

Recognition memory for human motor learning

Highlights

- Recognition memory for motor learning exceeds memory assessed using active movement
- Retrieval cues in the form of passive movements restore motor memory
- Encoding of human motor memory is at least in part somatic
- Information about motor learning is retained but inaccessible using active movement

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In brief

Kumar et al. introduce a test of recognition memory for human motor learning. Participants hold a robot arm that replays candidate movements and are asked if they had produced this movement during training. Recognition tests are able to uncover substantial information regarding learned movements that is not evident with active movement testing.

Article

Recognition memory for human motor learning

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SUMMARY

Motor skill retention is typically measured by asking participants to reproduce previously learned movements from memory. The analog of this retention test (recall memory) in human verbal memory is known to underestimate how much learning is actually retained. Here we asked whether information about previously learned movements, which can no longer be reproduced, is also retained. Following visuomotor adaptation, we used tests of recall that involved reproduction of previously learned movements and tests of recognition in which participants were asked whether a candidate limb displacement, produced by a robot arm held by the subject, corresponded to a movement direction that was experienced during active training. The main finding was that 24 h after training, estimates of recognition memory were about twice as accurate as those of recall memory. Thus, there is information about previously learned movements that is not retrieved using recall testing but can be accessed in tests of recognition. We conducted additional tests to assess whether, 24 h after learning, recall for previously learned movements could be improved by presenting passive movements as retrieval cues. These tests were conducted immediately prior to recall testing and involved the passive playback of a small number of movements, which were spread across the workspace and included both adapted and baseline movements, without being marked as such. This technique restored recall memory for movements to levels close to those of recognition memory performance. Thus, somatic information may enable retrieval of otherwise inaccessible motor memories.

INTRODUCTION

Almost everything we know in terms of behavior about how newly learned movements are retained comes from studies in which participants are asked to make active movements that reproduce from memory what they have previously learned. In the case of human verbal memory, the analog of this kind of retention test, a test of recall memory, substantially underestimates how much learning is actually retained.^{1,2} Could it be that we also retain information about previously learned movements like a particular tennis serve that we can no longer reproduce, and that appears to be forgotten? If motor memory behaves at all like other forms of human memory, it may be possible to access this information if we replay the somatic cues that accompanied the original learning. In the present study, we introduce a procedure in which, following motor learning, retention for movement is probed using tests of recognition in which participants passively hold the handle of a robot arm that replays candidate movements. Participants are asked to indicate whether or not each displacement of the arm produced by the robot matches the movement they themselves produced at the end of training. The key tests are done 24 h following initial training to eliminate transient retention and assess consolidated memory. We find that although subjects

are poor at reproducing previously learned movements, they are much more accurate at recognizing these movements when presented to them. There is a memory retrieval failure when testing relies on active movement reproduction. Substantial information regarding previously learned movements is retained that is uncovered using recognition tests.

The present studies use somatic cues in which participants passively experience a robotic arm reproducing their movements during tests of recognition memory. There is a variety of evidence consistent with the idea that somatic information forms a part of a motor memory and that motor memories can be re-activated by exposure to previously experienced somatic states. Somatic memory probes in the form of arm displacements that were experienced during active movement can be used to evaluate short-term motor memory.³ Cutaneous stimulation that reproduces somatic inputs during sequence learning enables the re-activation of long-term motor memories that were acquired over several days of practice.⁴ Somatic inputs, in the form of a robot replay of the arm displacements of participants learning a novel motor skill, have been shown to lead to memory formation that is similar in magnitude to that obtained during training with active movement.⁵ This suggests that at least part of memory for learned movements is somatic. Somatic involvement in motor memory storage is also suggested by the finding that, during motor skill learning, changes

Table 1. Experimental conditions

Experimental condition		5 min	24 h
Recall-5 min	rotation →	recall	
Recognition-5 min	rotation →	recognition	
Recall-5 min-null	null rotation →	recall	
Recognition-5 min-null	null rotation →	recognition	
Recall-24 h	rotation →		recall
Recognition-24 h	rotation →		recognition
Cued recall-24 h	rotation →	passive cue →	recall
Cued recall-24 h-null	null rotation →		recall

Participants were randomly assigned to one of eight conditions that differed based on whether they were tested for recall or recognition memory and whether tests were conducted 5 min or 24 h after training.

in the excitability of somatosensory cortex precede those in the motor cortex and predict the amount of motor learning observed later.⁶ The disruption of somatosensory cortex following adaptation learning blocks retention when tested 24 h later, which is consistent with its involvement in motor memory storage.⁷ These observations raise the possibility that there is information available in motor memory that can be selectively accessed using somatic cues.

In the present study, we assessed motor memory retention using visuomotor adaptation as an experimental model of learning. Using different groups of participants, we tested retention either 5 min after learning or following a 24 h delay (Table 1). In tests of retention, participants that were evaluated for recall memory were asked to move (without visual feedback) in the same direction as they moved at the end of training. Participants tested for recognition memory were asked in retention tests to indicate, also without visual feedback, whether or not the displacement of the arm produced by the robot matched the movements that they themselves had produced previously at the end of training. We found that whereas the difference between recall and recognition in tests of retention was not reliable immediately following learning, 24 h later, recognition memory far exceeded retention as assessed by recall. This indicates that there is information about previously learned movements that cannot be readily reproduced by subjects but can be accessed using somatic probes that are similar to those experienced during learning.

RESULTS

Subjects in these experiments held the handle of a robotic manipulandum (Figure 1A) and made point-to-point reaching movements with either unperturbed or rotated visual feedback (Figure 1B). The visuomotor rotation was increased gradually over 75 trials to 30 degrees and then maintained for another 75 trials. After visuomotor training, subjects were tested for recall or recognition memory either immediately (5 min) or after 24 h. In the recall memory test, subjects were asked to reproduce from memory the movements that they made at the end of

visuomotor training, without visual feedback of movement direction (Figure 1B). In the recognition memory test, the subject's arm was moved passively by the robot handle, and subjects were asked to indicate whether or not the limb displacement they experienced corresponded to the direction they had moved in at the end of training (Figure 1B). Figure 1C provides a summary of the different phases of experiment.

As documented previously, subjects showed adaptation to the perturbation. Over the course of training trials, hand trajectories in the visuomotor training task showed a gradual change in a movement direction that compensated for the imposed rotation (Figure 1D, left panel), and as a result the cursor went largely straight to the target throughout training. During the phase in which the rotation was held constant (hold phase), subjects maintained the learned hand direction (Figure 1D, left panel). For subjects in null rotation groups, hand angles were close to zero (Figure 1D, left panel).

As seen in Figure 2A, in the hold phase, adaptation was similar for all subjects that trained with rotated visual feedback ($F_{[4,45]} = 0.32$, $p = 0.86$, $\omega_p^2 = -0.06$). Similarly, there was no difference in the performance of subjects that trained with null rotation ($F_{[4,45]} = 0.29$, $p = 0.74$, $\omega_p^2 = -0.05$). For these latter subjects, the hand angle over the course of training was no different than baseline ($t_{[29]} = 1.18$, $p = 0.24$). The same pattern of performance was obtained in the trials with limited visual feedback that were interspersed between learning trials, and in which direction information was withheld. The hand angle in these trials showed a gradual shift in a direction opposite to the applied rotation (Figure 2B). Adaptation was similar for all the subjects that trained with rotated feedback ($F_{[4,45]} = 0.40$, $p = 0.80$, $\omega_p^2 = -0.05$). Similarly, there was no difference in performance among subjects that trained with null rotation ($F_{[4,45]} = 0.99$, $p = 0.38$, $\omega_p^2 = 0$). These latter subjects showed hand angles that were not different from no-feedback trials in the baseline session ($t_{[29]} = 2.04$, $p = 0.05$). Taken together, subjects adapted to the applied visuomotor rotation.

After the visuomotor training, subjects were tested for their memory of learned movement direction using recall or recognition memory tasks. These memory tests were conducted either 5 min after the initial training or after a 24 h delay. Hand direction during the recall test is shown in Figure 3A. Subjects that each learned a 30-degree visuomotor rotation made movements toward the learned direction. Subjects showed incomplete recall if tested immediately (Figure 3A, solid red line), and subjects that were tested 24 h later showed even less retention (Figure 3A, dashed red line). Subjects that received no perturbation during the training session had hand angles in the recall test that were close to zero (Figure 3A, solid gray line). In the recognition tasks, subjects responded whether each presented direction matched their own movements at the end of training. These responses followed a Gaussian-like distribution (Figure 3B) whose center value varied with the delay between training and the memory test. In the null rotation condition, the curve peaked at close to 100% "yes" responses with a center value close to zero.

For statistical analysis, in the recognition tests, we modeled participants' responses using a fitted Gaussian function (Figure 1D, right panel) and estimated the center of this Gaussian curve (see Recall and Recognition Performance for more details), which thus corresponds to the direction that subjects judged to be most similar to their memory of their own learned

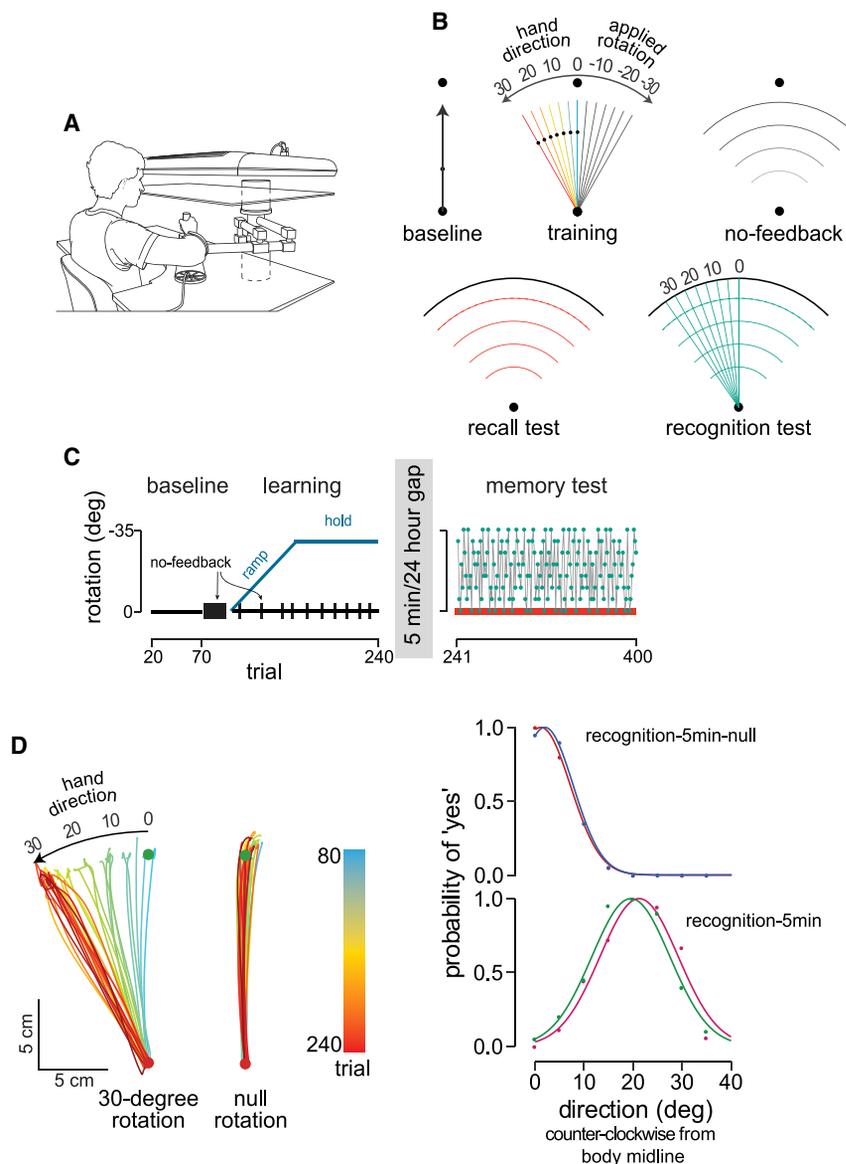


Figure 1. Participants were tested for retention of visuomotor adaptation using recall or recognition tests

(A) Participants made movements holding a robotic manipulandum.

(B) After baseline trials, a cursor was gradually rotated in a clockwise direction. No-feedback trials were interspersed during training, in which the only visual feedback was an expanding semi-circular arc. Subjects were tested for retention either 5 min or 24 h after initial training. In a recall test, subjects were asked to reproduce the movements that they made at the end of training. In a recognition test, the subject's arm was moved passively in each of eight different directions (green) and after each movement subjects reported whether the movement produced by the robotic arm was in the same direction as they themselves moved at the end of training.

(C) Participants trained either with a gradually introduced visuomotor rotation (blue) or with a null rotation (black). Directions used in the recognition test are shown with dots (cyan).

(D) Representative hand paths during training (left panel). Recognition memory performance of two subjects that initially trained with rotated or non-rotated feedback (right panel, bottom and top, respectively): each dot represents the probability of the subject responding "yes" for the presented direction, and lines represent the Gaussian fit for the individual subject.

movement. For comparison purposes, we averaged the hand angle in the recall tests. We will refer to the estimated center of the Gaussian fit and averaged recall as the remembered direction. Figure 3C shows the remembered directions in different conditions assessed through either recall or recognition tests. When the retention test was administered at 5 min after training, remembered direction was similar for both recall and recognition memory. However, in the retention test after a 24 h delay, subjects showed better recognition memory than recall. This pattern of performance was confirmed in statistical analysis, which revealed significant differences in retention among the different conditions ($F_{[5,54]} = 49.13$, $p < 0.001$, $\omega_p^2 = 0.80$). When tested 5 min after training, the remembered movement direction was not statistically different for recall or recognition memory ($p = 0.08$, Bayes factor [t test] = 1.47, i.e., weak evidence in favor of there being a difference). Twenty-four hours later, the remembered direction was significantly greater using a recognition test ($p < 0.001$). Memory in the recognition test showed no

decrement over time and was not significantly different when tested after either 5 min or 24 h ($p = 0.08$). In contrast, recall was significantly less when tested 24 h later ($p < 0.001$). Moreover, subjects in the recognition-24 h group showed similar memory of learned direction to those tested for recall memory 5 min after learning ($p > 0.99$).

In order to further investigate how recall and recognition measures varied across time, we ran a 2×2 ANOVA restricted to conditions with rotated feedback, with factor test (recall, recognition) and time point (5 min, 24 h) and performance (in degrees) as dependent variables. We found that there was a main effect of day ($F_{[1,36]} = 22.56$, $p < 0.001$) indicating that overall performance is better on day 1 than day 2. There was a significant main effect of the test ($F_{[1,36]} = 22.98$, $p < 0.001$) indicating that recognition was better than recall. The interaction between day and test was marginal ($F_{[1,36]} = 3.29$, $p = 0.077$). Bonferroni-Holm-corrected follow-up tests indicated no difference between recall and recognition on day 1 ($p = 0.13$), whereas recognition exceeded recall on day 2 ($p < 0.001$).

Subjects that were trained with a null rotation in the initial training session showed similar remembered directions in both recognition and recall memory tests ($p > 0.99$). Further, the remembered direction in these conditions was similar to average hand movements during the last 50 trials of hold phase of training ($p = 0.78$), which corresponded to a movement straight out to the

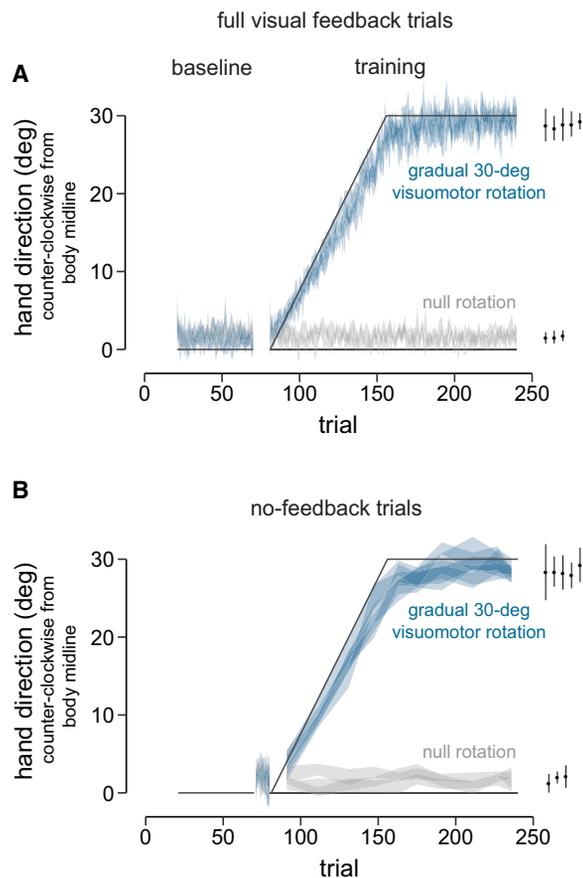


Figure 2. Subjects modified their movement direction to compensate for an imposed visual feedback rotation and the adjustment was maintained when direction feedback was withheld in no-feedback trials

(A) Learning curves showing mean hand direction across trials for each experimental condition (shaded areas and error bars, here and elsewhere, represent SEM). Lines in dark gray show the hand direction that would fully compensate the rotation. Hand angles were close to zero for those subjects who received no perturbation.

(B) Mean hand angle during no-feedback trials.

Black dots represent the mean hand direction for each experimental condition at the end of training (last 50 trials in A, last 4 no-feedback trials in B), showing that there were no significant differences across conditions.

target. This suggests that during the recognition test, subjects' responses were not biased toward any direction. Overall, these results indicate that the recognition memory is greater than active recall memory for the same learned movements. Recognition tests accessed information that is available, but not retrieved, in measures of recall.

We recruited two additional groups to assess whether we can improve recall memory for previously learned movements using non-specific somatic retrieval cues in which the robot replayed in random order a small number of movements that were spread across the workspace. As above, one group trained using a visuomotor rotation whereas the other performed the visuomotor task without any perturbation. Retention tests were conducted 24 h later, immediately preceded by the somatic retrieval cues (16 movements). Subjects were told to hold the

robot handle during these displacements but were not given any further instructions. Subjects' memory of the previous day's learning was then assessed using recall memory tests (Figures 4A and 4B). It can be seen that 24 h after initial training the remembered direction of subjects who received the passive movement retrieval cues was greater than that of subjects who had been tested without retrieval cues after the same 24 h interval ($p = 0.02$). The somatic cues restored recall memory for movements to levels close to those of recognition memory performance: active recall for these subjects was not significantly different from the remembered direction of subjects tested using recognition memory tests ($p = 0.42$). The passive exposure on its own did not bias subjects to move toward any specific direction: subjects who experienced the same set of 16 passive limb displacements 24 h after learning a null rotation showed a remembered memory direction similar to their hand directions toward the end of training ($p = 0.53$), and not significantly different from either recognition or recall memory following null rotation training without any exposure to the memory retrieval cues ($p = 0.99$).

In order to assess whether subjects' performance during recall and recognition memory tests was stable, we estimated the remembered direction over a sliding window of 24 trials separately for recall and recognition performance. For the recognition test, we fitted a Gaussian function to subjects' yes/no responses and estimated the center of the Gaussian curve (see Recall and Recognition Performance for more details) for each window, which thus corresponds to their remembered direction. Similarly, for recall performance, the remembered direction was computed as the mean hand angle using a sliding window. Figures 3D and 4C show the remembered direction across windows in different conditions. Subjects' performance was similar throughout the retention session irrespective of whether tested after 5 min or 24 h delay, and whether recall or recognition memory was assessed. For each subject, we then fitted a line to the recall data or to the estimated center from the recognition test as a function of the trial bin number (Huber robust regression). We extracted the slope and found that the average slope across groups was not different from zero ($t_{[79]} = 0.06$, $p = 0.94$), indicating stable performance. Further, the slopes were similar across different conditions ($F_{[7,72]} = 1.94$, $p = 0.08$, $\omega_p^2 = 0.07$), indicating that remembered directions were similar throughout the retention session across groups. However, in Figure 3D there is one group (recognition-5 min) that when tested in isolation showed a decline in performance during the testing session if an uncorrected test was used ($t_{[9]} = 2.95$, $p = 0.016$).

We performed a control experiment in order to assess whether the reduction in recall performance observed after 24 h was due to a memory retrieval failure, that is, an inability to access the somatic representation of learned movements, or to an inability to correctly reproduce a successfully retrieved movement (motor copy). Subjects were provided somatic targets by having the robot passively move the arm in a particular direction, after which subjects were asked to actively reproduce the movement. Figure 5 shows the mean hand angle in response to each passive displacement direction. We computed the signed direction error for each passive direction relative to the target direction and performed a one-way ANOVA to assess differences in this error as a function of displacement direction. There was no significant difference in error among the different directions ($F_{[9,63]} = 1.37$,

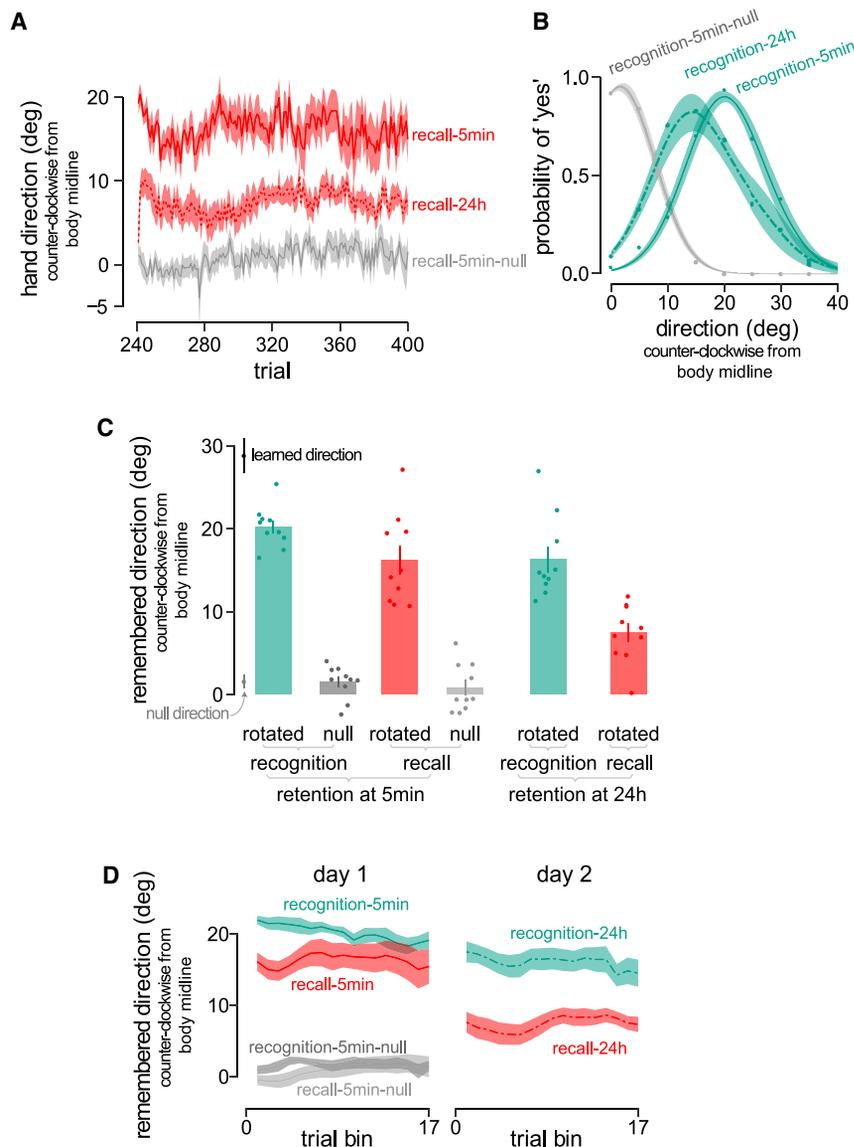


Figure 3. Recognition memory for previously learned movements substantially exceeds recall memory

(A) Mean hand direction during recall memory testing. Recall after 24 h (dashed red) shows a decrease relative to 5 min after training (solid red). Subjects that trained with null rotation showed hand directions close to zero (gray).

(B) Probability (shown as dots) of the subject saying “yes” for each presented movement direction (i.e., that direction was similar to their own movement at the end of training). Lines represent the average Gaussian fit in each group.

(C) Mean remembered direction assessed through recall or recognition (center of the Gaussian fit) memory tests; dots represent single subjects. When tested 24 h after initial training, recognition memory showed substantially greater retention than recall.

(D) Remembered direction estimated over a sliding window indicates that subjects show stable performance during testing. Shaded areas and error bars represent SEM.

gradually introduced 30-degree visuomotor rotation during reaching movements to a visual target. Retention tests were conducted 5 min after training or following a 24 h delay. Recall memory was assessed by asking subjects to reproduce the previously learned movements without visual feedback. In tests of recognition, which were also without visual feedback, a robot moved the subject’s arm in a number of candidate directions. Some of these directions matched those subjects moved in during training whereas other directions did not. Subjects were required to indicate whether or not the candidate movement was in the direction they had produced previously at the end of the training session. When tested 5 min after learning, estimates of recall and recognition

$p = 0.23$, $\omega_p^2 = 0.02$). Subjects showed a small average bias of 2.25 ± 0.96 degrees counterclockwise across all directions ($t_{[9]} = 2.31$, $p = 0.04$). This shows that subjects can successfully reproduce movements based on somatic information. It also addresses a potential concern that the discrepancy between recall and recognition performance is due to a bias in recall movements. The bias is in the same direction as recall memory, and thus would contribute to the over-estimation, not under-estimation, of recall retention. Taken together, these findings suggest that poorer performance in the recall test is due to a retrieval failure, i.e., inaccessibility of the previously learned movement, instead of a movement reproduction failure.

DISCUSSION

The present study tested whether somatic inputs can access information from motor memory that is not available when the task is to make active movements. Subjects learned to compensate for a

memory were roughly similar in magnitude, although statistical testing leaves open the possibility of a small difference in favor of recognition memory. The key finding was that following a 24 h delay, recognition memory was about twice as good as recall. The recognition tests show that much of the initial learning has been retained, but the motor memory is only partially accessible with recall tests in which subjects reproduce learned movements from memory.

The present study introduces measures of recognition memory for learned movements. These measures were shown to be stable and unbiased by several control analyses. Recognition memory response patterns for individual subjects closely followed a Gaussian distribution (Figure 1D) shown by high goodness-of-fit values. Recognition estimates within subjects were stable over time (Figure 3D). The fits showed good reproducibility because recognition estimates based on half of a subject’s data were within 1.8 degrees of estimates based on the other half. Between-subjects estimates of variability were low (Figure 3B) and similar to those observed in active movement recall

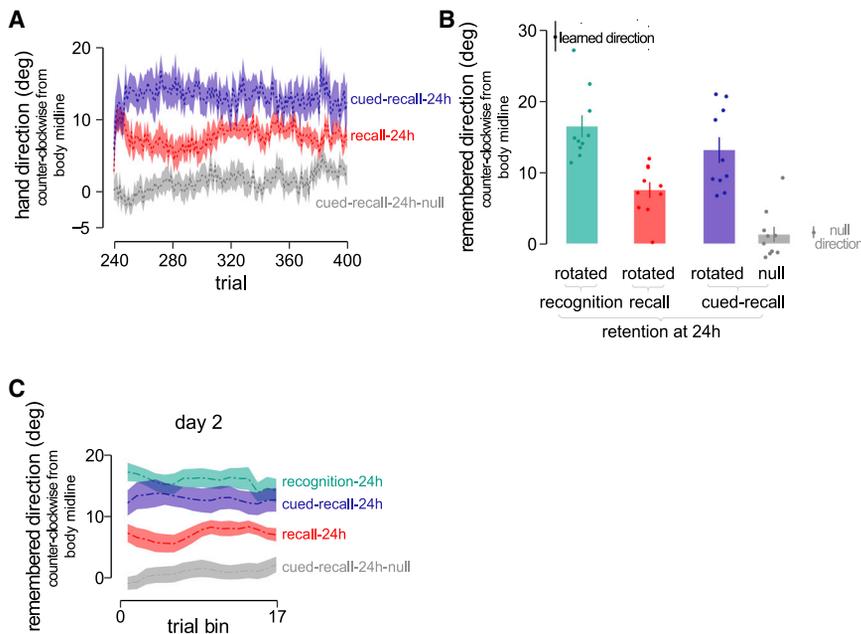


Figure 4. Somatic retrieval cues improve recall memory

(A) Mean hand direction in recall memory tests 24 h after training with rotated visual feedback or null rotation. The hand direction of subjects who received the passive movement retrieval cues prior to recall testing (purple) was greater than that of subjects without retrieval cues (red). The passive exposure on its own did not bias subjects to move in any specific direction because subjects who experienced the same set of 16 passive limb displacements after learning a null rotation produced recall movements similar to baseline (gray). (B) Mean remembered direction assessed through recall memory tests after somatic cues. Remembered directions without somatic cues are shown for reference (same data as Figure 3). Dots represent individuals. Recall after somatic cues (purple) was greater than recall without cues (red). (C) Remembered direction over a sliding window: performance is stable during testing. Shaded areas and error bars represent SEM.

(Figure 3C). Also, recognition memory estimates for people who had not undergone visuomotor learning were not significantly different from baseline (Figure 3D), showing that the test is not biased. Taken together, these analyses indicate that recognition memory estimates are both unbiased and robust.

The fact that there is recognition memory for previously learned movements is consistent with prior studies that have demonstrated that somatosensory inputs serve to access prior learning. Evidence for somatic access to motor memory comes from work on reinforcement learning in which passive displacements of the limb are used to probe memory for self-produced movements. Memory access is indicated by the fact that previous movements were identified accurately almost 75% of the time.³ In MR neuroimaging work, Yokoi et al.⁴ showed that when tactile stimuli obtained following 5 days of sequence learning were played back to passive subjects, a procedure that effectively tests for recognition memory, the experimenter-applied patterns of finger pressure activated the same set of parietal and frontal cortical areas that were active when subjects had to produce these same movements in tests that assessed recall.

The present results suggest that the encoding of learned movements is at least in part somatic in nature. This is supported by two observations: first that somatosensory information presented during recognition is able to access motor memory (Figure 3), and second that somatic retrieval cues (i.e., passive presentation of a set of movements) facilitated subsequent motor memory recall (Figure 4). These observations, together with the idea that retrieval cues are successful only to the extent that they match the information that is encoded (encoding specificity,⁸ see Frankland et al.⁹ for a neurobiological review), suggest that motor memories encode previously learned somatic states. Other evidence for this idea comes from work in which subjects were trained in a reinforcement learning task by a robot that passively displaced their arm. These subjects showed levels of retention in subsequent tests of recall memory that were

comparable to those of subjects that had trained by making active movements, showing that somatic information alone is sufficient for this type of learning.⁵ Similarly, the finding that the disruption of posterior somatosensory cortex activity following motor learning blocks subsequent retention of motor memory is consistent with the involvement of somatic regions of the brain in the storage of learned movements.⁷

The present data suggest that a substantial portion of the decrease in motor memory performance over time reflects an information access problem, and not necessarily a loss of information. There have been a number of studies that have observed a decrease in performance after a 24 h delay as compared to performance at the end of initial training. This has been reported in visuomotor rotation,¹⁰ force-field adaptation,^{11,12} and skill learning tasks.¹³ Our results replicated this phenomenon, where recall involving active movement was less after 24 h than after 5 min. However, recognition memory performance was comparable 24 h later to that observed shortly after learning, suggesting that the recall decrement is due to a retrieval failure and not due to a failure to retain information. After 24 h the information was not lost but only partly accessible when tested using recall. Somatic cues can be used to gain access to motor memories as was done in recognition testing.

The present finding that there is information available about previously learned movements that is not accessed in tests of recall, i.e., memory retrieval failure, has been addressed in previous work. Motor memory retrieval failures have been observed when there are competing motor memories, as, for example, occurs when one learns two opposing perturbations in close succession.^{14–18} Interference acts to block the expression of a motor memory rather than its retention: it has been shown that by adding time following washout trials at the end of learning, the interfering effects of washout on memory retrieval are reduced.¹⁹ Memory retrieval can also be impeded by the prior retrieval of other items (retrieval-induced forgetting), which occurs with motor memories as well.^{20,21} The phenomenon of savings is another

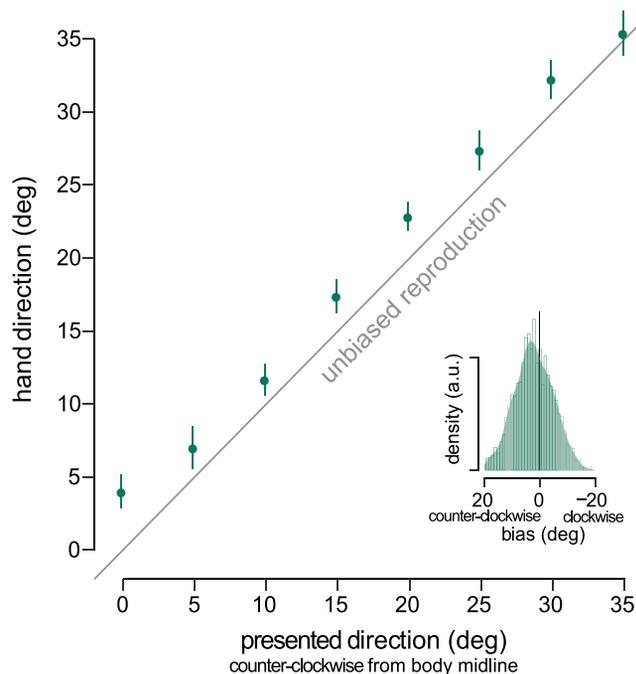


Figure 5. Subjects were able to accurately reproduce movements based on somatic cues (motor copy task)

The subject's arm was moved passively in eight different directions (similar to the recognition test), and then after each the subject was asked to reproduce the movement. Dots indicate average reproduced movement direction as a function of presented direction. Inlay shows the density of the signed difference between presented and reproduced movement direction pooled across all directions, indicating a small bias in the counterclockwise direction. Error bars represent SEM.

demonstration that there is information available that is not evident in initial recall performance. In savings, performance during re-learning improves more rapidly than during initial learning.^{14,15,22–29} These studies, taken together, show that information about previous motor learning is retained but is evident only when additional probing procedures are used. Our work on recognition memory builds on this by showing that somatic cues are one such avenue to access prior motor memories.

In tests of retention following visuomotor adaptation, when the perturbation is removed a washout is typically observed in which over the course of trials, movement direction returns to that observed with non-rotated feedback. In contrast, in the course of the present tests of recall, there is little if any evidence of memory decay, whether the tests are conducted 5 min or 24 h after learning or following presentation of somatosensory retrieval cues. Moreover, this stability is also seen in tests of recognition memory, which suggests that it is not attributable to active versus passive memory testing. The presence of this persistence under multiple experimental conditions indicates there is little loss of information over trials, although this may have been different had subjects been trained to adapt to multiple targets. One possible explanation why we do not observe washout is that it is typically observed when the visual target remains present, which is not the case here. A visual target creates a discrepancy between somatosensation and vision, which may drive washout. The target arc removes this discrepancy, and

under these conditions it is seen that information about prior movement direction is retained on a short-term basis and does not on its own decay.

The visuomotor rotation used to study adaptation was introduced gradually. However, the perturbation was relatively large (30 degrees), and in other work it has been found that with perturbations of this magnitude, both implicit learning and explicit aiming contribute to the resulting adaptation.^{28,30–33} Accordingly, here as well, there may be both implicit and explicit components to learning and motor memory. If this is the case, could differential decay rates of implicit and explicit learning possibly be the source of the differential patterns of retention observed in the recall and recognition tests after 24 h? A number of observations argue against this possibility. In the case of recognition memory, there is no evidence of memory decay after 24 h, which suggests there is little loss of information. In contrast, recall deteriorates after 24 h but cued recall is found to return performance to levels not different than those observed in recognition. This suggests that even in recall testing, motor memories have not decayed but rather are inaccessible using tests of active movement. Thus, while it is reasonable to assume that learning here may involve both implicit and explicit components, there is little evidence to indicate that the recall/recognition difference may be attributable to differential decay rates of implicit and explicit learning. Rather, the recall failure is presumably due to an inability to retrieve information that is available in motor memory.

Motor learning has been shown to be accompanied by somatosensory perceptual change. For example, following visuomotor rotation, subjects' sensed arm position is shifted in the direction of the imposed perturbation.^{34,35} This shift reduces the perceptual discrepancy between the seen direction of cursor movement and the sensed direction of the limb. Could this perceptual shift possibly account for the presently observed difference between recognition memory and active movement recall, since recognition relies on sensed limb position? In the present study, the subject has to learn to move to the left of the body midline to make the visual cursor move straight out to the target. Accordingly, one would expect that had measures of sensed limb position been taken following learning they would lie between the actual movement direction and the seen direction, i.e., biased toward the right of where they had actually moved. However, a perceptual shift in this direction could not account for larger estimates of recognition memory. If following adaptation in the present study, one's sensed arm position is biased to the right, this would be expected to introduce a similar bias to the right in tests of recognition, which is opposite to the observed direction of the discrepancy between recall and recognition. One other way in which somatosensory change may have contributed to the difference between recognition and recall is if recognition tests tap into a separate somatosensory memory that is created in parallel with motor learning. However, the fact that somatic retrieval cues facilitate subsequent recall involving active movement argues against this idea.

In summary, passive displacements of the upper limb were used to assess recognition memory for previously learned movements. Whereas tests of recall memory (active reproduction of previous learning) suggested a substantial loss of information when movements were reproduced after a 24 h delay, tests of

recognition showed little deterioration. When somatic retrieval cues were presented prior to recall testing (after a 24 h delay), memory for learned movements was restored to levels comparable to that observed in tests of recognition. Overall, the findings show that the encoding of previously learned movements is available in motor memory but only partially accessible using recall tests. The restoration of recall memory after the presentation of somatic retrieval cues argues for the presence of a somatic encoding of learned movements.

STAR★METHODS

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AUTHOR CONTRIBUTIONS

Conceptualization, Methodology, and Writing, N.K., F.T.v.V., and D.J.O.; Data Analysis, N.K. and F.T.v.V.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited Data		
Data used in figures	This Paper	https://doi.org/10.17632/4smw7ysnk2.1
Software and Algorithms		
Experiment Designing and Data Collection Tool	Custom Developed	https://github.com/florisvanvugt/inmotionpy
Python	Python Software Foundation (PSF)	http://www.python.org ; RRID: SCR_008394
R package: ez	CRAN Repository	https://cran.r-project.org/web/packages/ez/index.html
R package: ggplot2	CRAN Repository	https://ggplot2.tidyverse.org/index.html ; RRID: SCR_014601
R package: BayesFactor	CRAN Repository	https://cran.r-project.org/web/packages/BayesFactor/index.html

RESOURCE AVAILABILITY

Lead Contact

For further information communicate with Lead Contact, David Ostry (david.ostry@mcgill.ca).

Materials Availability

This study did not produce any new reagents or materials.

Data and Code Availability

Data used in creating figures have been deposited to Mendeley Data and are available at <https://doi.org/10.17632/4smw7ysnk2.1>.

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Participants

90 healthy right-handed individuals (67 men, 23 women, mean age 23.15 ± 4.8 years), 10 per experimental condition, participated in the study. Handedness was assessed using the Edinburgh Handedness Inventory. Subjects were naive as to the purpose of the experiment and the procedures were approved by McGill University Faculty of Medicine Institutional Review Board.

Setup

Subjects held a vertical handle attached to a two degree-of-freedom robotic arm (InMotion2, Interactive Motion Technologies) and made movements with the right hand in a standard point-to-point reaching task. A semi-silvered mirror, which served as a display screen, was placed just below eye level and blocked vision of the arm and the robot handle (Figure 1A). Two 16-bit optical encoders provided the position of the hand (Gurley Precision Instruments) at 200 Hz.

METHOD DETAILS

Visuomotor Training Task

Subjects were asked to perform point-to-point reaching movements from a start position to a target. The start position was indicated with a white circle (20 mm diameter) 30 cm in front of the subject. The target position, also indicated with a white circle (20 mm diameter), was 15 cm in front of the start position. During the movement, visual feedback of hand position was provided by a yellow cursor (5 mm diameter). The subject's elbow was supported by an air sled. At the start of each trial, the robot moved the subject's arm to the start position after which the start position turned green, signaling the subject to initiate the movement. After reaching the target, the color of the target changed to indicate whether the subject's movement was within the desired 800-1000ms range. No trials were removed for being too fast or too slow. Following the end of movement, the robot brought the arm back to the start position, without visual feedback of the movement path.

The visuomotor training task began with a familiarization phase in which subjects performed 20 practice movements with unaltered visual feedback. Subjects then performed 60 baseline trials which were the same as in the familiarization phase. The last 10 trials of baseline phase were performed under conditions of limited visual feedback. In these trials, the cursor was replaced by a semi-circular arc that grew in diameter as subjects moved toward the target (Figure 1B). Subjects were instructed to stop the movement as soon as the arc reached the target. In this way, movement amplitude was controlled without providing information about movement direction.

The baseline block was followed by a training session in which subjects performed movements with clockwise rotated visual feedback of hand position provided by the 5mm yellow cursor. In order to minimize subjects' awareness of the perturbation, the magnitude of rotation started at 0 and was increased by 0.4 degrees for each trial, until on the 76th trial, the rotated feedback had reached 30 degrees. It was then held at this level for a further 75 trials (Figure 1C). Ten trials with limited visual feedback were interspersed within the training session in which the cursor was replaced by an expanding half circle, as described above. The position of these trials was the same for all participants. Hand direction (the angle between the peak velocity point and a straight line to the target) in these trials provided a measure of learning. By the end of the training session, subjects compensated for the applied rotation by making movements in the opposite direction. Subjects were then tested for retention of this learning by using either a test of recall memory or recognition memory (described below). There were no additional movement trials between the last trial of the training session and first trial of recall or recognition memory test.

Recall Memory Test

In this task, subjects were asked to reproduce the movements that they had made at the end of the training session. A semi-circular arc was presented as a target in place of the white circle. The cursor feedback was withheld and instead participants were provided with a growing arc as they moved toward the target arc (Figure 1B). As in the preceding visuomotor training trials, feedback on movement duration was provided. The robot returned the subject's hand to the start position at the end of each movement. The design thus enabled the estimation of remembered movement direction, while controlling for movement amplitude and duration. A total of 160 trials were performed.

Recognition Memory Test

We developed a task to assess subjects' recognition memory for previously learned movements. Subjects were asked to hold the handle of the robot arm as candidate movement directions were presented passively. A target arc was displayed which was the same as that in the test of recall memory. However, instead of producing active movements, on each trial the subject's arm was moved passively by the robot in one of eight different directions ranging from 0 to 35 degrees relative to the body midline with a spacing of 5 degrees (Figure 1B). The displacements were straight and followed a minimum jerk velocity profile. Subjects were also presented with an expanding arc as visual feedback to indicate the amplitude of the passive movements. After each forward movement, the robot arm brought the participant's hand back to the start position. After each trial, participants were asked to report whether the movement produced by the robotic arm was in the same direction as they themselves produced at the end of visuomotor training. A total of 160 trials was performed in four blocks. The order of presentation of the passive limb directions was determined pseudo-randomly so that no direction was presented twice in a row and all other transitions were of similar probability. This order was kept constant across participants. Subjects in all experimental conditions using recognition testing were presented with the same set of directions.

Experimental Groups

Subjects learned a gradually introduced 30-deg visuomotor rotation and were tested either for recall or for recognition 5 min after training (*recall-5min* and *recognition-5min*, respectively). To test for retention of learning, subjects in two additional conditions were trained on visuomotor rotation and tested for recall (*recall-24 h*) or recognition (*recognition-24 h*) 24 h later. Ten subjects were tested in each condition, throughout the study.

We recruited two control groups in which subjects performed the visuomotor training without any rotation of the visual feedback. One of these was followed by a test of recall (*recall-5min null*) and the other by a test of recognition (*recognition-5min null*).

In two further conditions, subjects underwent initial training, as in the main experimental manipulations, with either a gradually introduced visuomotor rotation or an equal number of movements with a null rotation. Retention tests were conducted after 24 h. Prior to the memory test, subjects in each condition were exposed to 16 passive movements as memory retrieval cues, in the directions used in the recognition task (two displacements in each of 8 directions, in random order). In these exposure trials, visual information was withheld. No information about the purpose of these trials was provided and no judgment was required on the part of the subject. Afterward, subjects were tested for recall using active movements (as described above; *cued-recall-24* and *cued-recall-24 h null*).

In one further condition, we used a motor copy task to assess the possibility that participants may have an accurate somatosensory memory of the adapted movement but during recall trials their reproduction of this memory trace is biased toward a less adapted state. In this condition the participant's hand was passively moved out and back by the robotic arm in the same directions used in the recognition task (in random order). Subjects were then asked to actively reproduce the movement in the same direction. Visual feedback was limited to a target arc and a second arc which expanded with movement amplitude. As in other conditions, subjects in the motor copy condition performed the familiarization and baseline trials before the motor copy tests.

QUANTIFICATION AND STATISTICAL ANALYSIS

Preprocessing of Kinematic Data

The hand position of the participants was sampled at 200 Hz. The position time series was low-pass filtered at 40 Hz, using a zero-phase-lag Butterworth filter, and differentiated to produce velocities. Learning was quantified using the change in hand movement

angle across trials, which was calculated on a per trial basis as the angle between a line connecting the start position to the target, and a line connecting the start position and hand position at peak velocity.

Recall and Recognition Performance

In evaluating performance in the recognition task, we assumed that participant's yes/no responses for passive movement direction would follow a Gaussian distribution which was centered around a particular direction, which we aimed to estimate. The probability of a yes response ("yes, this is the direction of my movement at the end of training") was modeled by a Gaussian function of the presented direction x . For each presented direction, we computed the proportion of yes responses of the participant. We then fitted the following equation to these proportions: $p(\text{yes}) = a \cdot \exp(-(x-m)^2 / 2w^2)$ where m refers to the curve center, w to the curve width and a to the amplitude (peak). The fits were computed using Levenberg-Marquardt least-squares optimization in multiple steps. The parameter space was restricted so that width (w) could take only positive values and amplitude (a) could take values between 0 and 1. In order to achieve robustness we fitted in three steps: in the first step, we held the width parameter constant at 6 degrees and fitted for center and amplitude. In a second step, we used this preliminary estimate of the center to obtain the curve width. In the third step we used the curve width to obtain a final estimate of the curve center and amplitude.

These fits were computed for each subject and curve center was estimated. We computed the goodness of fit (R^2) between the observed proportion of yes responses of subjects with those predicted by the fitted Gaussian functions. Overall fit quality was on average $R^2 = 0.984$, CI: [0.972 0.99]. The Gaussian fit to the 'yes' responses of two representative subjects after learning a 30-deg visuomotor rotation or a null rotation is shown in [Figure 1D](#) (right panel).

In order to assess the stability over time in the recognition test, these fits were computed over sliding windows of 24 trials. The sliding window was computed at 8-trial intervals, which reflects the number of directions participants received in one cycle. That is, the Gaussian was fit to trials 1-24 yielding one estimate of curve center, and then repeated for trials 9-32, yielding another estimate of the curve center, etc. This sliding window method produced 17 windows which are referred to as trial bins. We computed the goodness of fit (R^2) between the observed proportion of yes responses of subjects with those predicted by the fitted Gaussian functions for each sliding window. Fits with $R^2 < .5$ were discarded from further analyses (6 cases i.e., 1.2% of the data). Overall fit quality was on average $R^2 = 0.929$, CI: [0.906 0.947].

To assess the validity of the fitting procedure, we split the data for each subject in half (first 80 trials, last 80 trials) and repeated our fitting procedure for each half. The center estimates obtained in the two halves showed a correlation of $r[28] = 0.976$, $p < 0.001$. The absolute difference between the center estimates of two halves was 1.80 [95% CI 1.28 2.31] degrees.

Recall memory was computed based on the hand direction at peak velocity relative to the straight line (body midline). Hand directions were averaged for each subject to compute the remembered direction. To assess the stability in recall performance over time, hand directions were averaged over a sliding window of 24 trials which yielded 17 trial bins of remembered directions for each subject. When the main analyses of this study were repeated using the hand direction estimated at the end of movement (instead of peak velocity) we found essentially the same pattern of results.

In the motor copy test, hand angle was calculated at peak velocity relative to the body midline. Bias in the active reproduction of copy direction was calculated as the difference between hand angle and the target displacement direction.

We compared retention across the different experimental conditions using ANOVA, with retention (in degrees) as the dependent variable and experimental condition as between-subject factor. This ANOVA includes all null and rotation learning conditions. All follow-up pairwise comparisons were corrected using the Holm-Bonferroni method. When statistical trends were found Bayes Factor t tests were also computed³⁶ using the `ttestBF` function from the BayesFactor R package (version 0.9.12-4.2), using a non-informative Jeffrey prior and r -scale value of $\sqrt{2}/2$. For all the tests that are done with ANOVA, we report F values, degrees of freedom, p values and effect sizes. For follow-up pairwise tests (Bonferroni-Holm corrected t tests), for purposes of readability we opted to report only p values.