Neural signatures of memory gain through active exploration in an oculomotor-auditory learning task

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February 2, 2023

Abstract

Active engagement improves learning and memory, and self- vs. externally generated stimuli are processed differently: perceptual intensity and neural responses are attenuated. Whether the attenuation is linked to memory formation remains to be understood. This study investigates whether active oculomotor control over auditory stimuli – controlling for movement and stimulus predictability – benefits associative learning, and studies the underlying neural mechanisms. Using EEG and eyetracking we explored the impact of control during learning on the processing and memory recall of arbitrary oculomotor-auditory associations. Participants (N=23) learned associations through active exploration or passive observation, using a gaze-controlled interface to generate sounds. Our results show faster learning progress in the active condition. ERPs time-locked to the onset of sound stimuli showed that learning progress was linked to an attenuation of the P3a component. The detection of matching movement-sound pairs triggered a target-matching P3b response. There was no general modulation of ERPs through active learning. However, participants could be divided into different learner types: those who benefited strongly from active control during learning and those who did not. The strength of the N1 attenuation effect for self-generated stimuli was correlated with memory gain in active learning. Our results show that control helps learning and memory and modulates sensory responses. Individual differences during sensory processing predict the strength of the memory benefit. Taken together, these results help to disentangle the effects of agency, unspecific motor-based neuromodulation, and stimulus predictability on ERP components and establish a link between self-generation effects and active learning memory gain.

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Declarations of interest: **None.**

Abstract

Active engagement improves learning and memory, and self- vs. externally generated stimuli are processed differently: perceptual intensity and neural responses are attenuated. Whether the attenuation is linked to memory formation remains to be understood. This study investigates whether active oculomotor control over auditory stimuli – controlling for movement and stimulus predictability – benefits associative learning, and studies the underlying neural mechanisms. Using EEG and eyetracking we explored the impact of control during learning on the processing and memory recall of arbitrary oculomotor-auditory associations. Participants (N=23) learned associations through active exploration or passive observation, using a gaze-controlled interface to generate sounds. Our results show faster learning progress in the active condition. ERPs time-locked to the onset of sound stimuli showed that learning progress was linked to an attenuation of the P3a component. The detection of matching movement-sound pairs triggered a target-matching P3b response. There was no general modulation of ERPs through active learning. However, participants could be divided into different learner types: those who benefited strongly from active control during learning and those who did not. The strength of the N1 attenuation effect for self-generated stimuli was correlated with memory gain in active learning. Our results show that control helps learning and memory and modulates sensory responses. Individual differences during sensory processing predict the strength of the memory benefit. Taken together, these results help to disentangle the effects of agency, unspecific motor-based neuromodulation, and stimulus predictability on ERP components and establish a link between self-generation effects and active learning memory gain.

Keywords: self-generation, multisensory associations, active learning, gaze-controlled interface

Introduction

We learn faster when we are actively engaged with the material – this is not just a folk wisdom, but it has been reproduced in a plethora of experimental settings (Markant et al., 2016). Active learning benefits for memory are, however, a very diverse phenomenon, and in order to study their cognitive and neural underpinnings, we have to choose a focus. In this study, we have asked ourselves whether memory gain through active learning could be linked to the previously established differences in the neural and perceptual processing of self- versus externally generated stimuli (Baess et al., 2011; Blakemore et al., 1998, 2000; Schäfer & Marcus, 1973). Specifically, we decided to study the effects of being in control over auditory stimuli on the learning progress of visuo-auditory contingencies, in an experimental setup that controls for the conflating factors of predictability and movement. We designed a variation of the classic self-generation paradigm (Schäfer & Marcus, 1973) using eye movement sonification. In a memory task, participants learned associations between movement-sound pairs. Their learning progress was tracked across several stages of learning on a behavioural and neural level.

Our first aim was to test whether actively controlling stimuli, beyond effects of movement and predictability, would lead to associative learning benefits on a behavioural level. Previous studies have shown that active control during complex tasks such as spatial navigation, as well as simpler experimental setups such as recognition memory tasks, can facilitate learning (Harman et al., 1999; James et al., 2002; Plancher et al., 2013). A related, somewhat more clearly defined phenomenon is the "production effect": Stimuli produced by oneself are remembered better than externally produced stimuli (Brown & Palmer, 2012; MacLeod et al., 2010). Even minimal amounts of control, such as controlling the pacing of information, have been found to improve memory (Markant et al., 2014). The effects of control are easily conflated with the effects of movement during learning, since in most studies on this question, participants use hand movements in order

to control stimuli in the active condition, while not moving at all in the passive condition (Craddock et al., 2011; Harman et al., 1999; Liu et al., 2007; Luursema & Verwey, 2011; Meijer & Van der Lubbe, 2011). Nevertheless, some studies have found memory benefits for active learning even when controlling for the factor of movement (Plancher et al., 2013; Trewartha et al., 2015). Theoretical and experimental accounts of the role of choice during learning suggest that controlling the flow – the pacing, the order – of information is crucial for the memory gain, since the learner is able to develop hypotheses and test them, or revisit items that they feel unsure about (Gureckis & Markant, 2012; Kruschke, 2008; Markant et al., 2016; Markant & Gureckis, 2010; Schulze et al., 2012). This is corroborated by the fact that motor activity unrelated to strategic control over the learning strategy does not improve memory performance (Voss et al., 2011). In order to get a better view of the role of control in the learning process of arbitrary motor-auditory contingencies, we developed a learning paradigm in which participants had to return several times to the same set of stimuli and were tested on their memory performance in between rounds of learning. We hypothesised that we would encounter a memory advantage for stimuli learned under active exploration. We expect that this memory advantage will express itself in participants learning the associations faster in the active condition.

A second aim of this study was to investigate the neural mechanisms underlying the putative memory benefits for active learning. To that aim, we isolated neurophysiological effects of control over acoustic stimuli from unspecific neuromodulatory effects caused by movements and effects of stimulus predictability. Control during stimulus generation could modulate brain responses at different levels of learning, and we probed a series of possible mechanisms.

Control over stimuli, accompanied by a Sense of Agency (SoA), is known to impact stimulus processing. Electrophysiological responses to self-generated stimuli tend to be attenuated relative to externally generated stimuli, even when the stimuli evoking the response are physically identical (Blakemore et al., 2000; Gentsch & Schütz-Bosbach, 2011; Hughes et al., 2013b; Hughes & Waszak, 2011; Kilteni et al., 2020; Mifsud et al., 2018; SanMiguel et al., 2013). Although they can be observed in all sensory modalities (auditory: Baess et al., 2011; visual: Hughes & Waszak, 2011; tactile: Kilteni et al., 2020, for some examples), attenuation effects on sensory processing have been extensively studied in the auditory domain, often comparing evoked electrophysiological responses to self-generated and externally-generated acoustic stimuli (Horváth, 2015; Schäfer & Marcus, 1973). Using electroencephalogram (EEG), a number of neuro-electrical markers of self-generated processing have been established: An attenuation of certain event-related potentials (ERPs), i.e. a diminished amplitude of different peaks that characterise the early cortical processing of self- as opposed to externally generated sounds. Attenuation for self-generated sounds has been observed in the N1 component (Bäß et al., 2008; Elijah et al., 2018; Mifsud et al., 2016; Neszmélyi & Horváth, 2017; Oestreich et al., 2016; Pinheiro et al., 2019; van Elk et al., 2014), the P2 component (Horváth & Burgyán, 2013; Knolle et al., 2012), and the Tb component (Paraskevoudi & SanMiguel, 2022; SanMiguel et al., 2013; Saupe et al., 2013). The nature of these effects is often assumed to be predictive, since efference copies of motor commands are thought to serve as a basis for precise anticipation of sensory stimulation (Miall & Wolpert, 1996). Correctly predicted sensory stimulation is thought to elicit smaller neural responses than wrongly predicted or surprising input, in line with the predictive coding theory of neural processing (Blakemore et al., 1998; Kilner et al., 2007). However, previous research has shown that motor activity during sensory processing also has unspecific modulatory effects that are not related to predictability – just being in motion affects the way we perceive stimuli (Horváth et al., 2012), and movement effects can be a conflating factor when trying to study the effects of predictability and control (Hazemann et al., 1975; Horváth, 2013; Paraskevoudi & SanMiguel, 2021; Press & Cook, 2015). Recent studies that investigated specifically effects of agency, controlling for predictability and movement, have found both attenuation and enhancement effects on the P2 component (Bolt & Loehr, 2021; Han et al., 2021), and modulations of the P3 component have also been observed (Burnside et al., 2019; Kühn et al., 2011). We hypothesized that if the known effects typically observed in the self-generation paradigms on the N1, P2 and P3 component are indeed related to agency and control, we should be able to reproduce them with our design, even though we used an unconventional experimental paradigm: Instead of hand or finger movements, participants used their eye movements to generate sounds. By using a gaze-controlled interface, we were able to compare an experimental condition

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in which participants *controlled* a cursor using their eye movements ("agent condition") with a condition in which participants*followed* a cursor with their gaze ("observer condition"), minimizing the motor differences between conditions. Eye movements are mostly automatic and usually used towards visual goals, and we have no expectations of auditory consequences of our eye movements (Mifsud & Whitford, 2017; Slobodenyuk, 2016). Importantly, two studies using self-generation paradigms have used saccades to generate sounds and found either no attenuation for eye-movement initiated sounds (Mifsud & Whitford, 2017) or weakened attenuation of the N1, but not the P2 component (Mifsud et al., 2016). Electrophysiological responses to gaze fixations have been measured in the context of brain-computer interfaces and gaze-controlled games (Ihme & Zander, 2011; Protzak et al., 2013), and certain markers of voluntary gaze control have been established: Voluntary gaze fixations that were made consciously in order to control an interface were characterised by a slow negative parieto-occipital wave evoked by the fixation which was absent or much decreased in fixations that did not control the interface (Protzak et al., 2013; Shishkin et al., 2016).

Rather than control affecting stimulus processing on a basic level, we also considered the possibility that control would specifically modulate learning processes. Repeated presentation of a given movement-sound pair, as was the case in our paradigm, leads to neural changes over time related to the learning progress – we develop internal models of the associations that we have learned (Kilner et al., 2007), and the sound's predictability based on the preceding movement increases gradually. Effects of predictability on ERP components strongly resemble those of self-generation: predictability often leads to sensory attenuation (Alink et al., 2010; Grotheer & Kovács, 2016; Kaiser & Schütz-Bosbach, 2018; Summerfield et al., 2008), and in fact sensory attenuation for self-generated stimuli is more pronounced when the outcome of the self-generated action matches the agents' expectation (Hughes et al., 2013a; Stenner et al., 2014). Controlling for temporal predictability can help us to understand the functional separation of modulations of established ERP components by self-generation (Klaffehn et al., 2019). By studying the evolution of ERP components in relation to learning we can shed light on the effects of increased predictability beyond the self-generation effects, which should be observable from the start of the learning process. In line with previous studies, we expected to find an increased attenuation of the N1 (Kaiser & Schütz-Bosbach, 2018) and P2 component during late stages of learning. Furthermore, modulations of the P3 component – with less clear directionality – have been observed as a function of learning (Polich, 2007; Turk et al., 2018). If control was to facilitate learning progress, we would expect stronger or earlier effects of learning when participants have control over the stimuli.

Further insight into the neural mechanisms behind the active learning memory advantage can be gained by studying evoked responses to incongruent sounds. In our paradigm, participants are regularly tested on their memory of movement-sound pairs; in those test trials, they are required to passively observe a cursor movement and listen to a sound, and judge whether the two are a matching pair or not, based on their previously learned associations. We hypothesised that control during acquisition strengthens the internal representation of the movement-sound association, so violations of the latter should elicit larger prediction error signals (Knolle et al., 2013; Mathias et al., 2015). Based on the previous literature, we expected incongruent stimuli to elicit mismatch responses like the N200 or an orienting response like the P3a (Knolle et al., 2013; Winkler et al., 2009). Alternatively, sounds congruent with learned associations can elicit "matching" responses: The P3b component in particular is thought to reflect the matching of a stimulus with a predicted item, and has been found to be larger with increased predictability (Molinaro & Carreiras, 2010; Roehm et al., 2007; Vespignani et al., 2010). This component is also referred to as "late positive component" (LPC), which is believed to reflect an explicit recollective process (Friedman & Johnson Jr., 2000), typically elicited by designs in which participants have to make a response related to the stimulus (Yang et al., 2019). It is considered part of the classical "old/new" effect; stimuli presented in a test phase which appear familiar to the participant elicit a stronger LPC (Woodruff et al., 2006). The LPC has been found to be a predictor of learning outcomes (Turk et al., 2018). We expected the strength of either the matching-responses to correctly predicted or the mismatch responses to incongruent sounds to be modulated by the factor of control during the learning phase.

Once a motor-auditory association is established, the increased predictability of sounds that comes with

learning should affect sound processing similarly regardless of whether sounds are presented during learning or during a test trial: we expected that sensory responses – specifically the N1 and P2 component – would be attenuated during late stages of learning, and we hypothesised that this effect could be modulated by the mode of acquisition of the motor-auditory associations. Previous studies have shown that during memory tests, stimuli that were previously self-generated can cause motor-reactivation even in the absence of movememt (Butler et al., 2011). The distinctiveness account of the production effect (Hommel, 2005) suggests that motor activation during learning builds stronger, more distinctive memory traces, which is thought to be reflected in more efficient learning; how we learned something affects how we will process it in the future. Movement during sound processing affects our memory of the sound, but is it necessary for the movement to be causally linked to the sound in order for this effect to come into play? If the latter was indeed necessary, we would expect to see an effect of agency – rather than movement – on the neural processing of the stimulus or the strength of the memory trace. Alternatively, if we do not find modulations by agency, that would give support to the idea that movement does not need to be causal to the stimulus in order to affect its processing or memory encoding (Horváth et al., 2012).

In the present study, our goal was to improve our understanding of how active control over sound stimuli affects their immediate sensory processing and encoding in memory. Towards these aims, we studied the way in which control during learning improves memory, and how it modulates neural responses during sound processing and memory encoding. Last but not least, our goal was to reveal a link between self-generation effects during sound processing and memory benefits of active control.

Methods

Participants

Twenty-five healthy undergraduate university students from the University of Barcelona volunteered in the study. Two participants were excluded from the analysis due to their low behavioural performance, based on a cut-off point determined by simulating the responses of 25 randomly responding individuals and choosing the highest performing one as the threshold (56% correctness in the behavioural task). The final sample included twenty-three participants (14 women, M = 21 years old, range: 18–31). No participant self-reported any hearing impairment, psychiatric disorder or use of nervous system-affecting substances at least 48 hours prior to the experiment. All participants gave written informed consent for their participation after the nature of the study was explained to them and they were monetarily compensated (10 Medical Association (Declaration of Helsinki) with the exception of pre-registration and was accepted by the Bioethics Committee of the University of Barcelona.
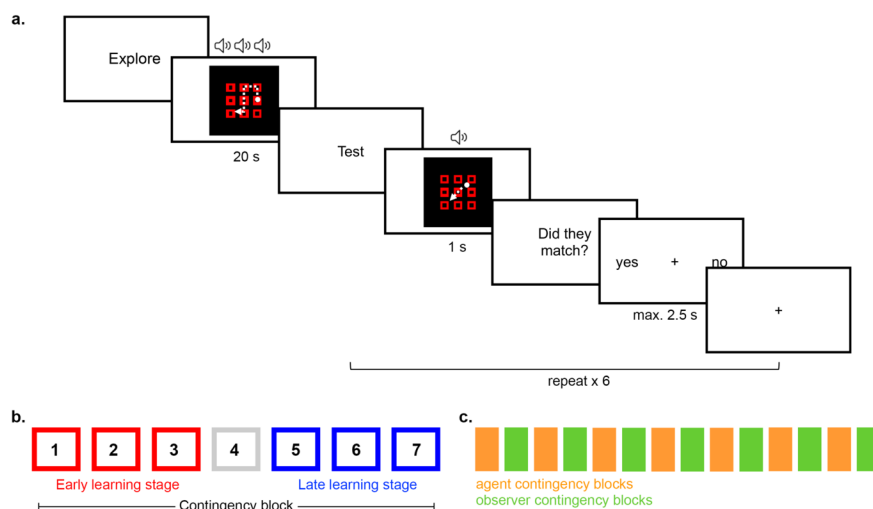
Experiment design

Experiment structure

The experiment consisted of two types of trials: acquisition trials and test trials. During acquisition trials, participants had 20 s to learn associations between movement directions of a white cursor over a grid of 9 red squares (Fig. 1), and 8 different sounds that were played depending on the cursor movements (see section on sound generation below). During test trials, participants were tested on their memory for the movement-sound associations.

The movement-sound associations were learned either as agents or as observers. Agent and observer experimental conditions differed only during acquisition trials. During acquisition trials in the agent condition, the cursor was controlled by the participant's gaze, while in the observer condition the cursor was animated by the computer. Thus, in the agent condition, the acquisition process required active exploration. Participants were instructed to perform saccades over the squares and generate as many different sounds as possible. In the observer condition, the cursor was animated using previously recorded eye movements from the same participant, and participants were asked to follow the cursor's movements and memorise the relationships between movements and sounds.

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Following each acquisition trial, participants were tested on their memory of the movement-sound associations in a series of 6 test trials. During test trials, participants were presented with a short animation of the cursor moving from one square to another in a straight line (executing one of the 8 possible movements). After a delay of 750 ms (matching the pattern of acquisition trials, see section "Visual stimulation and gaze-controlled sound generation"), one of the 8 sounds familiar from acquisition, either congruent or incongruent with the previously learned associations, was presented. 50% of test trials presented congruent movement-sound pairs. The order of the animations and sounds was based on a computer-generated, randomised list. At the end of each test trial, participants responded whether the movement and sound were a congruent pair by pressing one out of two buttons on a midi keyboard placed in front of them.

One acquisition trial and 6 test trials were considered a "learning block". During 7 consecutive learning blocks, participants were presented with the same movement-sound associations. Groups of 7 learning blocks with contingent movement-sound associations are referred to here as "contingency blocks". After the termination of the 7th learning block, the contingency block was finished and new sounds were loaded, so participants had to start their learning process anew. Contingency blocks alternated between the agent and observer conditions. The order of the conditions was counterbalanced across participants.

Figure 1. Experiment structure. a. Structure of a single learning block, consisting of one 20 s acquisition trial, followed by 6 test trials. During acquisition trials, participants either actively explored (agent condition) or passively observed (observer condition) the relationships between movement directions of a cursor and 8 different sound stimuli. In test trials, participants were tested on their memory of the associations. **b.** Structure of a contingency block. Each contingency block consisted of 7 learning blocks. The first three were considered the "early learning stage", and the last three were considered the "late learning stage".**c.** Structure of the experiment: The experiment consisted of 14 contingency blocks, 7 of which belonged to the agent condition and 7 of which to the observer condition.

In order to make the cursor move in a "gaze-like" style in the observer condition, it was computer-animated using the participant's own movements in acquisition trials of the preceding agent contingency block. In case the experiment started with the observer condition, we used the eye movement recordings from the training block, which always involved active exploration. In order to make eye movements less recognisable to the participant, we randomized the order of previously recorded trials across the learning blocks.

Training

Before starting the experiment, participants underwent two stages of training. First, a "free training" session with the purpose of adjusting the eye tracker, allowing the participants to familiarise themselves with the

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equipment, and learn how to use the gaze-controlled cursor. Participants sat facing a screen at 60 cm distance from their eyes. Their head position was stabilized for eye tracking via a chin and forehead rest, and they were wearing a pair of headphones connected to the experiment computer.

Participants were then instructed to move their gaze across the screen and "explore" the sounds that they were able to trigger by moving the cursor (for details, see section "Gaze-controlled sound generation"). During the free training, the experimenter ensured that the participant understood how to use the gaze-controlled cursor and was familiar with the experiment structure. The duration of the free training was variable but lasted typically around 5 minutes.

The subsequent "structured training" followed the same pattern as an agent experimental block, but with only 3 instead of 6 test trials.

Visual stimulation and gaze-controlled sound generation

Before the start of the free training and before every agent experimental block, the eye tracker was calibrated collecting fixation samples from known target points in order to map raw eye data to the participant's gaze position (standard in-built Eyelink calibration procedure). After the calibration was successful, the experiment screen appeared: a grid of 9 red squares over a black background. Each red square's side had a visual angle of 5° 18' 0.99", with gaps of 1° 28' 0.39" between squares. The center of each red square was marked by a small black square with a side length of 0° 49' 0.11". The gaze position of the participant appeared on the screen as a white dot (radius = 0° 19' 0.64"). A fixation on a square was defined as the gaze resting within a radius of 0° 29' 0.47" around the edges of the square. The distance between the chin and forehead rest and the screen was 60 cm, as suggested by the Eyelink 1000 user manual, which translates to an eye-screen distance of about 70 cm.

During the free training, the structured training and the agent experimental condition, participants were able to generate sounds by moving their gaze from one square on the screen to another, adjacent square. The possible movement directions that could trigger a sound were: vertical up and down, horizontal left and right, and diagonal up-right, up-left, down-right, and down-left. A participant could move their gaze from one square to another, and in order to trigger a sound, a fixation on the target square with a duration of 750 ms was required. In the case that the participant interrupted the fixation before the delay period of 750 ms ended, no sound was played.

Sound stimuli

Sound stimuli were synthesized speech sounds created with Google text-to-speech API through Python set to a male Spanish speaker with a sampling rate of 16000 Hz. The sound stimuli were then manually manipulated in Praat using the Vocal Toolkit (Boersma, 2002) to have the same duration and flat pitch. Sounds were normalized and resampled to 96000 Hz. Each sound was a 500 ms /CV/ syllable delivered at 70 dB, formed by a random combination of one of 8 different pitches, vowels and consonants. Pitch (in Hz) was either 90, 120, 150, 180, 210, 240, 270 or 300; the consonant was either [f], [g], [l], [m], [p], [r], [s] or [t]; the vowel was either [a], [e], [i], [o] or [u]. Per participant, 14 sets of 8 different sounds were generated. In each contingency-block, 8 sounds were randomly paired with the 8 possible movement directions.

Apparatus

An ATI Radeon HD 2400 monitor and Sennheiser KD380 PRO noise cancelling headphones were used for presentation of visual and auditory stimuli, respectively. A midi keyboard, the Korg nanoPAD2, was used to record participants' responses. This keyboard was chosen because key presses don't produce any sounds. The presentation of the stimuli and recording of participants' responses was controlled using MATLAB R2017a (The Mathworks Inc.), the Psychophysics Toolbox extension (Brainard, 1997; Kleiner et al., 2007; Pelli, 1997), and the Eyelink add-in toolbox for eyetracker control.

EEG was recorded using Curry 8 Neuroscan software and a Neuroscan SynAmps RT amplifier (NeuroScan, Compumedics, Charlotte, NC, USA). Continuous DC recordings were acquired using Ag/AgCl electrodes

attached to a nylon cap (Quick-Cap; Compumedics, Charlotte, NC, USA) at 64 standard locations following the 10% extension of the international 10-20 system (Chatrian, Lettich, & Nelson, 1985; Oostenveld & Praamstra, 2001). Further electrodes were placed on the tip of the nose (online reference), and above and below the left eye (vertical electrooculogram, VEOG). Further two electrodes were placed next to the outer canthi of both eyes referenced to the common reference (horizontal electrooculogram, HEOG). The ground electrode was located at AFz. Impedances were required to be below 10 kΩ during the whole recording session and data was sampled at 500 Hz.

Horizontal and vertical gaze position of the left eye were recorded using the EyeLink 1000 desktop mount (SR Research) at a sampling rate of 1,000 Hz.

Behavioural data analysis

We analysed the percentage of correct responses (%Correct) to the question of whether the movement-sound pair presented in a test trial was congruent ("Did they match?"). Missing responses were counted as false. Test trials presenting unseen sound-movement pairs were excluded from the analysis to avoid forced guessing. After performing this exclusion, we calculated the %Correct of each participant per learning block, distinguishing between associations acquired in the agent and observer condition. We performed a repeated-measures ANOVA with the factors agency (agent/observer) and learning block (seven levels).

During initial stages of learning, participants were expected to perform very poorly on the memory task due to the little exposure to the associations. During late stages, they were expected to be proficient.

EEG data analysis

Preprocessing

EEG data was preprocessed using EEGLAB (Delorme & Makeig, 2004). After a high-pass filter was applied to the data (0.5 Hz high-pass, Kaiser window, Kaiser β 5.653, filter order 1812), the continuous recording of each participant was inspected, and non-stereotypical artefacts were manually rejected. Then, eye movements were removed from the data using Independent Component Analysis (SOBI algorithm). Independent components representing eye movement artefacts were rejected based on visual inspection and the remaining components were projected back into electrode space. A low-pass filter was applied (30 Hz low-pass, Kaiser window, Kaiser β 5.653, filter order 1812). Malfunctioning electrodes were interpolated (spherical interpolation). A -100 ms to 500 ms epoch was defined around each sound both during acquisition and test trials (-100 to 0 ms baseline correction). A 75 µV maximal signal-change per epoch threshold was used to reject remaining artefacts. Participant averages were calculated for each event of interest, as well as the grand averages using all participants. We obtained ERPs for acquisition sounds in agent and observer acquisition mode, as well as early (blocks 1 to 3) and late (blocks 5 to 7) learning stages. For test sound ERPs, we calculated averaged ERPs for test sounds acquired in agent versus observer mode, early versus late learning stages, and congruent versus incongruent test sounds (relative to the associations between movements and sounds learned in acquisition trials). The mean number of trials per subject-level average was 361, with a standard deviation of 185 trials.

Statistical analyses

Both in acquisition and test sounds, statistical comparisons were conducted to extract agency and learning stage effects and their interactions. In test sounds, we analysed the effects of congruency and the interaction between congruency and the factors agency and learning stage.

Data-driven approach

A mass-univariate non-parametric randomization procedure was used as a first statistical assessment of the EEG data (Maris, 2004; Maris and Oostenveld, 2007). For this procedure, a Delaunay triangulation was used to define clusters of neighbouring electrodes over a 2D projection of the electrode montage, connecting nearby electrodes independently of the physical distance between them. Clusters were defined in order to

contain a minimum of two electrodes. Two dimensional (time, electrode) analyses were conducted on the ERP amplitudes between 0 and 400 ms post-stimulus.

For each of the comparisons performed, the amplitude at each time point and electrode underwent a 2-tailed dependent t-test. The significance probability (p-value) of the t-statistic was determined by calculating the proportion of 2D samples from 10000 random partitions of the data that would have a larger test statistic as a result than the actually observed test statistic (Monte Carlo method). Then, clusters were created by grouping adjacent 2D points exceeding a significance level of 0.05 (two-tailed). A cluster-level statistic was calculated by taking the sum of the t-statistics within every cluster. The significance probability of the clusters was assessed with the described non-parametric Monte Carlo method. Corrected values of p below 0.05 were considered significant. For each significant cluster we report its temporal spread, cluster statistic and p value.

Using this procedure, statistical comparisons were conducted both in acquisition and test sounds comparing the agent and the observer conditions (subtracting observer from agent condition) to test for agency effects and comparing the early and late learning stages (subtracting early from late learning stages) to test for learning effects. Subsequently, we tested for interactions between agency and learning stage comparing the difference between agent and observer across learning stages and the difference between learning stages across agency conditions. In test sounds, we tested for effects of congruency contrasting congruent and incongruent sounds. Finally, we investigated if congruency effects were modulated by the factors agency and learning stage by comparing the difference between congruent and incongruent trials (incongruent subtracted from congruent) in the agent versus observer condition, and in the late versus early learning stage.

As discussed frequently (e.g. Sassenhagen & Draschkow, 2019), cluster-based statistical analyses controlling for multiple comparisons (Maris, 2004; Maris and Oostenveld, 2007) may lead to an overestimation of the temporal and spatial characteristics of the effects, so it is recommendable to avoid very specific time-space claims about the data. We are aware of these limitations, and we try to relate the findings from the cluster-based analysis to classic ERP components based on the shapes and scalp topographies of the obtained waveforms.

Targeted-component analysis

As a complementary, ERP-focused approach, we examined the responses for all comparisons of interest in the N1, P2 and P3 time windows at the Fz, Cz and Pz electrodes. The windows were defined after visual inspection of the data by locating the highest negative or positive (depending on the component of interest) peak in the usual latencies and electrodes for each component, and defining a window centered on the peak and adjusted to the width of the component, as reported by previous works (SanMiguel et al., 2013). We observed morphological differences between responses to acquisition sounds and test sounds, thus windows were defined separately for the two types of sounds, based on the peaks observed in either the average of all acquisition sounds or all test sounds. The N1 was measured at the Fz electrode in the window 80-120 ms in acquisition sounds and 110-140 ms in test sounds. The P2 was measured at Cz in the window 180-240 ms in acquisition sounds and 210-270 ms in test sounds. Both components showed reversed polarity at the mastoid electrodes in these windows. The P3 component was measured at the Fz electrode (P3a) and the Pz electrode (P3b), respectively, in the 310-390 ms time-window in acquisition sounds and the 340-400 ms time-window in test sounds.

We ran repeated-measures ANOVAs in order to test for differences on the mean amplitude of each component at the selected electrodes between conditions of interest. Specifically, for the acquisition sounds, we ran a two-way ANOVA with the factors *agency* (two levels: agent and observer) and *learning stage* (two levels: early and late) for each ERP component of interest.

We ran two separate ANOVAs for each component for the test sounds. A one-way ANOVA with the factor movement-sound congruency (levels: congruent and incongruent) and a two-way ANOVA with the factors agency and learning stage. We also analysed whether the effects of congruency were modulated by agency and learning stage by using the differences between amplitudes in congruent and incongruent trials as the

dependent variable in a two-way ANOVA with the factors agency and learning stage.

Correlation analysis

We aimed to identify electrophysiological markers related to the performance benefits associated with active learning amongst a small set of pre-defined candidate ERP components. Thus, we tested for significant correlations, using Pearson's coefficient, between each participant's effect of agency on the percentage of correct responses and the effect of agency on the N1, P2 and P3 in acquisition sounds (amplitude of acquisition sound ERPs in agent condition – observer condition). Given that agency effects on the behavioural data were restricted to the early learning stage (see results), we used only the performance data from the early learning stage (%Correct in agent–%Correct in passive) for this correlation analysis.

Behavioural results

Behavioural results show that active exploration led to faster learning and better memory performance. However, given enough training, passive viewing led to similarly good performance (fig. 2).

A two-way ANOVA was run with the factors agency (agent versus observer) and learning block (1 to 7) and the dependent variable %Correct.

We found a significant main effect of agency [$F_{(1, 22)}$= 11.865, p < .001, $\eta_p^2 = 0.32$] and learning block [$F_{(6,132)}$ = 16.534, p < .001, $\eta_p^2 = 0.39$], and a significant interaction between the two factors [$F_{(6,132)}$ = 6.635, p < .001, $\eta_p^2 = 0.20$]. Post-hoc t-tests (Bonferroni corrected) showed that memory performance in the agent condition was significantly higher than in the observer condition in the first, second and fourth learning block. The effect of agency on %Correct was inversely correlated with learning block ($r_{(5)}$ = -3.922, p = .01). Post-hoc t-tests showed that the difference between agent and observer was significantly larger in the first learning block than in the last learning block [$t_{(22)}$ = 4.291, p < 0.001, $d = 1.105$]. The effect of learning was significantly smaller in the agent compared to the observer condition [$t_{(22)}$ = -4.291, p < 0.001, $d = -0.656$] (subtracting learning block 1 from learning block 7 in agent versus observer condition). This shows that agency accelerates memory encoding for arbitrary audiovisual associations.
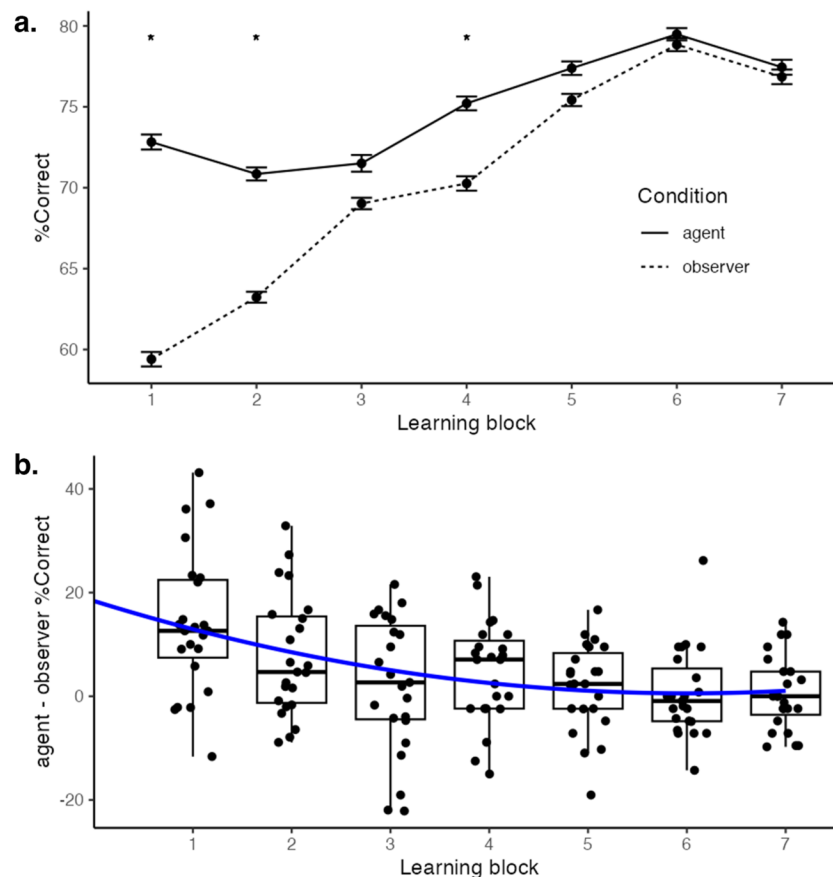
Figure 2. Effect of agency and learning block on %Correct.a. %Correct mean and standard error across all participants (N=23) in the agent condition *(solid line)* and observer condition (*dotted line*) across learning blocks. Asterisks mark learning blocks in which significant differences between conditions were found in post-hoc tests. **b.** Difference between the agent and observer conditions for each participant across learning blocks *(black dots)*, as well as the median and interquartile range across participants (*boxplots*). The difference between the agent and observer conditions is inversely correlated with learning block. An exponential curve was fitted to the data (*blue solid line*) to illustrate the decreasing effect of agency with the progress of learning. The effect of agency decreases rapidly during the first three learning blocks and then remains constantly low in the remaining four learning blocks.

Electrophysiological results

For each effect and interaction studied, we present here two complementary approaches: a data-driven analysis using cluster-based permutation tests, and an ERP component driven analysis using ANOVAs to assess effects on targeted ERP components.
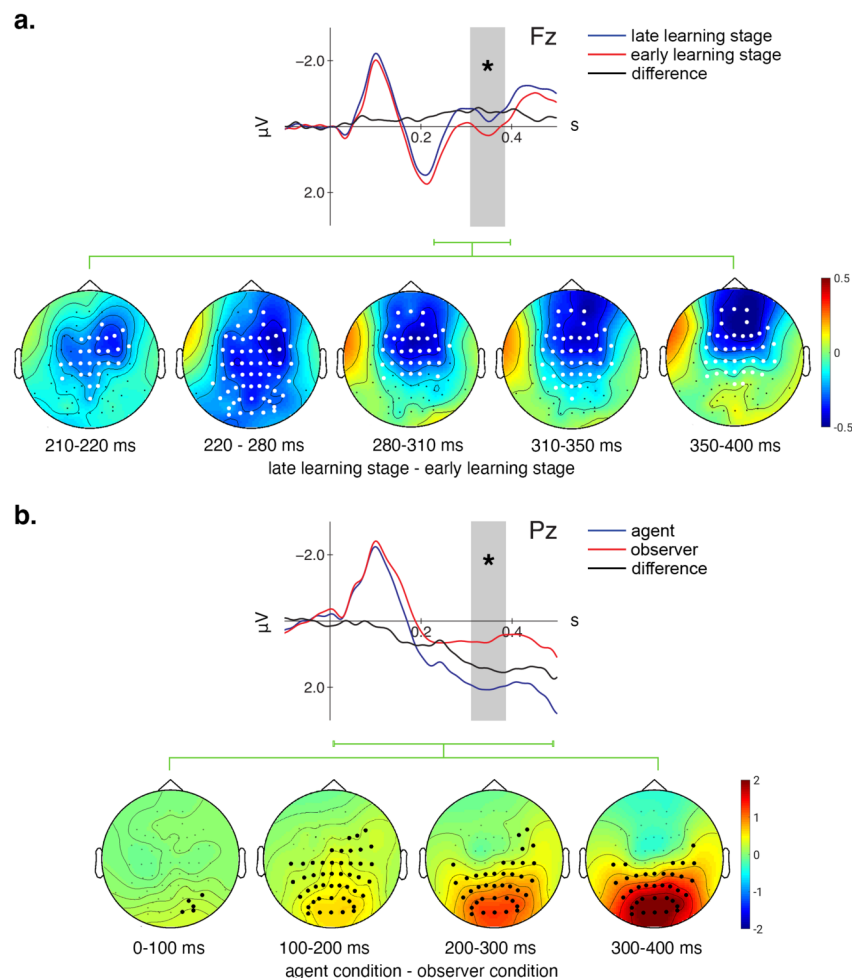
Acquisition sounds

Learning progress was reflected in ERPs as an attenuation of the P3a component. The cluster-based analysis comparing early and late acquisition sounds (late – early learning stage) revealed a negative cluster with a fronto-central distribution (T = 4659.8, p < .01; 220 ms to 400 ms), encompassing the P2 and P3a components (figure 3a). The targeted-component ANOVA yielded a significant main effect of learning stage

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on the amplitudes of the P3a component at Fz [$F_{(1,22)} = 14.436$, $p < .001$, $\eta_{\mathrm{p}}^2 = 0.40$], reflecting more negative values with increased learning stage.

Regarding the effect of agency, we found more positive ERPs in parietal electrodes in the agent compared to the observer condition (figure 3b). The cluster-based permutation test comparing the agent and observer conditions detected a significant positive cluster with an occipito-parietal distribution ($T = 10900$, $p < .01$; 60 ms to 400 ms). The cluster temporally encompasses the P2 and P3 components, revealing overall more positive amplitudes in the agent condition. The targeted-component ANOVA detected a significant main effect of agency on the P3b component at Pz [$F = 25.706$, $p < .0001$, $\eta_{\mathrm{p}}^2 = 0.54$]. The occipito-parietal distribution of the effect led us to suspect that the observed differences are due to motor differences related to the control of the sound stimuli. To explore this possibility, we conducted further analyses, which can be found in the supplementary materials.

In order to study possible interactions between agency and learning stage using cluster-based permutation tests, we subtracted the early learning stage from the late learning stage in both the agent and observer condition and then ran a cluster-based analysis (late minus early learning stage in agent condition versus late minus early learning stage in observer condition). Studying this interaction, possible confounding factors due to eye movement differences (see discussion in supplementary materials) were eliminated from the data. However, this analysis yielded no significant results. We also tested for interaction effects in the targeted-component ANOVAs, but this also did not produce any significant interaction effects. All in all, no interactions between the factors agency and learning stage were detected.

Figure 3. Effects of learning stage and agency on acquisition sound ERPs and topographical cluster plots. a. Grand-averaged ERP wave forms of the late learning stage (*blue*) and the early learning stage (*red*) acquisition sounds, plus the difference wave (early subtracted from late; *black*) at the Fz electrode. The P3a time window is highlighted. The asterisk indicates a significant difference across learning stages. Below, a series of 5 topographical plots shows the difference between late and early learning stage (late - early) across time and sensor space. Electrodes belonging to the significant negative cluster are highlighted in white. **b.** Grand-averaged ERP wave forms of the agent condition (*blue*) and the observer condition (*red*) acquisition sounds, plus the difference wave (observer subtracted from agent; *black*) at the Pz electrode. The P3b time window is highlighted. The asterisk indicates a significant difference across agency conditions. Below, a series of 4 topographical plots shows the difference between agent and observer condition (agent - observer) across time and sensor space. Electrodes belonging to the significant positive cluster are highlighted in black.

Test sounds

Congruency between movement and sound triggered a late positive deflection that was absent in incongruent sounds (figure 4). The cluster-based permutation test comparing congruent and incongruent test sounds detected a significant positive cluster (T = 4946.6, p = .004; 240 ms to 400 ms) that starts at occipito-parietal electrodes and spreads across the entire skull. The cluster temporally encompasses the P2 and

P3 components, revealing overall more positive amplitudes for congruent sounds. The targeted-component ANOVAs found a significant main effect of congruency on the P3 component in Fz [$F_{(1,22)} = 12.342$, p=.001, $\eta_p^2 = 0.36$] and Pz [$F = 20.589$, $p < .001$, $\eta_p^2 = 0.48$], corresponding to the P3a and the P3b. The effects of congruency were not modulated by agency or by learning stage.

We found no effects of agency nor learning stage on test sounds, and no interactions. Both the cluster-based approach and the targeted-component analysis yielded no significant results.
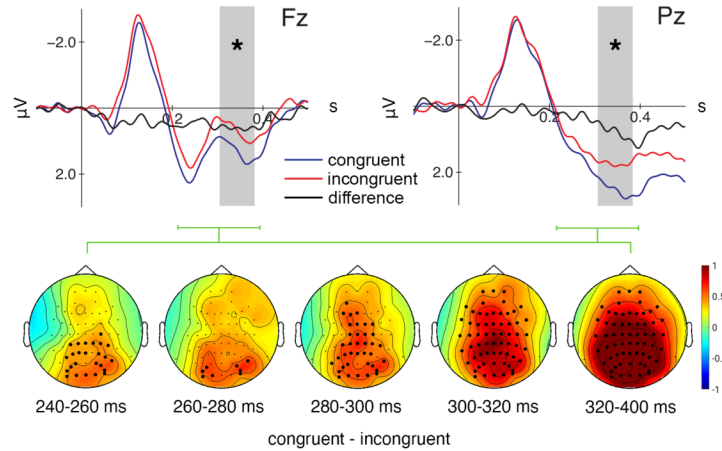
Figure 4. Effects of congruency on test sound ERPs. Congruent (*blue*) and incongruent (*red*) test sound evoked grand-averaged ERPs, as well as their difference wave (congruent – incongruent, in *black*) are plotted at the Fz and the Pz electrodes. A series of topographical plots showing the difference between congruent and incongruent sounds across time and sensor space illustrates the spread of the significant positive cluster across time. Sensors exhibiting significant differences across conditions are highlighted in *black*.

### Correlations between neural and behavioural effects of agency

Differences in %Correct between the agent and observer condition exhibited a great variability across individuals (M = 9.7%, SD = 7.1%, range = 0-26%). Thus, active learning was more efficient than learning from observation for some, but not all participants. Aiming to uncover the neural underpinnings of active learning benefits, we tested for possible correlations between the benefit that a participant would have of agent over observer acquisition for their memory of the movement-sound associations, and the degree to which agency modulated auditory ERPs during early stages of acquisition, when the active learning benefits were maximal.

We found a significant correlation between agency effects on N1 amplitude of acquisition sounds at Fz in the early learning stage and agency effects in memory performance [$r_{(21)} = 0.6$, p = .002]. The stronger the N1 agency effect that a participant experienced during early acquisition, the stronger the memory advantage for the agent vs. the observer conditions (figure 5).

In order to visualize this finding, we decided to split the participants into two groups, using the median of the difference between agent and observer %Correct as a cutoff point (M = 7.8%).

Participants who had stronger behavioural agency effects than the median were considered "active learners" (N = 11), and participants that fell below that median of behavioural effects were considered "indifferent learners" (N = 12).

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We compared the overall performance (agent + observer condition) of active and indifferent learners. Active learners performed overall better in the behavioural task (M = 78%, SD = 13%) as compared to indifferent learners (M = 68%, SD = 11%). A two-sample t-test showed that this difference is statistically significant [$t_{(21)}$ = 3.844, p < .001, d = 0.80].
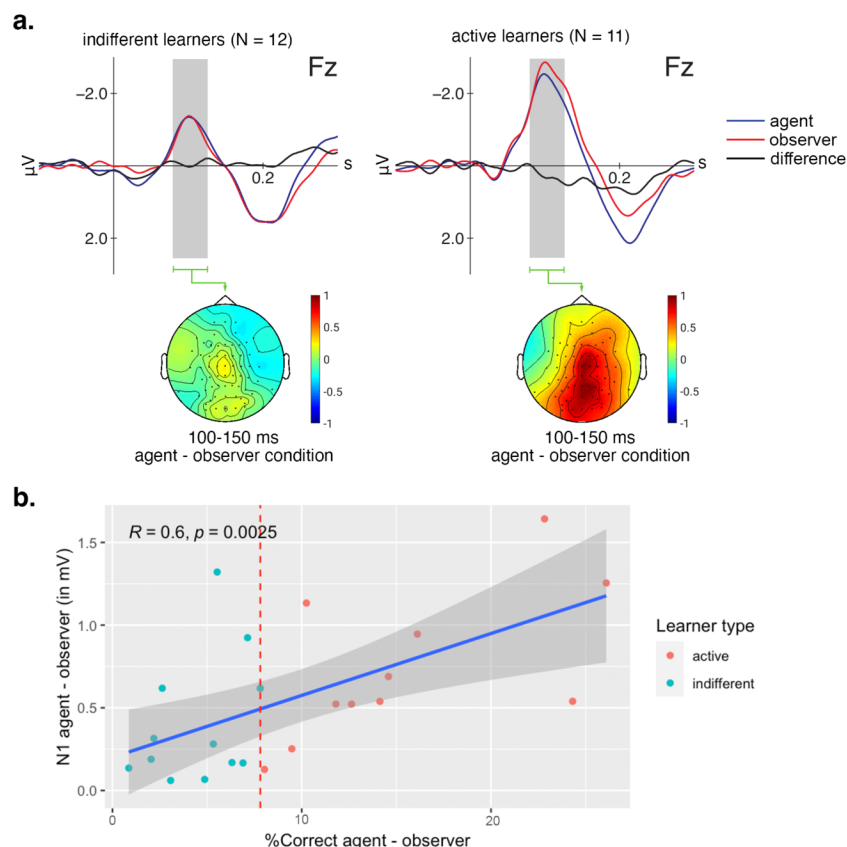
Figure 5. Correlation between memory performance and neural responses. a. ERPs contrasting the agent and observer condition at the Fz electrode in participants who exhibited a strong memory benefit in the agent relative to the observer condition (active learners) and in participants that did not exhibit a strong memory advantage for the agent condition (indifferent learners). Below, topographical plots that show the distribution of the effect in the N1 time window. **b.** The difference between the N1 amplitude in the agent versus observer conditions during the first learning stage is plotted on the y-axis, and the difference between the agent and the observer condition in the %Correct during the memory task is plotted on the x-axis. A linear regression is fitted to the data (*blue*). A dotted line indicates the median on the x-axis, based on which participants were sorted into the "active learners" and "indifferent learners" groups.

Discussion

The aim of this study was to investigate the neural mechanisms underlying the benefits of active control for associative learning while controlling for the factors of movement and predictability, which in the existing literature often conflate the effects of agency during learning. Using a gaze-controlled interface in a motor-auditory associative memory task, we showed that control over stimuli alone – controlling for unspecific neuromodulatory effects through movement and stimulus predictability – can lead to learning benefits on a

behavioural level.

We found higher movement-sound association memory accuracy for associations studied with active oculomotor control of visual exploration versus objects studied passively. This active-learning advantage for memory occurred despite the fact that visuo-auditory information was matched between the agent and observer study conditions. However, some participants did not seem to follow this pattern, exhibiting small or no differences between the agent and observer learning condition. We found that we could distinguish amongst participants based on their learner type, that is to say that some participants indeed exhibited the expected memory benefit for active learning, while others did not. Interestingly, this behavioural difference was correlated with the individual participant's degree of N1 attenuation, a well-established marker of self-generation during sound perception. We found that the stronger sensory processing differences between self- and externally generated stimuli – represented by the attenuation of the N1 component – a participant exhibited, the more they would benefit from control during learning, and the better their overall performance.

A large body of research shows that, chiefly, being in control of information during learning is beneficial for memory encoding. Beyond the well-known production effect (Brown & Palmer, 2012; MacDonald & MacLeod, 1998; MacLeod et al., 2010), an advantage for active, self-directed over passive learning methods is an established fact in educational contexts (Tomporowski et al., 2015) and has been observed in different modalities and domains of learning (Butler et al., 2011; Cohen, 1989; Gathercole & Conway, 1988; James et al., 2002; Kuhn et al., 2000; Schulze et al., 2012). Low-intensity exercise or simple motor-activity (such as walking or finger tapping) produces mixed results in relation to memory performance, with some studies finding memory benefits (Schaefer et al., 2010; Schmidt-Kassow, Deusser, et al., 2013; Schmidt-Kassow et al., 2010, 2014; Schmidt-Kassow, Heinemann, et al., 2013) and others memory impairment (Lajoie et al., 1996; Li et al., 2001; Lindenberger et al., 2000; Yogev-Seligmann et al., 2008). In many of the studies on the benefits of production for memory the effects of movement and the effects of being in control cannot be interpreted separately (Mama & Icht, 2016; Ozubko et al., 2012; Rummell et al., 2016). Some studies have tried to single out the effect of agency from conflating factors and found benefits for learning and memory (Chi, 2009; Gureckis & Markant, 2012; Markant et al., 2016). In this study we tried to relate self-generation effects during sensory processing to memory benefits of active learning. Taking into consideration the substantial evidence suggesting that self-generation effects are in part due to unspecific neuromodulation through motor activity, we asked ourselves whether or not the established self-generation effects would be reproducible in a paradigm that specifically singles out the effect of agency while controlling for movement. Additionally, we used eye movements for sound generation. Eye movements don't trigger sounds in real life, so participants had to learn the associations between their movements and the different sounds from scratch. The fact that the production effect was reproduced in this set-up suggests that agency contributes significantly to the phenomenon, beyond the effects of coincidental proximity to a motor act. Specifically, we found that the attenuation of the N1 component could predict the strength of the active learning memory benefits an individual participant would experience.

The production effect is frequently explained with the distinctiveness account – the idea that retrieval of an event from memory is facilitated if the event is embedded in a network of associations rather than remembered in isolation (Hommel, 2005). An alternative explanatory approach is the idea that being in control is rewarding, that motivation is higher, and that it activates more strongly those areas of the brain that process reward (Leotti & Delgado, 2011), facilitating memory encoding. It has been hypothesized that feeling in control over something makes it self-relevant, which by default might be remembered better (Kim & Johnson, 2012). In experiments comparing the memory encoding of stimuli that are either under the control of the participant or under the control of the experimenter, there is also an inherent information processing advantage in control conditions: Self-directed learners can decide when they want to see what information. They can select the information that has the biggest effect on reducing their uncertainty and optimise the flow of information according to their needs. This makes the learning experience more efficient (Gureckis & Markant, 2012; Markant & Gureckis, 2010; Schulz & Bonawitz, 2007). In this study, the correlational finding between the attenuation of the N1 component and the memory performance of individual subjects suggests that whatever differences in performance we find are at least partly due to perceptual differences

during learning, rather than conflating factors such as information efficiency.

It is not yet well understood how active production leads to improved memory performance on a neural level, and so far there are few established links between sensorimotor processing and memory gains. Our study contributes to this discussion by delivering evidence towards a link between the way we process a self-generated stimulus and the strength of its memory trace. Linking the differences in memory encoding that were found on a behavioural level to the differences in sensory processing during the learning phases of our experimental task, we were able to establish a connection between self-generation effects on ERP components and the production effect on memory. Memory performance was correlated with the degree of attenuation of the N1 component in self- versus externally generated sounds. We can draw two tentative conclusions from this: That there are individual differences in the strength of the self-generation effect on the N1 component, and that there is a link between the processing of self-generated sounds and their memory encoding.

Due to physical differences between eye movements in the agent and observer condition, we were not able to interpret the effect of agency on acquisition sound ERPs directly. Nevertheless, we were able to study whether the effects of the other two factors, learning stage and congruency, were modulated by agency. Contrary to our expectations, we did not find that the effects of learning progress and identity predictability (i.e. congruency with learned associations) themselves on neural processing were modulated by agency. Observing the change of ERP components over the course of the learning process, we found an attenuation of the P3a component in acquisition. We expected that faster learning through agency during acquisition might speed up this process, which would have led to a stronger attenuation earlier during learning. Studying test sounds, which we manipulated to be either congruent or incongruent with the learned movement-sound associations, we found a late positivity for congruent sounds. A movement-sound association strengthened by agency during learning should have reflected in a stronger congruency effect overall. Neither of these effects was modulated by agency during learning.

The P3a component is an orienting response typically associated with novel stimuli (Polich, 2007). We found an attenuation of the P3a with learning. Why was the attenuation effect not enhanced, or established earlier in the learning process, by agency during acquisition? The behavioural results suggest that the effect of agency should be most visible in the early and intermediate stages of learning, while towards the end, both conditions become similar. We could speculate that we would have found an earlier attenuation in the agent condition, had we been able to perform a more fine-grained analysis. Our design allowed us to separate into early and late learning stages. Maybe an analysis using more levels for this factor – which in our case was not possible due to an insufficient number of trials – would have detected an effect during intermediate stages of learning.

The congruency effects that we found were not exactly what we had anticipated, but they were nevertheless conclusive. We had expected that sounds that were incongruent with the learned associations between movements and sounds would trigger some form of mismatch response, possibly an audio-visual mismatch negativity (avMMN), which has been observed in response to violations of cross-modal predictions, similar to what was found by Winkler and colleagues (Winkler et al., 2009). We hypothesized that the way in which associations have been learned (either passively or as motor-associations) would impact the strength of the prediction error elicited by violations of those learned associations. Specifically, we expected to observe differences in certain ERPs that had previously been linked to deviant or target processing, like the N2b and the P3a (Knolle et al., 2013). We expected that deviating from an association learned as linked to a motor act will trigger a more efficient processing and yield stronger N2b and P3a responses. What we found instead was that test sounds that were congruent with learned associations between movements and sounds triggered a late positive component with a central distribution, which we could call P3. The P3 is often considered an index of context or internal model updating (Polich, 2007; Reed et al., 2022), and depending on the nature of the experimental task, it has also been observed as a response to target stimuli (Hillyard & Kutas, 1983; Nieuwenhuis et al., 2005; O'Connell et al., 2012; Twomey et al., 2016; Verleger et al., 2017). We found a P3 triggered by congruent sounds, so if we want to integrate this finding into existing theories,

we should consider it a marker of model updating based on a positive match – participants see an animation, predict the upcoming sound, and when the prediction is matched, the model is reinforced. Alternatively, we could think of this component as a late positive component (LPC). This component has been hypothesized to be correlate of the working memory updating processes (Donchin, 1981; Donchin & Coles, 1988; Polich, 2007). It has been found in experiments where stimuli are task-relevant or response-dependent (Pritchard, 1981; Snyder & Hillyard, 1976). In one experiment, it was elicited when participants had to detect and respond to deviant stimuli, but not when they were instructed to ignore deviants (Maidhof et al., 2010). The LPC may reflect participants detecting a stimulus they had been looking out for (Mathias et al., 2015). Just like in this experiment, Mathias and colleagues found that the LPC was not modulated by active or passive acquisition mode, which they see as support for the idea that the LPC depends on the stimulus' task relevance rather than the degree of deviation from a memory representation.

Conclusion

We found that active control during the learning of movement-sound associations using a gaze-controlled interface facilitates memory encoding. We found that the degree of attenuation of the N1 component for self-generated sounds correlated with the behavioural performance of each participant: the stronger the sensory processing differences during learning, the stronger the memory gain for active learning, and the better the overall performance on the memory task. This finding suggests that memory benefits of active learning are at least in part linked to perceptual differences during sensory processing, and that there may be a continuum of variation in the self-generation N1 attenuation effect across the population that allows us to assess different learner "profiles". Although we did not find across-the-board modulation of neural responses by the factor of agency during learning, we see neural responses being modulated by increasing stimulus predictability, and we found that during memory recall, matching association pairs triggered a target matching response.

CRediT authorship contribution statement

Stefanie Sturm: Conceptualization, Data acquisition, Formal Analysis, Methodology, Software, Investigation, Writing – Original draft preparation, Visualization. ***Jordi Costa-Faidella:*** Conceptualization, Formal Analysis, Methodology, Software, Writing – Original draft preparation, Supervision. Iria SanMiguel: Conceptualization, Formal Analysis, Methodology, Software, Writing – Original draft preparation, Supervision, Project administration, Funding acquisition.

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