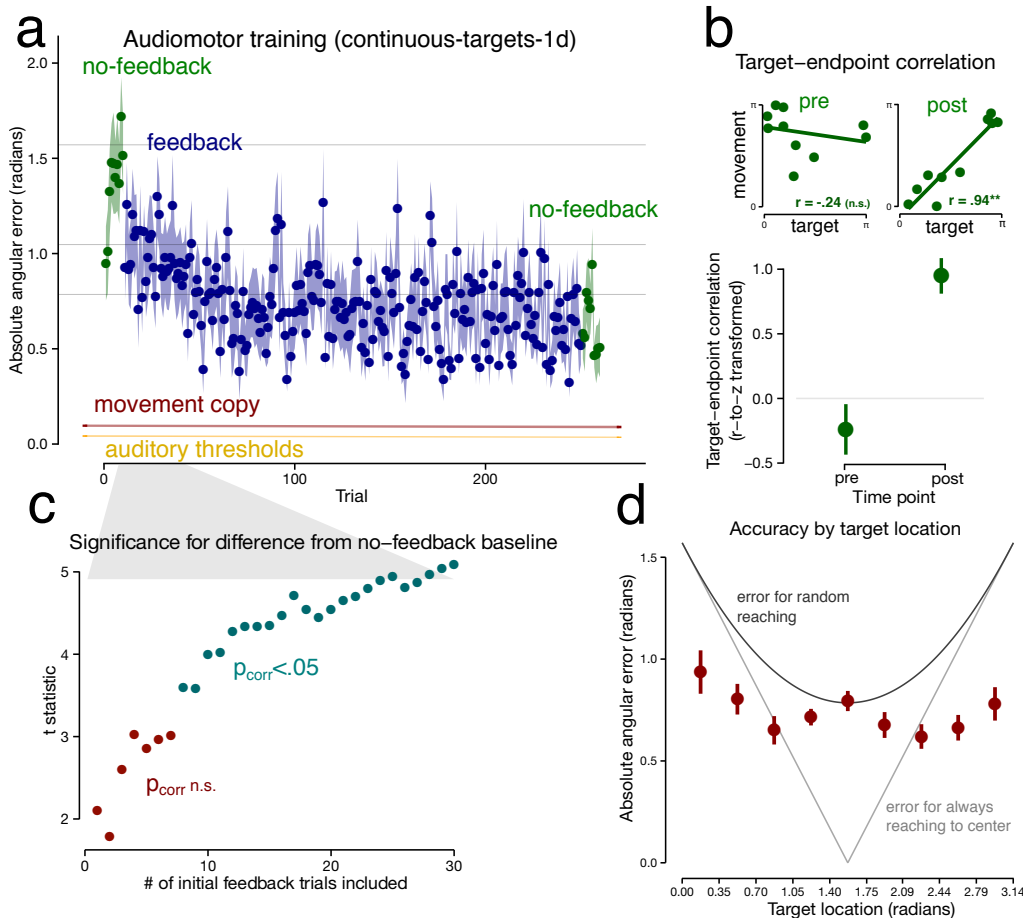


Figure 4: An audiomotor point map is acquired even when participants make movements to auditory targets that are never repeated. **a**, Absolute angular error between the target and movement endpoint is shown to improve as a function of trial (continuous-1d experiment). Dots indicate means across subjects and the shaded area the SEM. Performance on auditory (yellow) and motor (red) tests remained stable and are shown for reference, translated into motor coordinates (in radians, mean and SEM; the variability is so small that it appears as a line). **b**, Correlations between the target and movement angle for a representative subject indicate that at the outset there was no prior information about the mapping (no correlation; top left panel) whereas after learning movement directions vary systematically with auditory target location (top right panel). This was true for subjects overall (main panel) (data r-to-z Fisher-transformed; error bars indicate SEM). **c**, In order to study at what point over the course of training the movements became different from chance reaching, we took the initial n trials with feedback, for various n , and computed a t-test against the no-feedback pre training trials. Colour coding indicates that movement error reduction reaches significance after 8 movements, indicating very rapid learning. **d**, Absolute angular error for various bins of target location (in radians), indicating that subjects' performance deviated from chance error levels that would be expected if subjects would always reach to the center (grey; the theoretically optimal strategy if the mapping was unknown to them) or if subjects would reach randomly (in black).

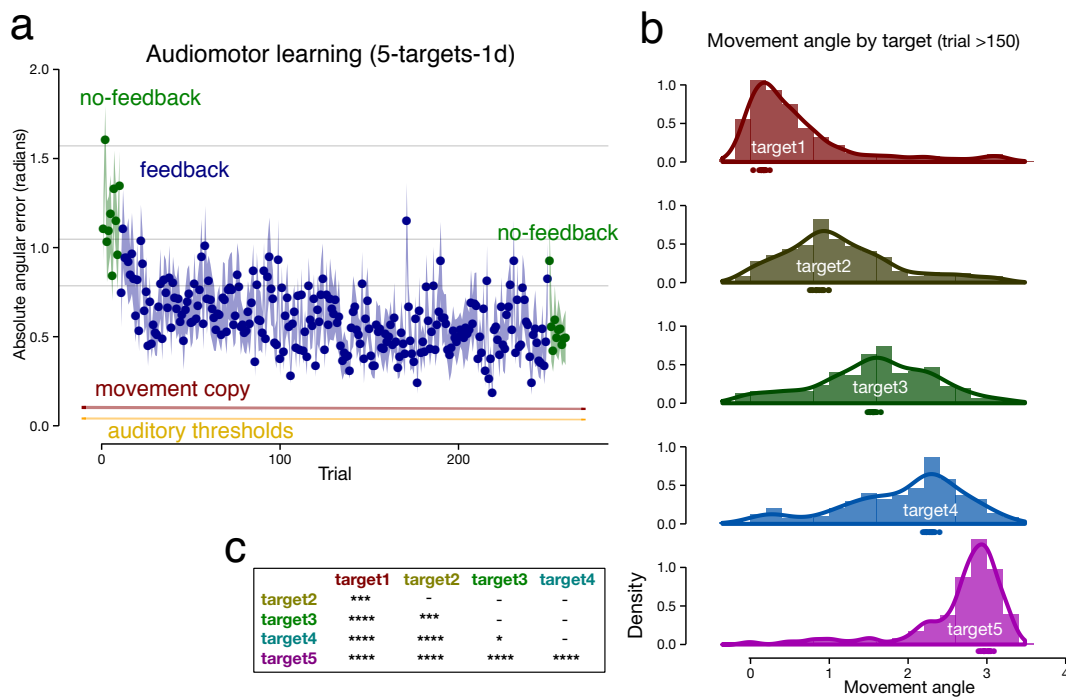


Figure 5: The acquired audiomotor point map encodes multiple targets (five or more). **a**, Angular error over time (5-targets-1d). **b**, Movement angles as a function of the target presented for all subjects combined (targets are numbered in counter clockwise order starting from the right). Actual locations of the targets varied between subjects and are indicated by dots below the histograms. Lines indicate kernel density estimates. **c**, Pairwise comparisons of the reaching endpoints for the individual targets were all significant (t-tests with Bonferroni-corrected p-values: * $p < .05$, ** $p < .01$, *** $p < .001$ **** $p < .0001$).

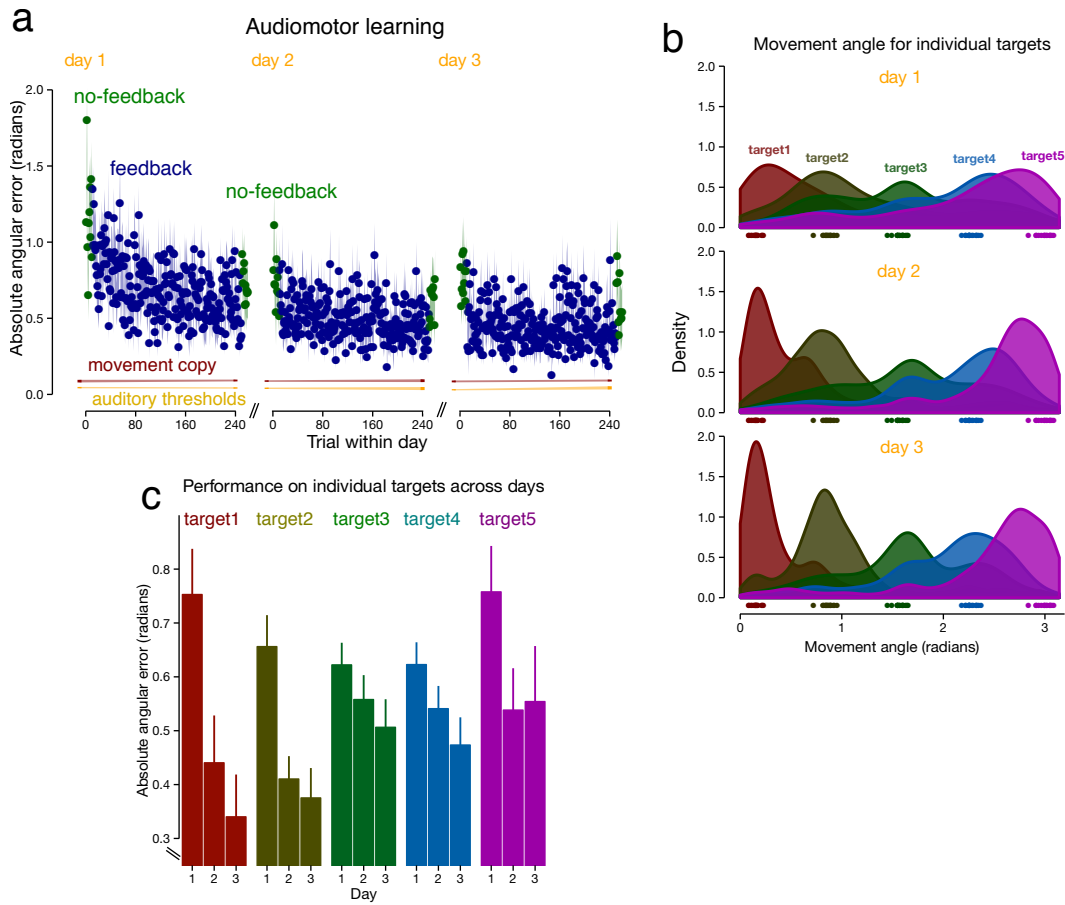


Figure 6: **The audiomotor map is retained and learning continues across days** (5-targets-3d experiment). **a**, Mean absolute error across trials on the three days. **b**, Density estimation of movements to each of the five targets for all subjects combined show that movements become progressively more clustered around actual target locations (indicated with dots below the horizontal axes). **c**, Average absolute angular error for the individual targets across the three days.

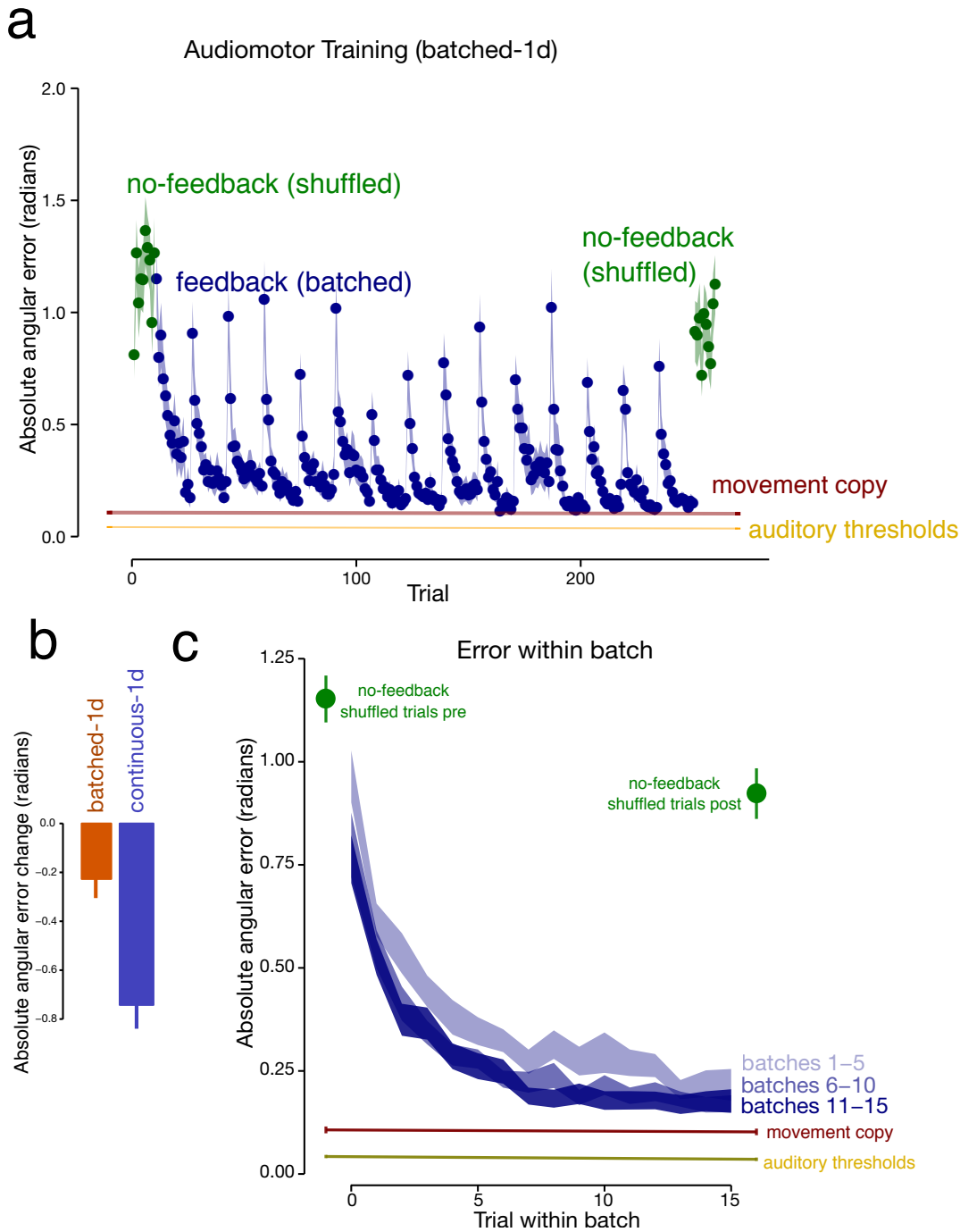


Figure 7: When error correction is made possible, convergence to targets is observed and this convergence itself changes over time, which is evidence for error map acquisition. a, Audiomotor training trials indicate a sharp decline in error over the course of repeated presentations of a single target. **b,** However, point map learning is *less* when targets are repeated than when they are random on every trial (cf. Figure 4) as shown by average reduction in angular absolute error during the no-feedback trials. **c,** Average errors in groups of 5 batches. A sharp initial decline in error ends in asymptotic performance that is close to the movement copy error (in red). Green dots indicate average error on no-feedback trials before and after audiomotor training.

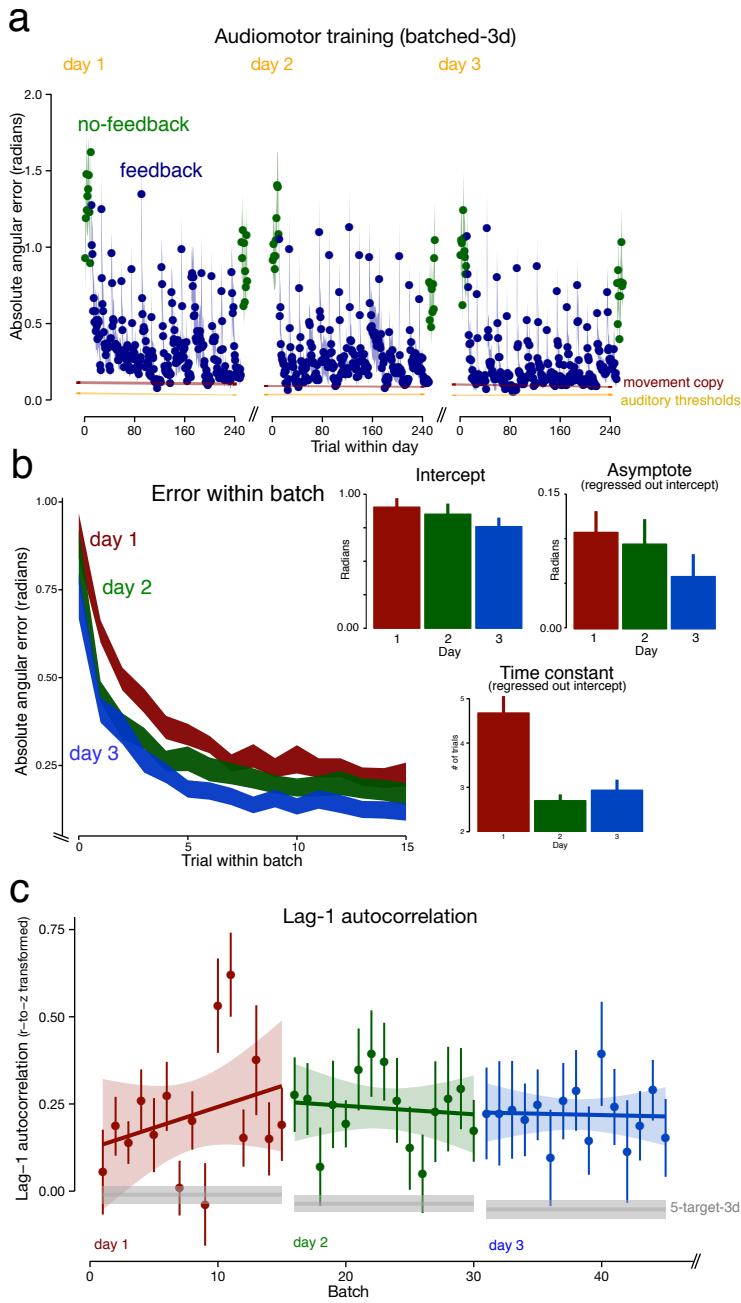


Figure 8: Error map learning is itself a learning process, observed as improved convergence on to the target across days. **a**, Error as a function of trial across days. **b**, Error as a function of repeated presentation of the same target across the three days. The barplot indicates that the time constant decreases (rate of convergence on to the target increases) and the asymptote decreases and this cannot be explained by the intercept of learning curves (see barplots). **c**, Lag-1 autocorrelation (ACF1) calculated for each new target increases over the course of the first day (red) and then remains stable at a small but non-zero level for following days (green and blue). For random trials, ACF1 remains at zero (in grey; calculated over chronologically ordered series of 16 movements to the same target in the five-target 3-day experiment, omitting intermediate trials to different targets), suggesting that a different learning process operates in the repeated and random target studies.

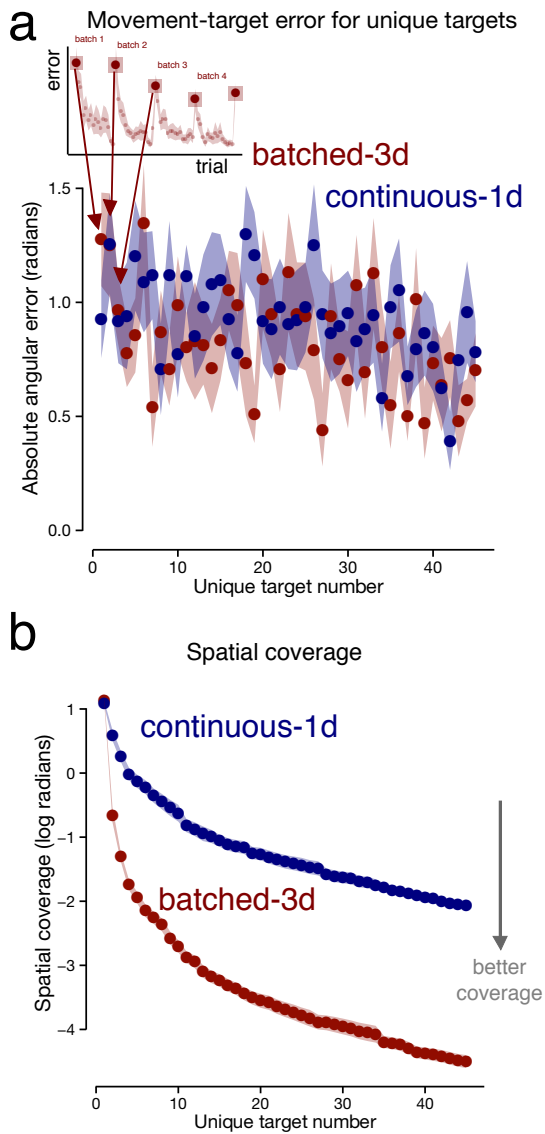


Figure 9: Point and error map learning are independent. a, Repeated movements to the same target do no contribute to learning a point map. Independence of the mappings is indicated by plotting the error on the first trial of every new target (red; trial selection is illustrated in the inlay figure where green markers indicate the first trial of every new target which is shown in the main panel) against the errors that occurred when targets were selected randomly and never repeated (continuous-1d experiment; Fig. 4). It is seen that even though subjects that moved repeatedly to the same target showed much better asymptotic performance at the end of each batch, the improvement from the start of one batch to the start of the next was no different than that observed for subjects tested with random targets. This indicates that the learning process that operates with repetitions of the same target (error map learning) is independent of the process by which a point map is acquired. **b, Repeated-targets participants received ample exposure to the audiomotor workspace.** Spatial coverage computes how far any given point in the interval is to the closest movement, therefore as the set of movements cover the space more densely the distance to the closest point is less (see supplementary materials). For the repeated-targets experiment we calculate the spatial coverage based on all intermediate movements, but plot only the first trial to every new target to allow comparison with the continuous-1d experiment coverage. The repeated-targets participants' coverage of the space is greater than that of the continuous-1d participants, indicating that their identical performance on the random trials (panel a) cannot be explained as a lack of spatial coverage. **c, A visual-auditory observation experiment reveals some learning indicating that a cognitive strategy, if used at all, could only lead to a limited improvement in performance.**

A Supplementary Materials

A.1 Computational architecture

Here we present an theoretical rationale for the existence of a point and error map based on a computational architecture of a sensorimotor controller. In order to study how sensorimotor relations may be encoded in the brain, we considered the following computational architecture. We let this model perform the task that our subjects did, that is with a one-dimensional one-to-one sensory-to-motor mapping on a fixed interval $[0, \pi]$, however, the model and its results generalise straightforwardly to multiple dimensions. Since the mapping is one-on-one we will refer to auditory or motor coordinates in common coordinates on the given interval $[0, \pi]$ (Fig. 1a). We assumed for simplicity of presentation that the point map and error map consisted of look-up tables. The point map is a lookup table that maps sensory results to motor commands. Further, we assumed that the sensorimotor controller, given a sensory target, would first perform a nearest-neighbour lookup in the point map (Fig. 1d). For the sake of simplicity, we assume that this lookup is error-free and so are the performance of the movement and perception of the target and feedback. The initial movement will in many cases still not be succesful in exactly reproducing the target (Fig. 1d). The controller continues to compute the error (in sensory coordinates) and then look up the corresponding motor correction in the error map, which is also an error-free look-up table. Note that the sensory error is coded as a difference between two sounds and motor correction is the difference between two movements (an original movement and its corrected version). We assume that the error map does not depend on space, that is, the sensory-motor gradient can locally be approximated by a single function that is the same everywhere. The sensorimotor controller then applies the motor correction to the first movement to yield the second movement. We assume that the error is corrected completely and that there is only one correction step. This means that the multiple error correction steps that plausibly happen in reality are here merged into a single correction for simplicity of presentation.

The idea is that as you learn a motor skill, you populate these maps with informational units (a history of prior movements), here represented as entries in a lookup table. As more content is added, the spatial resolution of the maps increases. Assuming that these maps together can only hold a limited amount

of information, what is the best way to allocate information units between a point map and error map? The cost was defined as the sum of units in the point map and the units in the error map, reflecting the idea that the bigger the lookup table, the higher the cost associated with encoding it. Furthermore, we assume that the model places whatever number of units are allocated to each of the point and error maps in the optimal way, that is, so that the expected error for reaching to a target in space is minimal (after the correction step) (see Fig. 1f for illustrations of the optimal placement of various point/error map ratios). A proof of what is the optimal placement is included below.

The problem of optimising this controller is then reduced to finding which division of units between point and error maps yields the most accurate reaching. Given the numbers of units in the point and error maps, the expected reaching error is completely determined based on the assumptions presented so far and can be calculated analytically (Fig. 1g). The optimal allocation of resources between a point and error map divides the units equally between the two maps, which yields smaller reaching errors than allocating all units to either the point or error map (Fig. 1g).

A.1.1 Formal definition

Consider the set of all possible movement endpoints M and the set of all possible sounds S . The model here is essentially a function $f : S \rightarrow M$, where given a sound s the model selects a movement with endpoint $f(s)$.

The model introduced here consists first of a point map that is a look-up table of n_p pairs of movements and sounds $P = \{(m_i, s_i) | i \in \{1, 2, \dots, n_p\}\}$ where m_i is the movement of the i -th lookup pair and s_i is the corresponding sound. Given P let us write $P_S = \{s_i | (m_i, s_i) \in P\}$. We assume that the model has access to a sensory comparison function which we call N and which is not part of the model proper and does not undergo learning. The comparison function N takes as input a sensory candidate sound c and a set of reference sounds R . The comparison function then returns the reference sound $r \in R$ that is most similar to the candidate sound c . The model needs no further acoustic or other information about the sounds in order to function. The comparison function could be based on a simple spectral comparison of the sounds in question. For practical purposes of the modeling here we assume the comparison function

satisfies this condition $N(c, R) = \operatorname{argmin}_{r' \in R} |r' - c|$, that is, we assume that the subjects have a way of accurately assessing which sounds are more similar, but this information is not part of the audiomotor map per se. Given a target the model queries the sensory comparison function with the target sound and the set of sounds in its lookup table, and then returns the movement corresponding to the sound returned by the sensory comparison function. That is, it works as a generic look-up function L_P defined as follows: $L_P(s_t) = m_i$ iff $s_i = N(s_t, P_S)$. Similarly for the error map except that it is a look-up table of movement changes and sound changes $E = \{(\Delta m, \Delta s_i) | i \in 1, 2, \dots, n_e\}$.

Our architecture selects reaching movements as follows (illustrated informally in Figure 1). Call s_t an auditory target presented on a given trial. The model first makes a reaching movement $m_1 = L_P(s_t)$, which generates an error $s_t - L_P(s_t)$ giving rise to a movement correction $\Delta m =_{\text{def}} L_E[s_t - L_P(s_t)]$ so that the next (second) movement is $m_2 = L_P(s_t) + \Delta m =_{\text{def}} M_{P,E}(s)$. The error of this second movement, i.e. the residual after the corrective movement, is $s_t - (L_P(s_t) + \Delta m)$. This completes the model definition.

A.1.2 Optimal placement of map points for a single look-up step

In what follows, we will simplify notation by referring to sounds by the movement to which they are linked as specified by Figure 2 of the main manuscript (for example, the sound with oscillator frequencies 220, 780, 1200 will be referred to as $.3\pi$, which is the movement angle subjects would have to produce to generate that sound). With this simplification, any look-up table $\{(m_i, s_i)\}$ we can now simply write as $\{m_i\}$. In such a case, the lookup function can be written more simply as $L_X(y) = \operatorname{argmin}_{x \in X} |y - x|$. We can then write the point and error maps both as points along a single dimension, i.e. $P = \{p_i\}$ for $i \in 1, 2, \dots, n_p$ and the error map as units $E = \{e_i\}$ for $i \in 1, 2, \dots, n_e$.

Here we show what is the best placement of a fixed number of points over a given interval so they optimally cover the space relative to a look-up function described above. Given a closed interval $[0, w]$ and a number n of points $X = \{x_i\}$ (for $i \in \{1, \dots, n\}$) to be placed in that interval, the task is to minimise the average distance from any point in the interval $[0, w]$ to the closest of the points x_i , i.e. minimise

$$C_X = \int_0^w |p - L_X(p)| dp = \sum_{p \in [0, w]} \min_{i \in \{1, \dots, n\}} ||x_i - p||$$

The above equation can be rewritten to $C_X = \frac{1}{2}x_1^2 + \frac{1}{2}(w - x_n)^2 + \frac{1}{2^2}\sum_{i=1}^{n-1}(x_{i+1} - x_i)^2$. Setting all $\frac{\delta C_X}{\delta x_i} = 0$ we find the following equations that hold true for the optimal placement of points $X = \{x_i\}$:

$$x_i = \begin{cases} \frac{1}{3}x_2 & \text{if } i = 1 \\ \frac{1}{3}x_{n-1} + \frac{2}{3}w & \text{if } i = n \\ \frac{1}{2}(x_{i-1} + x_{i+1}) & \text{otherwise} \end{cases}$$

From this, it follows that the optimal placement is $x_i = (w/2n)(2i - 1)$.

A.1.3 Optimality of dual map architecture

In this section, we set out to show that a dual map architecture is optimal. That is, given a number of units n that can be divided between a point (n_p units, a free parameter) and error map (n_e units, a free parameter), we aim to show that the optimal allocation is one in which the units are divided equally between the two maps, i.e. $n_p \approx n_e \approx n/2$.

As indicated previously, given a point map P and error map E , the final (corrected) movement for a given sensory target s is given by $M_{P,E}(s) = L_P(s) + L_E[s - L_P(s)]$ (see section above).

Proposition. Given a number of units n_p to allocate to the point map P and a number of units n_e to allocate to the error map E , the optimal placement of these units is given by $P = \{(2i - 1)\frac{w}{2n_p} | i \in \{1, 2, \dots, n_p\}\}$ and $E = \{-\frac{w}{2n_p} + (2i - 1)\frac{w}{2n_p n_e} | i \in 1, 2, \dots, n_e\}$.

Proof sketch. The indicated placement of the point map units is what gives the smallest error for the first reach (see section A.1.2) and therefore leaves the smallest residual error after the first reaching movement. Specifically, the error is now limited to an interval $|s_t - L_P(s_t)| \in [-\frac{w}{2n_p}, +\frac{w}{2n_p}]$. So now the problem is to place the units in the error map to maximally reduce this error, which is analogous to placing units on the interval $[0, 2\frac{w}{2n_p}]$ and then shifting by $-\frac{w}{2n_p}$. Using the reasoning from section A.1.2 the optimal placement of units over the interval $[0, 2\frac{w}{2n_p}]$ therefore is given by $E' = \{(2i - 1)\frac{w}{2n_p n_e} | i \in 1, 2, \dots, n_e\}$ which after shifting is equal to E above. \square

Corrolary. If P and E are chosen optimally (as specified above) then there exists an equivalent single-lookup map X such that $M_{P,E}(s) = L_X(s)$, and we will call this map the *effective map*.

For example, Figure 1f shows the effective map as green dots for various combinations of point and error maps.

Proposition. Given a number of units n which can be divided between a point map (n_p units) or an error map (n_e units), i.e. $n_p + n_e = n$, the optimal such division is $n_p = n_e = \frac{n}{2}$ or as close to it as can be achieved using discrete units.

Proof. Given a choice of n_p and n_e the optimal placement of units is given in the previous proposition. The expected error of the two-step reaching can then be shown to be $C_{P,E} = \int_0^w |p - M_{P,E}(p)| dp = \int_0^w |p - (L_p(p) + L_E[p - L_p(p)])| dp = n_p n_e (\frac{w}{2n_p n_e})^2$. Now we can substitute $n_e = n - n_p$ so that $C_{P,E} = \frac{w^2}{2^2} (n - n_p) n_p$. Now the problem is reduced to minimising $C_{P,E}$ as a function of $n_p \in 1, 2, \dots, n-1$. Solving $\frac{\delta C_{P,E}}{\delta n_p} = 0$ yields $n - 2n_p = 0$ and $n_p = n/2$. In other words, the optimal residual error is lowest for equal division of units between the point and error maps. \square

A.2 Learning could not be explained as perceptual or motor learning

Across our experiments, we found that auditory perceptual thresholds and motor copy errors could not explain the improvements in reaching towards auditory targets (Fig. S1). This critically shows that learning could not be explained as perceptual or motor learning but was attributable to the learning of the sensorimotor mapping.

In the 5-targets-1d experiment, motor-copy absolute angular errors were not significantly different after training than before ($F(1,16)=.58$, $p=.46$) nor were auditory psychometric curve midpoints ($F(1,14.00)=2.74$, $p=.12$). Further, motor-copy angular error and auditory psychometric curve midpoints were not significant as covariates to no-feedback improvement ($F(1,24.82)=.42$, $p=.52$; and $F(1,232.33)=.01$, $p=.91$, respectively).

In the 5-targets-3d experiment, auditory psychophysical thresholds were not different across days ($F(2,70.00)=.88$, $p=.42$) nor differed between before and after audiomotor learning sessions on a day ($F(1,70.00)=.50$,

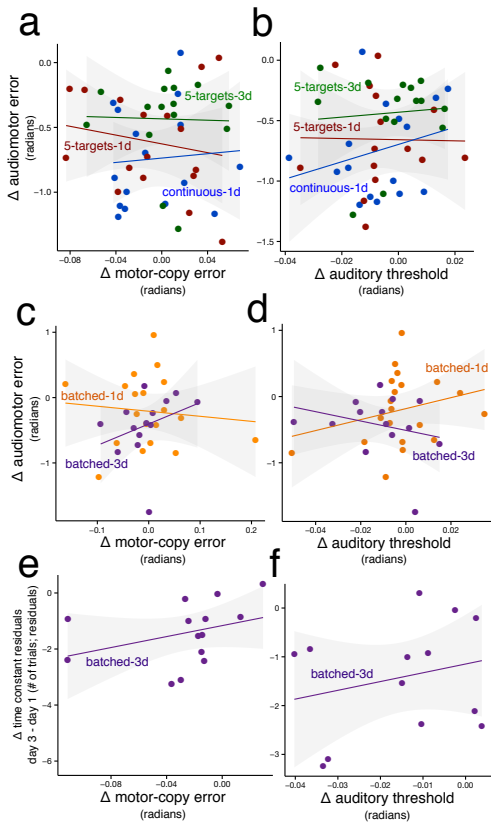


Figure S1: Auditory psychophysical and motor-copy changes cannot explain the improvement in the audiomotor trials. Change in angular error (in radians) in the motor-copy trials (**a,c,e**) and change in auditory psychophysical curve midpoint (**b,d,f**). The dependent variable is the change in angular error in the no-feedback audiomotor trials (**a-d**) and the change in time constant of the batch learning curve (after regressing out its intercept and asymptote) (**e,f**).

$p=.48$). Motor-copy thresholds also did not differ across days ($F(2,70.00)=.02$, $p=.98$) or before vs. after training ($F(1,70.00)=.78$, $p=.38$). Auditory or motor learning alone could not explain the no-feedback audiomotor trials improvement, because of non-significant covariates auditory thresholds ($F(1,247.62)=.27$, $p=.61$) and motor-copy error ($F(1,286.62)=.03$, $p=.86$) (Fig. 6a).

In the repeated-targets (1-day) experiment, the improvement in no-feedback trial reaching could not be explained by a change in auditory threshold ($F(1,50.59)=1.76$, $p=.19$) or motor-copy error ($F(1,186.28)$, $p=.48$).

In the repeated targets (3-day) experiment the no-feedback trial reaching improvement could not be explained as an auditory change ($F(1,56.31)=1.39$, $p=.24$) or motor-copy change ($F(1,134.70)=1.38$, $p=.24$) (Fig. 8a).

A.3 Reaction times and movement times

Figure S2 shows the reaction times for the various experiments reported in the main manuscript, measured from the offset of the target sound which is when subjects were allowed to start moving. It can be seen that there is a trend for reaction times to decrease in the course of the continuous-targets experiment but not in the 5-target experiments. In the repeated target experiments it can be seen that, first, reaction times fall during the first half of the first day, and second, that reaction times are longer for the first trial of each batch of movements to the same targets (Fig. S2b). This latter fact is presumably due to the fact that subjects on subsequent trials to the same target have already heard this target on the previous trial and can therefore initiate their movement more rapidly. Panel (Fig. S2c) shows that the follow-up movements to the same targets gradually become more rapid in the course of the three days of training. In sum, in cases where in the main manuscript reductions in errors were observed, the reaction times thus also decrease or remain constant, suggesting that learning that was observed is not due to a speed-accuracy trade-off.

As for movement duration, we did not observe any changes across the experiments. Movement durations were 844 (SD 156) ms in the continuous-targets experiment, 909 (SD 91) ms in the 5-targets-1 day experiment, 889 (SD 143) ms in the 5-targets-3 day experiment. In the repeated targets 1-day experiment movement durations were 903 (SD 169) ms and in the 3-day experiment they were 959 (SD 150) ms.

A.4 Signed error analysis

The present study has coded reaching error as absolute deviation from a target. However, the signed error is the preferred and appropriate method for analysing data from sensorimotor adaptation studies because it estimates a bias. In sensorimotor adaptation studies such a bias (consistent mislocalisation) is elicited using a perturbation: participants are expected to exhibit a bias in reaching once a perturbation is introduced. For example, if a visual cursor is rotated clockwise by 10 degrees, one expects all subjects to initially exhibit a 10 degrees clockwise (signed) error which in the course of the experiment they reduce, as illustrated by the simulations the reviewer performed. Thus, in sensorimotor adaptation studies the aim is to learn to counteract a perturbation. In the present studies, however, no perturbation is applied and

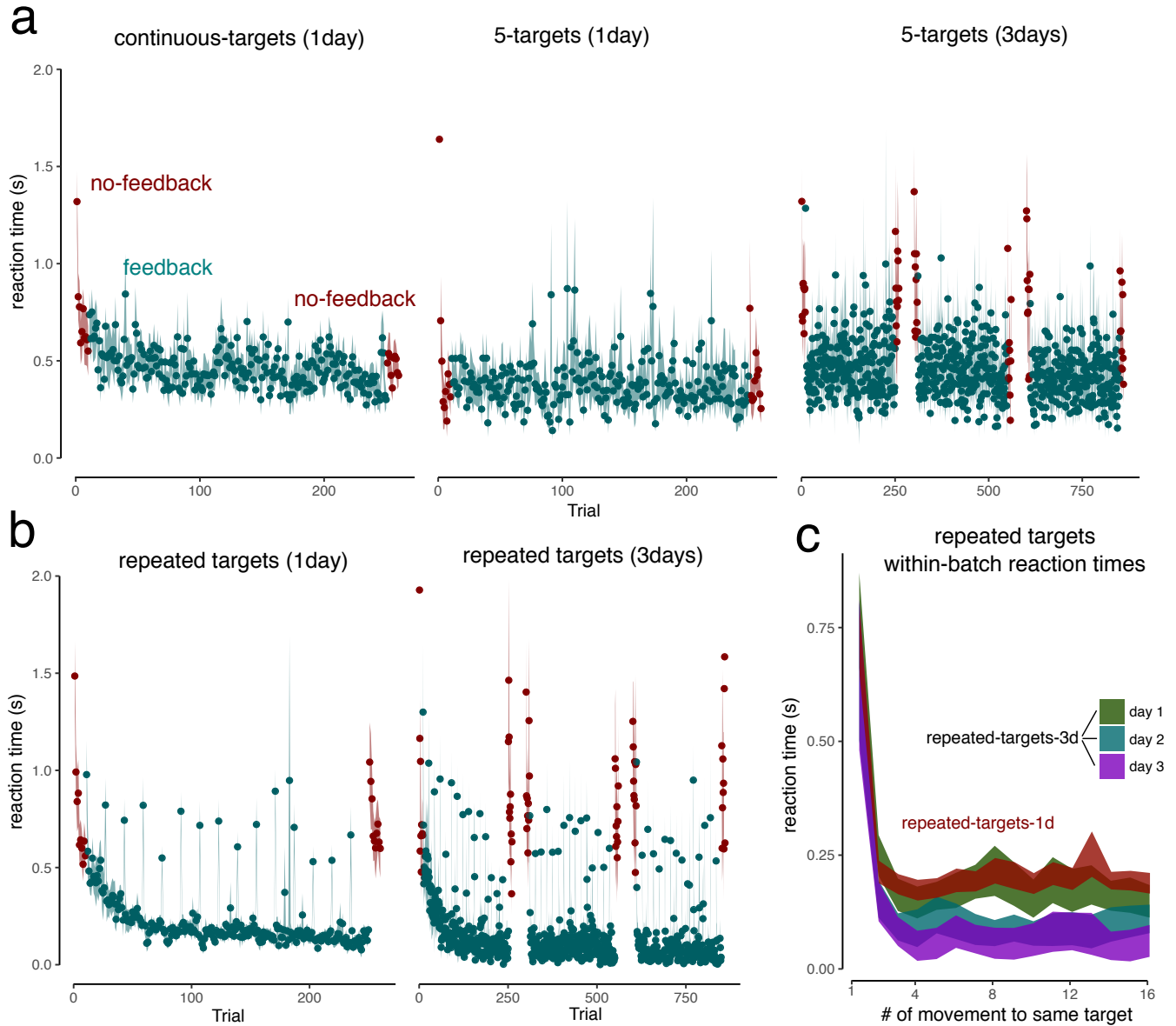


Figure S2: Reaction times measured in the experiments reported in the main manuscript. **a**, Reaction times in the shuffled target conditions (continuous targets, 5 targets 1 day and 3 day). **b**, Reaction times for the repeated target conditions (1 day and 3 day). **c**, Reaction times as a function of the number of the movement to a given target, indicating that the first movement to each target was initiated more slowly than subsequent movements to the same target. Across days the movements to subsequent targets were faster.

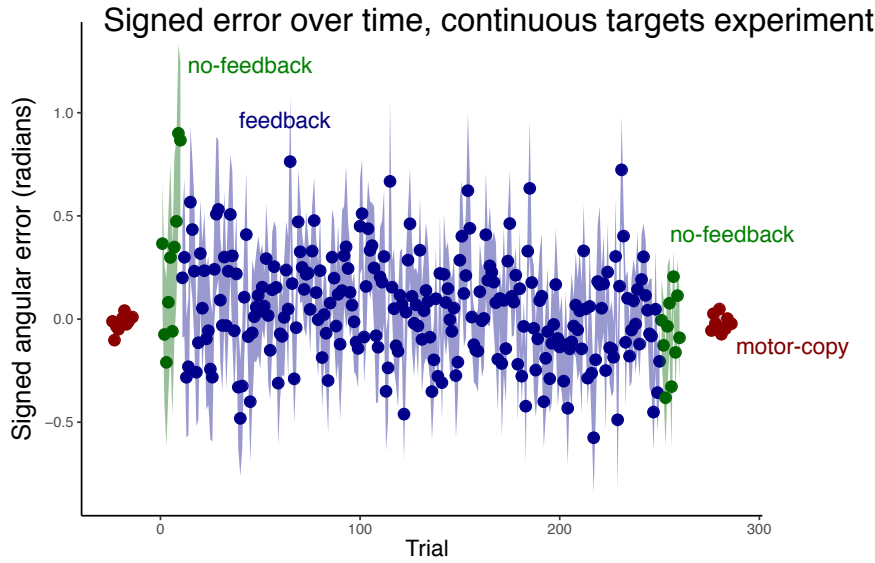


Figure S3: **Signed error performance analysis** for the continuous target experiment (cf. Fig. 4a of the main manuscript). Green dots indicate no-feedback trials before and after learning, blue indicates training trials. Red dots mark performance on motor-copy trials in the absence of sounds.

learning is of a different nature. Subjects come to this task without a mapping between movements and sounds and as a result, they cannot be consistently mislocating sounds. Indeed, in the random continuous targets we computed signed errors and plotted these in the figure below (Figure S3). During no-feedback trials prior to learning, this bias is not significantly different from zero [$t(15)=1.31$, $p=.21$] and there was no change between no-feedback trial bias after vs. before learning [$F(1,15)=1.86$, $p=.19$]. When this figure is compared with the learning showed in Figure 4a of the main manuscript it can be seen that the signed error measure misses information about learning that is captured when learning is assessed as a change in absolute error.

A.4.1 Individual subject bias analysis

The previous section suggested that subjects do not exhibit a consistent signed error, but the signed error may nevertheless be consistent within subjects. In order to capture learning that may involve correcting a random subject-specific bias, the following analysis was performed. For each subject, the sign was computed for the first trial, and then all errors for that subject were multiplied by that sign. Essentially, this computes a measure of error in the direction of the first error. Across subjects the value of this new

error metric on the first trial equals the absolute error. But subsequent trials may be of opposite sign (if they are on the other side of the target than the first trial) or the same sign (if they are on the same side of the target of the first trial).

We computed this analysis on the data we previously collected. For all subjects, we computed the sign of the first trial of the no-feedback block and used this to flip (or not) the errors on the learning trials. We found that this signed error did not show significant change in the course of the experiment (Fig. S4a). Indeed, comparing the first ten trials with the last ten trials on a per-subject basis revealed no significant difference ($t(15)=-.34$ $p=.74$). Interestingly, even taking together all trials for a given subject and averaging them, the sign of this average (flipped) error was not significantly positive ($t(15)=1.46$, $p=.16$), as would be expected if there was a bias that was gradually corrected. We then computed this same metric for the experiment where participants moved to five targets in shuffled order, and we found the same pattern of results (Fig. S4b): there was no difference in signed (flipped) error on the first vs. last ten trials of learning ($t(16)=.93$, $p=.37$). Across multiple days, there was moreover no tendency for the signed, flipped error to decrease (Fig. S4c) even when we compared the largest learning interval from the first 10 trials of day 1 to the last 10 trials of day 3 ($t(14)=1.22$, $p=.24$).

A.5 Repeated vs. random target differences are not due to working memory limitations

An alternative explanation for the performance differences between the repeated and random target conditions might be that point map learning is dependent on recent memory. At any point in the experiment random participants have recently experienced a wider range of targets than the repeated target participants. However, if memory span is critical in this task, one might reasonably expect that in the 5-targets experiments the error on a particular trial would increase systematically as a function of the number of trials elapsed since the same target was last presented. However, we found no such effect in the 5-targets-1d or 5-targets-3d experiments ($F(1,15.05)=1.60$, $p=.22$) (Fig. S5c). This indicates that memory decay for previously visited locations does not explain the fact that performance was identical between

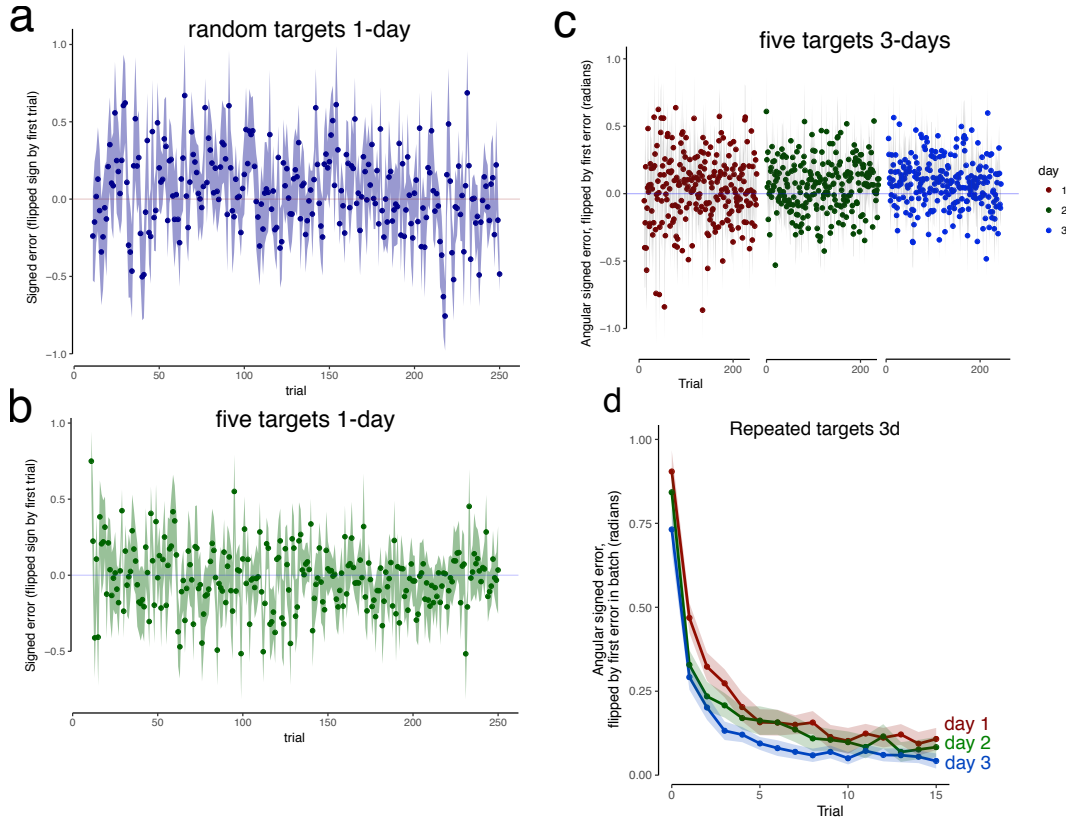


Figure S4: Signed error analysis of data reported in the main manuscript. **a**, Flipped-sign analysis for data in the random targets single day experiment. All errors are flipped according to the sign of the error on the first trial (no-feedback). **b**, Idem for five-targets 1-day experiment. **c**, Idem for five-target 3-day experiment. **d**, Signed analysis of the 3-day repeated target condition where the signs of the error on each trial were flipped according to the sign of the error for the first presentation of the target. It can be seen that sign-flipped errors decrease, suggesting that subjects engage in error correction, and that the convergence on to the target becomes more rapid across days and asymptotic performance improves. Both of these findings match those observed in the absolute error scores presented in the main manuscript.

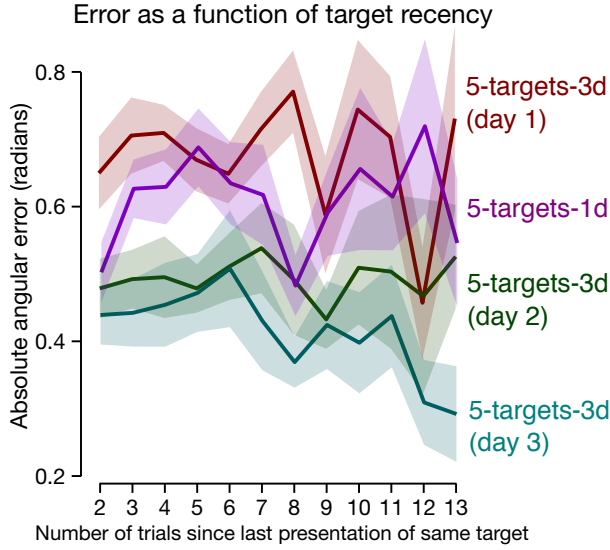


Figure S5: **Differences between random and repeated target trials cannot be explained a short memory span.** If the difference in learning between repeated and random targets is due to memory, it would be expected that the movement error in the 5-target random experiments should depend on the number of trials between two presentations of the same target. However, this graph indicates that error does not vary as a function of the number of intervening trials.

the repeated and random target experiments. Performance is different in repeated and random target conditions, not because there is more opportunity for forgetting when target presentation is randomized, but rather because these tasks rely on different maps.

A.6 Spatial coverage

In order to quantify participants' exposure to the auditory-motor workspace, we defined a spatial coverage metric as follows. Given a set of movements M (for example, all movements up to a certain trial, performed by the subject), and given a point p in the interval $[0, w]$, define the minimum distance from p to any of the movements as $d(p) = \min_{m \in M} ||m - p||$. The spatial coverage is then the expected value of $d(p)$ for any $p \in [0, w]$. This implicitly assumes that all targets in the workspace are equally likely to be presented on a given trial. Figure S6a illustrates the spatial coverage for various sets of movements M plotted as red dots. The spatial coverage is then mathematically equivalent to the green area. The figure illustrates the mathematically correct intuition that adding movements in the proximity of already existing movements does not improve the spatial coverage whereas adding movements to parts of the space not yet covered does.

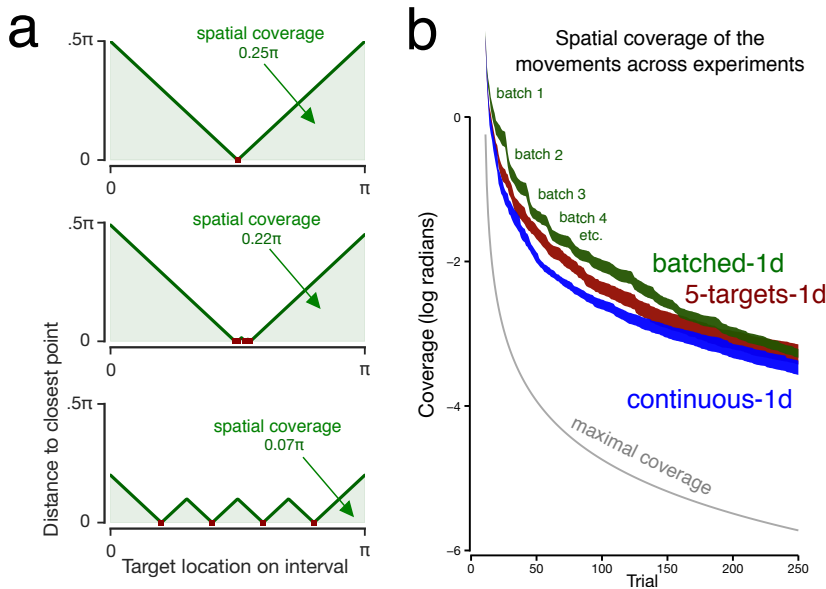


Figure S6: Definition of spatial coverage. **a**, Three possible scenarios are illustrated (top, middle, bottom). The red markers indicate the set of points whose spatial coverage is calculated (in our case, these are movement endpoints). For every point on the interval $[0, \pi]$ the absolute distance to the closest of the red points is indicated by the green line. Spatial coverage is then defined as the average distance to the closest point, i.e. the area under the green curve. The top scenario illustrates a single point placed so as to maximise spatial coverage. The middle scenario illustrates that when multiple points are added to roughly the same location, the effect on spatial coverage is minimal. When the same number of points are divided more or less equally across space, the coverage is improved (smaller residual error). This shows that the spatial coverage metric varies with the spread of the data points. **b**, Spatial coverage for the movements produced by subjects in the 1-day experiments. The grey line indicate the maximal coverage that could be achieved with the same number of movements. The batch structure is clearly visible as a stepwise improvement in coverage. The movements in the continuous-1d experiment exhibit greater coverage of the space than the 5-targets-1d experiment, indicating that our metric is capable of picking up fine differences in movement distribution. Note that the auditory targets for each trial do not enter in to the calculation of spatial coverage. The opaque areas indicate the mean plus and minus the standard error.

Figure S6b shows the empirical spatial coverage obtained in the single day experiments, revealing two observations. First the batch structure is evident in the repeated targets (1-day) experiment, indicating that the spatial coverage improves more rapidly in the beginning of a batch and more slowly towards the end of the batch. Second, we find that although the angular errors in the 5-targets-1d and continuous-1d experiments were essentially indistinguishable, the continuous-1d participants exhibit more dense coverage of the space, suggesting that their acquisition of the sensorimotor map exceeded five targets.