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1 **Sensory suppression and increased neuromodulation during**
2 **actions disrupt memory encoding of unpredictable self-**
3 **initiated stimuli**

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22 **Abstract**

23 Actions modulate sensory processing by attenuating responses to self- compared to
24 externally-generated inputs, which is traditionally attributed to stimulus-specific motor
25 predictions. Yet, suppression has been also found for stimuli merely coinciding with actions,
26 pointing to unspecific processes that may be driven by neuromodulatory systems.
27 Meanwhile, the differential processing for self-generated stimuli raises the possibility of
28 producing effects also on memory for these stimuli, however, evidence remains mixed as to
29 the direction of the effects. Here, we assessed the effects of actions on sensory processing
30 and memory encoding of concomitant, but unpredictable sounds, using a combination of self-
31 generation and memory recognition task concurrently with EEG and pupil recordings. At
32 encoding, subjects performed button presses that half of the time generated a sound (motor-
33 auditory; MA) and listened to passively presented sounds (auditory-only; A). At retrieval,
34 two sounds were presented and participants had to respond which one was present before.
35 We measured memory bias and memory performance by having sequences where either both
36 or only one of the test sounds were presented at encoding, respectively. Results showed worse
37 memory performance – but no differences in memory bias – and attenuated responses and
38 larger pupil diameter for MA compared to A sounds. Critically, the larger the sensory
39 attenuation and pupil diameter, the worse the memory performance for MA sounds.
40 Nevertheless, sensory attenuation did not correlate with pupil dilation. Collectively, our
41 findings suggest that sensory attenuation and neuromodulatory processes coexist during
42 actions, and both relate to disrupted memory for concurrent, albeit unpredictable sounds.

43 *Keywords:* self-generation, memory, pupillometry, EEG, auditory processing

44 **1. Introduction**

45 Forming predictions about upcoming events in the environment is crucial for all behaving
46 organisms. A critical instance of such predictive processing is our ability to anticipate the
47 sensory consequences of our own actions, which is essential for building a sense of self and
48 shapes our perception of sense of agency (Gallagher, 2000). Although predictions have been
49 suggested to facilitate perceptual processing in the wider sensory literature, most studies from
50 the action domain point to attenuated processing for the predicted self-produced events
51 (Schröger et al., 2015; Press et al. 2020), with only a few exceptions showing the opposite
52 effect (e.g., Reznik et al., 2014; Eliades & Wang, 2008). Several lines of research have shown
53 that actions suppress the processing of the self-generated reafferent input (so-called self-
54 generation effect) in a wide range of species (Chagnaud et al., 2015; Kelley et al., 2010; Kim
55 et al., 2015; Requarth & Sawtell, 2011; Roy et al., 2001; Schneider et al., 2014) and
56 irrespective of sensory modality (auditory; Baess et al., 2011; Horváth, 2013a; Horváth,
57 2013b; Martikainen, 2004; Mifsud & Whitford, 2017; SanMiguel et al., 2013; Saupe et al.,
58 2013; Schafer & Marcus, 1973; Timm et al., 2013; Klaffehn et al., 2019; Weller et al., 2016;
59 Pyasik et al., 2018, visual; Hughes & Waszak, 2011; Mifsud et al., 2018; Roussel et al., 2013;
60 Roussel et al., 2014, and tactile; Blakemore et al., 1998; Hesse et al., 2010; Kilteni et al.,
61 2020). Dominant *cancellation* models attribute this attenuation to stimulus-specific
62 prediction signals generated via internal forward modelling (Wolpert et al., 1995) before or
63 during an action that are sent from the motor to the corresponding sensory cortices (Sperry,
64 1950; von Holst, 1954). These motor-induced predictions of sensory reafference (i.e.,
65 corollary discharge) are compared to the sensory input generated by one's actions, and only
66 the difference between the two (i.e., prediction error) is sent to higher stages of the neuronal
67 hierarchy for further processing (Friston, 2005), ultimately suppressing the processing of the
68 anticipated event in order to prioritize the most informative unexpected inputs (Sperry, 1950;
69 von Holst, 1954).

70 So far, self-generation effects in the auditory domain have been typically assessed using
71 the *contingent* self-generation paradigm, where neural responses to sounds generated by the
72 participants in a fully predictable fashion are compared to the responses elicited by
73 externally-generated sounds. Most of these studies have shown attenuated auditory N1 and
74 P2 event-related potential (ERP) amplitudes, with especially the former being considered a

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75 proxy of suppressed processing of self-produced sounds in the auditory cortex, driven by
76 motor predictions (for a review see Schröger et al., 2015). However, it is known that the
77 auditory N1 response is not a unitary phenomenon but rather reflects the overlap of several
78 components (SanMiguel et al., 2013), among which two are proposed to be stimulus-specific
79 and to reflect processing in primary and secondary auditory areas (Näätänen & Picton, 1987).
80 The first one is generated by tangentially oriented sources in the auditory cortex, has a
81 frontocentral distribution, and shows polarity reversal at the mastoids. Nevertheless, the few
82 studies that have analyzed N1 amplitudes at the mastoids have reported no suppression
83 (Timm et al., 2013; SanMiguel et al., 2013) or even enhanced amplitude in response to self-
84 generated sounds (Horváth et al., 2012). The second one, usually referred to as the “T
85 complex”, is generated by radial sources in the superior temporal gyrus and is typically
86 identified as the first and second negative peaks (i.e., Na and Tb, respectively) observable on
87 anterior temporal sites (Toninquist-Uhlen et al., 2003; Wolpaw & Penry, 1975). Reports of
88 self-generation effects on the “T complex” remain scarce, but the few studies that have
89 assessed it reported attenuation of Tb for self-generated sounds (Horváth, 2013b; SanMiguel
90 et al., 2013). Inevitably, if N1-suppression indeed reflects modulations in auditory areas
91 driven by stimulus-specific motor predictions, then the self-generation effects should be
92 specific to the expected stimulus and mediated by sensory specific areas.

93 However, the stimulus-specificity of the effects has been challenged by data showing that
94 the N1-suppression may mostly affect the stimulus-unspecific component of N1 (SanMiguel
95 et al., 2013), which is thought to be the cortical projection of a reticular process that facilitates
96 motor activity (Näätänen & Picton, 1987). Further evidence supporting the lack of stimulus-
97 specificity of the effects comes from work showing that suppression of responses can be also
98 observed in the absence of a predictive relationship between the action and the sound.
99 Horváth et al. (2012) employed a *coincidence* rather than a *contingent* task, where
100 participants had to press a button several times and concurrently, but independently from the
101 actions, a sound sequence with random between-sound intervals was presented. They showed
102 that despite the absence of contingent relationship between the action and the sound, the
103 auditory N1 was attenuated for sounds that coincided with a button press, indicating that the
104 N1-suppression for self-produced sounds may be also driven by the temporal proximity
105 between action and sound, rather than by a stimulus-specific prediction of the expected

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106 sensory input. These findings challenge the predictions made by the cancellation account,
107 since if this attenuation was to be attributed to stimulus-specific motor predictions, then it
108 should only be found in paradigms where the stimulus can be indeed predicted by the action,
109 and it should mainly reflect the attenuation of the sensory components of N1 (generated in
110 auditory cortex).

111 Indeed, a significant number of non-predictive processes are also known to modulate
112 perceptual and neural responses during motor acts (Press et al., 2020; Press & Cook, 2015),
113 which may point to an unspecific gating mechanism during movement (i.e., a “halo of
114 neuromodulation”) that modulates processing of sounds presented close in time to a motor
115 act even in the absence of a causal relationship between the action and the sensory stimulus
116 (e.g., Hazemann et al., 1975; Makeig et al., 1996; Horváth, 2013a, b; Horváth et al., 2012).
117 This mechanism may be mediated by arousal-related unspecific modulatory processes which
118 receive influences from motor areas (Näätänen & Picton, 1987). Specifically, the locus
119 coeruleus norepinephrine (LC-NE) system has been implicated as a possible reticular
120 candidate responsible for mediating the unspecific gating of sensory processing around the
121 motor acts. Supporting evidence comes from animal work showing that the auditory cortex
122 receives inputs from both motor and neuromodulatory areas (mostly from the basal
123 forebrain), which are simultaneously active during movement and form synapses onto many
124 of the same auditory cortical excitatory and inhibitory neurons (Nelson & Mooney, 2016; for
125 a review see Schneider & Mooney, 2018). Critically, the neurons in the basal forebrain
126 receive inputs from subcortical regions, including the locus coeruleus, suggesting that this
127 overlap of motor and neuromodulatory inputs in auditory areas may result in a diverse set of
128 motor and neuromodulatory influences, thereby pointing to coexisting, but possibly
129 independent, stimulus-specific and unspecific effects during movement (Nelson & Mooney,
130 2016). More importantly, the link between LC-NE activity and motor behavior is supported
131 by animal (Lee & Margolis, 2016; McGinley et al., 2015; Stringer et al., 2019; Vinck et al.,
132 2015) and human work (Simpson, 1969; Strauch et al., 2020; Yerba et al., 2019) showing a
133 close association between engaging in motor activities (e.g., whisking or button press in
134 Go/No-Go tasks) and pupil dilation, which has been shown to track the activity of the LC-
135 NE system (Aston-Jones & Cohen, 2005; Vinck et al., 2015).

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136 Although most studies have focused on the effects of self-generation on the immediate
137 sensory processing, previous work has reported modulatory effects of movements on
138 hippocampal and parahippocampal activity (Halgren, 1991; Mukamel et al., 2010; Rummell
139 et al., 2016), suggesting that the differential processing of self- and externally-generated
140 stimuli may also have consequences for memory encoding. One line of evidence shows that
141 spoken words are better remembered than words that are passively listened to (MacDonald
142 & MacLeod, 1998) and played melodies can be better recognized compared to melodies that
143 are passively presented to the participants (Brown & Palmer, 2012), suggesting that self-
144 generated stimuli are encoded more efficiently in memory than the passively presented ones
145 (so-called *production effect*). These memory improvements for self-produced stimuli have
146 been attributed to the increased distinctiveness of those items because producing them
147 provides extra mnemonic information (i.e., a memory trace of having spoken the words) that
148 is not present for silently read words (Conway & Gathercole, 1987; Mama & Icht, 2016;
149 Ozubko et al., 2012). Additional evidence suggests that the action-induced memory
150 enhancement may be driven by the engagement of the noradrenergic system, as shown by
151 the increased pupil dilation and locus coeruleus activity in response to stimuli tied with – but
152 not produced by – actions (i.e., Go-events in a Go/No-Go task; Yerba et al., 2019). However,
153 predictive coding theories suggest that learning and memory are driven by the amount of
154 surprise (i.e., prediction error) associated with an item (Bar, 2009; Krawczyk et al., 2017;
155 Pine et al., 2018). Specifically, the larger prediction errors elicited by unpredicted items at
156 encoding are thought to result in greater synaptic change, reduced prediction error for this
157 item at retrieval (Greve et al., 2017; Heilbron & Chait, 2018; Henson & Gagnepain, 2010;
158 Pine et al., 2018), and ultimately enhanced memory performance. The latter findings are
159 consistent with studies reporting that items leading to high prediction error tend to produce
160 greater hippocampus fMRI signal in the study phase of a recognition memory experiment,
161 and that this increase in hippocampal activity is associated with enhanced subsequent
162 recollection in the test phase (Gagnepain et al., 2011; Henson & Gagnepain, 2010; Pine et
163 al., 2018). In sum, this framework would predict memory enhancements for the externally-
164 generated sounds in a typical *contingent* paradigm where they inherently elicit larger
165 prediction error compared to the more predictable self-generated stimuli.

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166 To the best of our knowledge, there have been no attempts to simultaneously address the
167 effects of self-generation on sensory processing and memory encoding of sounds and assess
168 the possible relationship between these two phenomena. Meanwhile, the findings as to the
169 direction of the motor-driven effects on memory encoding of self-generated stimuli
170 (enhanced vs. reduced memory performance) remain mixed but point to differential memory
171 representations for events that have been experienced as self-initiated and those that have
172 been experienced as externally-generated. Further, recent evidence contradicts the traditional
173 view of sensory suppression being due to stimulus-specific motor predictions, thereby raising
174 the need to examine the possible role of stimulus-unspecific neuromodulatory mechanisms
175 both on sensory processing and memory encoding of sounds merely coinciding with motor
176 actions.

177 In this study, we examined whether and how motor actions affect sensory processing and
178 memory encoding of concomitant, but unpredictable sounds, by employing a combination of
179 a self-generation and memory recognition task, while monitoring the brain's and the pupil's
180 responses to sounds that were either presented passively or that coincided in time with a
181 motor act. The aim of this study was twofold: First, we aimed to clarify the role of the
182 neuromodulatory LC-NE system in the motor-driven modulation of auditory processing of
183 self-generated sounds. Based on previous work, we expected to replicate the sensory
184 suppression effects when sounds merely coincide with, rather than being predicted by the
185 action. Thus, we expected to observe typical self-generation effects at encoding (i.e.,
186 attenuated N1, P2, Tb responses and enhanced P3, Hórvath et al., 2012; SanMiguel et al.,
187 2013). Moreover, we hypothesized that these typical self-generation effects are related to
188 neuromodulatory processes, thus we expected them to correlate with increased pupil diameter
189 for motor-auditory events (McGinley et al., 2015; Yerba et al., 2019). Second, we sought out
190 to examine whether the differential sensory processing of stimuli paired with an action affects
191 their encoding in memory. To this end, we examined whether coincidence with an action at
192 encoding enhances or impairs memory recall at retrieval, and we hypothesized that the
193 potential differences in the memory encoding of sounds presented with or without a
194 concomitant action should be driven by, and thus correlate with, the differential
195 neurophysiological responses (i.e., event-related potentials and pupil diameter) at encoding
196 for sounds that were either paired with an action or not.

197 **2. Methods**

198 **2.1. Participants**

199 Twenty-six healthy, normal-hearing subjects, participated in the present study.
200 Participants were typically undergraduate university students at the University of Barcelona.
201 Data from three participants had to be excluded due to technical problems, inability to comply
202 with the task instructions, or excessive artifacts in the EEG recording, leaving data from
203 twenty-three participants (6 men, 17 women, $M_{age} = 24.82$, age range: 21-36). None of them
204 had any hearing impairments, suffered, or had suffered from psychiatric disorders or had
205 taken substances affecting the central nervous system the 48 hours prior to the experiment.
206 All participants gave written informed consent for their participation after the nature of the
207 study was explained to them and they were monetarily compensated (10 euros per hour).
208 Additional materials included a personal data questionnaire, a data protection document, and
209 five personality trait questionnaires. The study was accepted by the Bioethics Committee of
210 the University of Barcelona.

211

212 **2.2. General experimental design**

213 Each trial consisted of three phases: the encoding phase, the retention phase and the
214 retrieval phase.

215 *Encoding phase:* At the start of each trial, subjects were presented with a row of six
216 vertical lines on the screen, separated in semi-random distances from each other. The
217 positions of vertical lines were distributed based on the sequence presented in each trial.
218 During the whole duration of the encoding period (12 seconds), a horizontal line moved at a
219 stable pace across the screen from left to right, intersecting each of the vertical lines as it
220 advanced. Participants were asked to press a button every time the horizontal line reached
221 one of the vertical ones. Only half of these presses produced a sound (Motor-auditory event;
222 MA). The other half did not result in the presentation of a sound (Motor-only event; M).
223 Additionally, three more sounds were presented passively to the participants without being
224 triggered by a button press (Auditory-only event; A). Thus, in every trial, the encoding set
225 consisted of nine events, three motor-only (M) and six sounds (i.e., three of them triggered
226 by a button and the other three presented passively between presses; MA and A events,
227 respectively). The event-to-event onset asynchrony varied from 0.8 s to 2.4 s, in steps of 0.05

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228 s, while the sound-to-sound onset asynchrony varied between 1.6 and 2.4 seconds in steps of
229 0.05. Participants were asked to pay attention to all the sounds presented. The encoding phase
230 finished when the horizontal line had intersected all the vertical ones and arrived at the right
231 of the screen. If the task was performed correctly (i.e., all required button presses were
232 performed), the trial continued into the retention phase. Otherwise, an error message
233 appeared on the screen indicating that the participant did not press the button every time the
234 horizontal line reached a vertical one, and a new trial began.

235 *Retention phase:* During the subsequent retention phase, participants were presented with
236 a fixation cross on the screen for 3 s and they were asked to remember all the sounds that
237 were previously presented in the encoding phase.

238 *Retrieval phase:* In the retrieval phase, participants were presented with two sounds with
239 a 2 s sound-to-sound onset asynchrony (indicated by the visual stimuli “Sound 1” and “Sound
240 2”, respectively). Subsequently, a question appeared on the screen, prompting participants to
241 respond whether the first or the second test sound was presented during the encoding phase.
242 The response window was 2 seconds. After the end of the response window, a fixation was
243 presented for 2 seconds (inter-trial interval) before the start of the next trial.

244

245 **2.3. Stimuli**

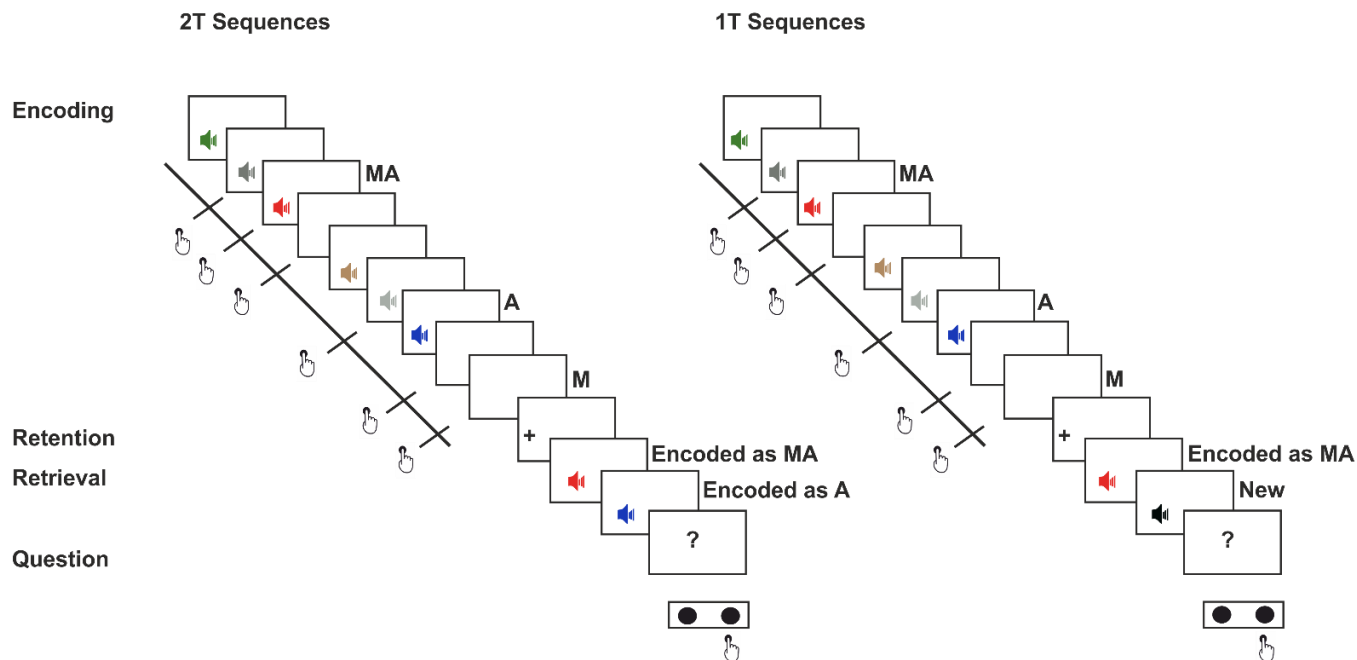
246 **2.3.1. Sequences**

247 Two types of sequences were created, differing in whether both or only one of the test
248 sounds presented at retrieval were also present during the encoding phase. In the “Two Test
249 Sounds at Encoding” (henceforth 2T; Figure 1) and unbeknownst to the participants, the two
250 test sounds presented passively at retrieval were also presented in the encoding sequence,
251 one as a motor-auditory (Encoded as MA) and the other one as an auditory-only event
252 (Encoded as A). In the “One Test Sound at Encoding” (henceforth, 1T; Figure 1), only one
253 of the test sounds at retrieval was presented at encoding, either as a MA (Encoded as MA) or
254 as an A event (Encoded as A), while the other sound was new (New sound). The 1T
255 sequences were introduced only for the behavioral data and were not used for the EEG and
256 pupillometry analyses. This design allowed us to have enough trials for Encoded as A and
257 Encoded as MA sounds at retrieval, keep the experiment’s duration within a reasonable time,
258 and obtain an additional objective measure of memory performance in the 1T sequences

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259 besides the measure of memory bias obtained in the 2T sequences. Five of the 1T sequences
260 were randomly chosen to be used during the practice block.

261



262

263 **Figure 1.** Schematic representation of the experimental design. Each trial consisted of three
264 phases (encoding, retention, retrieval). During the encoding phase, a horizontal line moved
265 at a stable pace across the screen from left to right, intersecting each of the six vertical lines
266 as it advanced. Participants were asked to press a button every time the horizontal line
267 reached one of the vertical ones. Only half of these presses produced a sound (Motor-
268 auditory; MA). The other half did not result in the presentation of a sound (Motor-only; M).
269 Additionally, three more sounds were presented passively to the participants without being
270 triggered by a button press (Auditory-only condition; A). The encoding phase finished when
271 the horizontal line had intersected all the vertical ones and arrived at the right of the screen.
272 During the subsequent retention phase, participants were presented with a fixation cross on
273 the screen for 3 s and they were asked to remember all the sounds that were previously
274 presented in the encoding phase. In the retrieval phase, we employed two types of sequences:
275 2T (left) and 1T (right) sequences. Participants were presented with two sounds separated by
276 a 2 s sound-to-sound onset asynchrony. In the 2T sequences, both sounds at retrieval were
277 presented also at encoding, one Encoded as A and the other Encoded as MA. In the 1T
278 sequences, only one of the two sounds was presented before, either Encoded as A or Encoded
279 as MA, while the other sound was new. After the presentation of the test sounds, a question
280 appeared on the screen, prompting participants to respond whether the first or the second test
281 sound was presented during the encoding phase. The response window was 2 s and the inter-
282 trial interval was set to 2 s.

283

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284 Importantly, the same sounds in the same encoding sequence positions were used as
285 either A or MA in different trials, which allowed us to compare between physically identical
286 auditory sequences that only differed in the actions performed. Additionally, we controlled
287 for the order of the sounds at encoding that would be later used as test at retrieval for the 2T
288 sequences, the order of the two retrieval sounds, and the position of the test sounds in the
289 encoding sequence counterbalancing it across trials. Specifically, related to the latter, we
290 discarded the first and last position of the encoding sequence for placing test sounds to avoid
291 primacy and recency effects, which refer to an improvement in memory retention for stimuli
292 that have been presented first or last in a list, respectively (Mondor & Morin, 2004).
293 However, we included 20 catch trials with test sounds in those positions, which were
294 randomly interleaved with the experimental sequences described above and discarded from
295 all analyses.

296

297 **2.3.2. Auditory stimuli**

298 For the main experiment, 255 different, environmental, natural, complex, and non-
299 identifiable sounds were gathered from the libraries of McDermott Sound Library
300 (<http://mcdermottlab.mit.edu/svnh/Natural-Sound/Stimuli.html>) and Adobe
301 (https://offers.adobe.com/en/na/audition/offers/audition_dlc.html). These sounds were then
302 edited to all have 250 ms of duration, a sampling rate of 44.1 kHz and to be played at 16 bits,
303 mono and with 50-55 dB of intensity. Subsequently, six volunteers that did not participate in
304 the main experiment rated the 255 sounds based on their identifiability (i.e., how easy it was
305 to assign a name to them). All sounds were presented to them in a randomized order and each
306 sound was presented twice. The volunteers rated them in a scale from 1-3 (1 = identifiable,
307 2 = not sure, 3 = not identifiable), and the mean score for each sound was calculated. The
308 108 less identifiable sounds were selected to construct the unique experimental sound
309 sequences. The sounds used in the practice block consisted of 35 pure tones of different
310 frequencies, ranging from 300 Hz to 3700 Hz in steps of 100.

311

312 **2.4. Apparatus**

313 The visual stimuli were presented on an ATI Radeon HD 2400 monitor. The auditory
314 stimuli were presented via the Sennheiser KD 380 PRO noise cancelling headphones. To

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315 record participants' button presses and behavioural responses, we used the Korg nanoPAD2.
316 The buttons of this device do not produce any mechanical noise when pressed, and, thus, do
317 not interfere with our auditory stimuli. The presentation of the stimuli and recording of
318 participants' button presses and responses were controlled using MATLAB R2017a (The
319 Mathworks Inc., 2017), the Psychophysics Toolbox extension (Brainard, 1997; Kleiner et al.,
320 2007; Pelli, 1997), and the Eyelink add-in toolbox for eyetracker control.

321 EEG activity was acquired with Neuroscan 4.4 software and Neuroscan SynAmps RT
322 amplifier (NeuroScan, Compumedics, Charlotte, NC, USA). We recorded continuously with
323 Ag/AgCl electrodes from 64 standard locations according to the 10% extension of the
324 International 10–20 system (Chatrian, Lettich, & Nelson, 1985; Oostenveld & Praamstra,
325 2001) mounted in a nylon cap (Quick-Cap; Compumedics, Charlotte, NC, USA). An
326 additional electrode was placed at the tip of the nose (serving as online reference). The
327 vertical electrooculogram (EOG) was measured with two electrodes placed above and below
328 the left eye, and the horizontal EOG with two electrodes placed on the outer canthi of the
329 eyes referenced to the common reference (unipolar montage). The ground electrode was
330 placed at AFz. All impedances were kept below 10 k Ω during the whole recording session
331 and data was sampled at 500 Hz.

332 Concurrently with the EEG recording, horizontal and vertical gaze position, as well as the
333 area of the pupil, were recorded using EyeLink 1000 desktop mount (SR Research, sampling
334 rate: 1,000 Hz; left eye recordings except for three participants for whom the right eye was
335 recorded instead). The pupil was assessed in the centroid mode of the eye tracker, which uses
336 a center-of-mass algorithm. This algorithm detects the pupil area by identifying the number
337 of black pixels and its center on the video image. Importantly, in contrast to methods using
338 ellipse fitting for the measurement of the pupil, this method is hardly affected by noise (S-R
339 Research Eyelink-CL Manual, p. 71).

340

341 **2.5. Procedure**

342 Prior to the start of the experiment, participants were asked to complete several
343 questionnaires. Subsequently, participants were seated in an electrically and acoustically
344 shielded room and were asked to place their head on a chinrest at approximately 60 cm from
345 the screen. Eyetracker calibration was performed first at the start of the experiment and then

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346 every six blocks. In order to familiarize themselves with the task, participants first completed
347 a practice block of 5 trials and repeated it as many times as they needed to make sure they
348 understood how to perform the task. During the main experiment, participants completed a
349 total of 236 trials: 56 1T trials, 160 2T trials and 20 catch trials. These were divided in 24
350 blocks, 20 of them comprised of 10 trials (9 experimental and 1 catch trial) and the remaining
351 4 comprised of 9 trials (all of them experimental trials). At the end of each block, a message
352 appeared informing participants about the number of errors (i.e., not pressing the button when
353 required) and extra-presses (i.e., more than the required button presses) at the encoding phase,
354 as well as the number of missed responses at retrieval for this block. Catch trials, as well as
355 trials including errors in button-pressing and missed responses were discarded from further
356 analyses. Participants took a break of approximately 5 minutes every six blocks to prevent
357 fatigue. The experiment lasted for approximately 1.5 hour excluding the EEG preparation.

358

359 **2.6. Data analysis**

360 **2.6.1. Behavioral analysis**

361 To test for differences in memory bias (2T sequences) and memory performance (1T
362 sequences) for sounds encoded as A or MA, we performed two different analyses. For the 1T
363 sequences, we calculated the percent correct for the sounds at retrieval (i.e., memory
364 performance), separately for those that were Encoded as MA and Encoded as A, which was
365 subsequently submitted to a two-sided paired sample *t*-test. For the 2T-trial sequences, we
366 calculated the percent recall for sounds Encoded as MA and Encoded as A and tested for
367 differences in memory bias, using a two-sided paired samples *t*-test. We complemented the
368 frequentist *t*-tests with corresponding Bayesian *t*-tests, separately for the 1T and 2T
369 sequences. For both Bayesian comparisons, the Bayes factor (BF_{10}) for the alternative
370 hypothesis (i.e., the difference of the means is not equal to zero) was calculated. Specifically,
371 the null hypothesis corresponded to a standardized effect size $\delta = 0$, and the alternative
372 hypothesis was defined as a Cauchy prior distribution centered around 0 with a scaling factor
373 of $r = 0.707$ (Rouder et al., 2012). In line with the Bayes Factor interpretation (Lee &
374 Wagenmakers, 2013) and with previous work reporting Bayes Factors (Korka et al., 2019;
375 Korka et al., 2020; Marzecová et al., 2018), data were taken as moderate evidence for the
376 alternative hypothesis if the BF_{10} was greater than 3, while values close to 1 were considered

377 only weakly informative. Values greater than 10 were considered strong evidence for the
378 alternative (or null) hypothesis.

379

380 **2.6.2. EEG preprocessing**

381 EEG data was analyzed with EEGLAB (Delorme & Makeig, 2004) and plotted with
382 EEProbe (ANT Neuro). Data were high-pass filtered (0.5 Hz high-pass, Kaiser window,
383 Kaiser β 5.653, filter order 1812), manually inspected so as to reject atypical artifacts and
384 identify malfunctioning electrodes, and corrected for eye movements with Independent
385 Component Analysis, using the compiled version of runica (binica) that uses the logistic
386 infomax ICA algorithm (Onton & Makeig, 2006). Components capturing eye movement
387 artifacts were rejected by visual inspection and the remaining components were then
388 projected back into electrode space. Data was then low-pass filtered (30 Hz low-pass, Kaiser
389 window, Kaiser β 5.653, filter order 1812), remaining artifacts were rejected by applying a
390 75 μ V maximal signal-change per epoch threshold, and malfunctioning electrodes were
391 interpolated (spherical interpolation). A -100 to $+500$ ms epoch was defined around each
392 event both at the encoding and the retrieval phase. The data was subsequently baseline
393 corrected (100 ms prior to the event). We calculated the average wave for each event of
394 interest, as well as the grand average for the whole sample. Specifically, we obtained the
395 averages for the MA, A, and M events at encoding, while for the retrieval data, we binned
396 the responses to motor-auditory and auditory-only sounds as a function of memory (i.e.,
397 Encoded as MA and Encoded as A at retrieval that were remembered or forgotten). For each
398 condition of interest the number of remaining trials used for the analyses after trial rejection
399 were: Auditory-only ($M = 424.9$, $SD = 46.9$), Motor-auditory ($M = 427.2$, $SD = 40.6$), Motor-
400 only ($M = 429$, $SD = 40.8$), Encoded as A and forgotten ($M = 68$, $SD = 11.7$), Encoded as A
401 and remembered ($M = 64$, $SD = 14.7$), Encoded as MA and forgotten ($M = 64.1$, $SD = 14.2$),
402 Encoded as MA and remembered ($M = 67.7$, $SD = 11.9$).

403 To assess self-generation effects at encoding, MA sound responses were corrected for
404 motor activity by subtracting the motor-only (M) averages from the motor-auditory (MA)
405 averages, since the signal obtained in the MA condition represents the brain signal elicited
406 by the sound, but also by the planning and execution of the finger movement to press the
407 button. We, therefore, obtained a motor-corrected wave that only included the brain signal

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408 elicited by the MA sound. Self-generation effects at encoding were then assessed by
409 comparing responses to MA sounds corrected for motor activity (MA–M) with the responses
410 elicited by the auditory-only sounds (A). Self-generation effects are presented in all figures
411 as the difference wave between the motor-auditory (corrected) sound responses and the
412 auditory-only sound responses (A–[MA–M]). No motor correction was performed at
413 retrieval since the Encoded as MA sounds were presented passively.

414

415 **2.6.3. ERP analysis**

416 For all the effects of interest at encoding, we examined responses separately for the N1
417 and P2 at Cz (N1, P2) and at the mastoids (henceforth, N1_{mast}, P2_{mast}), the P3 component at
418 Pz, and the N1 subcomponents Na and Tb at T7 and T8. The same components except for P3
419 were examined at retrieval. The windows were defined after visual inspection of the data by
420 locating the highest negative or positive (depending on the component of interest) peak in
421 the usual latencies for each component as reported by previous work (SanMiguel et al., 2013).
422 Specifically, time windows for N1 (and N1_{mast}), P2 (and P2_{mast}), Na, and Tb were defined on
423 the grand-averaged waveforms of the auditory-only sounds as previously reported (e.g.,
424 SanMiguel et al., 2013). Na and Tb were identified as the first and second negative peaks,
425 respectively, identifiable after sound onset on electrodes T7 and T8, as recommended by
426 Tonnquist-Uhlen et al. (2003). N1/N1_{mast} and P2/P2_{mast} were identified as the negative and
427 positive peaks occurring in the window ~70 to 150 ms, and ~150 to 250 ms after stimulus
428 onset on Cz, respectively, showing reversed polarity at the mastoid electrodes. P3 at encoding
429 was identified as the peak of the difference wave (A – [MA–M]) in the P3 window range
430 based on previous work (e.g., Baess et al., 2008). The time windows for the N1/N1_{mast},
431 P2/P2_{mast}, P3, Na, and Tb peaks were centered on the identified peaks ± 13, 25, 15, 10, and
432 15 ms, respectively. For the encoding data, we performed paired samples *t*-tests with the
433 factor Sound Type (A vs. MA) to test for differences in N1, P2 and P3, and a repeated
434 measures ANOVA with factors Sound Type (A vs. MA) x Laterality (M1 vs. M2 or T7 vs.
435 T8) to test for differences in N1_{mast}, P2_{mast} and Na, Tb, respectively. For the retrieval data we
436 performed 2x2 ANOVAs with the factors Sound Type (Encoded as A vs. Encoded as MA)
437 and Memory (Remembered vs. Forgotten) on N1 and P2, while for the N1_{mast}, P2_{mast}, Na, and

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438 Tb an additional factor Laterality was introduced in the ANOVAs (i.e., M1 vs. M2 or T7 vs.
439 T8).

440

441 **2.6.4. Pupillometry analysis**

442 Missing data and blinks, as detected by the EyeLink software, were padded by 100 ms and
443 linearly interpolated. Additional blinks were found using peak detection on the velocity of
444 the pupil signal and linearly interpolated (Urai et al., 2017). Blinks separated by less than 250
445 ms were aggregated to a single blink. The interpolated pupil time series were bandpass
446 filtered using a 0.05–4 Hz third-order Butterworth filter. Low-pass filtering reduces
447 measurement noise not likely to originate from physiological sources, as the pupil functions
448 as a low-pass filter on fast inputs (Binda et al., 2013; Hoeks & Levelt, 1993). High-pass
449 filtering removes slow drifts from the signal that are not accounted for by the model in the
450 subsequent deconvolution analysis. First, we estimated the effect of blinks and saccades on
451 the pupil response through deconvolution and removed these responses from the data using
452 linear regression using a procedure detailed in previous work (Knapen et al., 2010; Urai et
453 al., 2017). The residual bandpass filtered pupil time series was used for the evoked analyses
454 (van Slooten et al., 2018). After zscoring per trial, we epoched trials (epoching window -0.5
455 to 1.5 post-event), baseline corrected each trial by subtracting the mean pupil diameter
456 500 ms before onset of the event and resampled to 100 Hz.

457 For each participant, we first obtained the average evoked response for the main events of
458 interest. Specifically, we obtained the averages for the A and MA events at encoding, while
459 at retrieval we obtained the averages for the Encoded as A and Encoded as MA sounds,
460 separately for the remembered and the forgotten ones. We used non-parametric permutation
461 statistics to test for the group-level significance of the individual averages, separately for
462 encoding and retrieval. Specifically, we computed t values of the difference between the two
463 conditions of interest and thresholded these t values at a p value of 0.05. Each cluster was
464 constituted by the samples that passed the threshold of the p value. The cluster statistics was
465 chosen as the sum of the paired t -values of all the samples in the cluster. First, we compared
466 the pupil response to motor-auditory and auditory-only events at encoding. For the retrieval
467 data, we aimed to test for possible main effects of Sound Type (Encoded as A vs. Encoded
468 as MA) and Memory (Remembered vs. Forgotten), as well as for possible interactions

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469 between the two. For the main effects of Sound Type and Memory at retrieval, the
470 permutation statistics were performed between Encoded as A and Encoded as MA sounds
471 (irrespective of their memory) and between Remembered and Forgotten sounds (irrespective
472 of how they were encoded before), respectively. To test for possible interactions, the cluster-
473 permutation test was performed on the difference waves ([Encoded as A and remembered –
474 Encoded as MA and remembered] and [Encoded as A and forgotten – Encoded as MA and
475 forgotten]). For each statistical test, this procedure was performed by randomly switching
476 labels of individual observations between these paired sets of values. We repeated this
477 procedure 10,000 times and computed the difference between the group means on each
478 permutation. The obtained p value was the fraction of permutations that exceeded the
479 observed difference between the means (i.e., two-sided dependent samples tests). The pupil
480 preprocessing and analysis was performed with custom software based on previous work
481 (Urai et al., 2017) using Fieldtrip (Oostenveld et al., 2011).

482

483 **2.6.5. Correlations**

484 Finally, we hypothesized that the electrophysiological and neuromodulatory effects at
485 encoding (i.e., sensory suppression and pupil dilation for MA events) might be driving any
486 memory encoding differences between A and MA sounds, and that neuromodulation might
487 be behind the suppression of ERP responses to MA sounds. To assess these relationships, we
488 tested for possible correlations between the behavioural, electrophysiological and
489 neuromodulatory (i.e., pupil diameter) effects of actions. Only those differences between MA
490 and A events that were found to be significant in the previous analyses were introduced in
491 the correlation analyses. For all the behavioural and the electrophysiological effects, we first
492 calculated the difference by subtracting the MA from A values (i.e., difference in memory
493 and ERP amplitude for each component of interest between A and MA). Regarding the ERPs
494 identified in two electrodes (e.g., Na, Tb, N1_{mast}, P2_{mast}), we calculated the mean amplitude
495 across the two (T7/T8 and M1/M2, respectively). For the pupil data, we used the peak of the
496 difference wave between A and MA events at encoding. We then submitted these values to
497 a Pearson correlation coefficient to test for correlations between a) the effects on ERPs at
498 encoding and memory performance/bias (1T and 2T sequences, respectively), b) the
499 neuromodulatory effects at encoding and memory performance/bias (1T and 2T sequences,

500 respectively), and c) the effects on the ERPs and the neuromodulatory effects at encoding. In
501 all correlations, for the ERPs, the larger the attenuation effects for the negative (N1, P2_{mast},
502 Na, Tb) and positive (N1_{mast}, P2, P3) components, the more negative and positive the values,
503 respectively. Conversely, for the pupil and the behavioural data, the more negative the value,
504 the larger the pupil diameter and the worse the memory performance for MA sounds.

505

506 **3. Results**

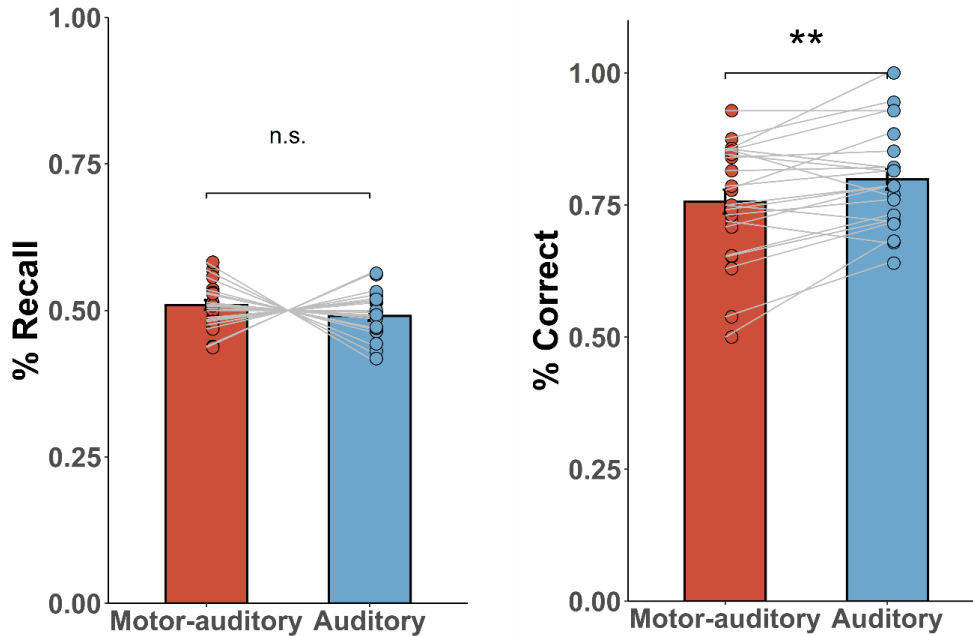
507 All statistical analyses were performed using R (version 3.6.0). For all the *t*-tests
508 performed, we first confirmed that the assumption of normality was not violated (Shapiro–
509 Wilk normality test $p > .05$).

510

511 **3.1. Behavioural performance**

512 For the analysis of the behavioural data, we calculated the percent correct (i.e., memory
513 performance in the 1T sequences) and the percent recall (memory bias in the 2T sequences)
514 for sounds that were encoded as motor-auditory or auditory-only (see Figure 2). For the 1T
515 sequences, we obtained significantly better memory performance for sounds that were
516 encoded as auditory-only compared to those that coincided with participants' motor acts in
517 the previous encoding phase, $t(22) = 3.15$, $p = .005$, $d = 0.66$ ($M_{MA} = .757$, $M_A = .799$, SD_{MA}
518 $= .108$, $SD_A = .0924$). This difference, however, was not reflected in memory bias since we
519 did not find significant differences between the Encoded as A and Encoded as MA sounds in
520 the 2T sequences, where both of the test sounds were presented at encoding, $t(22) = 1.14$, p
521 $= .267$ ($M_{MA} = .509$, $M_A = .491$, $SD_{MA} = .0395$, $SD_A = .0395$). The absence of significant
522 differences in memory bias may suggest that they remembered both sounds as evident by the
523 generally high accuracy (i.e., mean performance in the 1T sequences = 0.78 with standard
524 deviation of 0.1) which led them to choose randomly between A and MA sounds in 2T
525 sequences. We complemented the frequentist *t*-tests with corresponding Bayesian *t*-tests,
526 separately for memory performance (1T sequences) and memory bias (2T sequences). The
527 Bayesian *t*-tests for the 1T and 2T sequences yielded similar results as the ones obtained from
528 the frequentist *t*-tests. Specifically, this analysis brought strong evidence for the alternative
529 hypothesis in the case of 1T sequences ($BF_{10} = 9.375$), while the Bayesian *t*-test for the 2T
530 sequences, brought weak evidence for the alternative hypothesis ($BF_{10} = 0.389$).

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531

532 **Figure 2.** Summary of the behavioural results, separately for memory bias in the 2T
533 sequences (left) and memory performance in the 1T sequences (right). Error bars depict
534 standard error of the mean. For memory bias (i.e., percent recall in 2T sequences), there were
535 no significant differences between motor-auditory and auditory-only sounds (two-tailed
536 paired samples t-test, $p > .050$, $M_{MA} = .509$, $M_A = .491$, $SD_{MA} = .0395$, $SD_A = .0395$), in line
537 with the Bayesian analysis that provided weak evidence for the alternative hypothesis
538 ($BF_{10} = 0.389$). For memory performance (i.e., percent correct in 1T sequences), there was a
539 significant difference between motor-auditory and auditory-only sounds (two-tailed paired
540 samples t-test, $t(22) = 3.15$, $p = .005$, $d = 0.66$), with higher accuracy for the latter ($M_{MA} =$
541 $.757$, $M_A = .799$, $SD_{MA} = .108$, $SD_A = .0924$), which was also supported by the Bayesian
542 analysis that brought strong evidence in favor of the alternative hypothesis ($BF_{10} = 9.375$).

543

544

545 3.2. Electrophysiological responses at encoding

546 Figure 3a shows all the studied peaks identified on the passive sound responses for the
547 encoding conditions at the relevant electrodes for each peak. The motor-auditory sounds at
548 encoding were motor corrected (see Methods). The time windows defined for each peak were
549 the following: Na 72–92 ms, Tb 120–150 ms, N1/N1_{mast} 94–120 ms, P2/ P2_{mast} 174–224 ms,
550 P3 256–286.

551 First, we performed a one-sided t -test to test for possible differences in N1 amplitude
552 between A and MA sounds at encoding, with the hypothesis of attenuated responses for the
553 latter. Indeed, we obtained a significant attenuation for the N1, $t(22) = -1.89$, $p = .036$, $d = -$
554 0.39 , with lower amplitudes for sounds that coincided with a motor act, compared to those

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555 that were passively presented to the participants (Figure 3a-b, see Table 1 for all the mean
 556 amplitudes per condition). We also tested for differences in N1 (with reversed polarity) at
 557 the mastoids (N1_{mast}) using a repeated measures ANOVA with factors Sound Type (MA vs.
 558 A) and Laterality (M1 vs. M2). We obtained a significant enhancement for the MA sounds
 559 $F(1, 22) = 15.68, p < .001, \eta_p^2 = .42$, suggesting that besides the attenuation for MA sounds
 560 observed at vertex, further modulatory effects of sound-action coincidence occur (Figure 3).
 561 We also found a significant main effect of Laterality, $F(1, 22) = 5.96, p = .023, \eta_p^2 = .21$, with
 562 lower amplitudes at M1 compared to M2, while the interaction between Sound Type and
 563 Laterality did not reach significance, $F(1, 22) = 3.55, p = .073$.

564

565 **Table 1.** Mean amplitudes and standard deviation per component and condition across 23
 566 participants.

Components	Electrodes	Auditory-only		Motor-auditory		Encoded as		Encoded as		Encoded as		Encoded as A	
		(A)	(MA)	(MA)	(MA)	MA and	MA and	A and	and	forgotten	remembered	forgotten	remembered
N1	Cz	-3.14	1.79	-2.66	1.98	-3.89	2.01	-4.51	2.28	-4.13	2.45	-4.19	2.22
P2	Cz	4.95	2.49	3.83	2.01	7.16	4.38	7.37	3.51	7.33	3.96	7.76	4.25
P3	Pz	-0.08	1.29	1.49	1.43	-	-	-	-	-	-	-	-
N1 _{mast}	M1	0.26	0.87	0.67	0.84	0.51	1.33	0.27	1.02	0.59	0.95	0.53	1.29
	M2	0.43	0.99	1.03	0.98	0.65	1.12	0.61	1.41	0.83	1.38	0.86	1.33
P2 _{mast}	M1	-0.75	0.79	-0.19	0.81	-1.88	1.51	-2.53	1.71	-2.03	1.32	-2.24	1.42
	M2	-0.56	1.01	0.05	0.87	-2.24	1.43	-2.63	1.64	-2.18	1.57	-2.45	1.55
Na	T7	-0.89	0.94	-0.97	1.18	-1.23	1.37	-1.48	1.19	-1.11	1.02	-0.86	1.09
	T8	-0.47	0.76	-0.45	1.03	-0.89	1.36	-1.21	1.30	-0.82	1.68	-0.59	1.12
Tb	T7	-1.91	1.01	-1.75	1.12	-2.89	1.73	-3.26	1.94	-2.97	1.66	-2.34	1.53
	T8	-2.18	1.40	-1.54	1.56	-3.68	2.25	-3.62	1.94	-3.40	2.19	-2.81	1.63

567

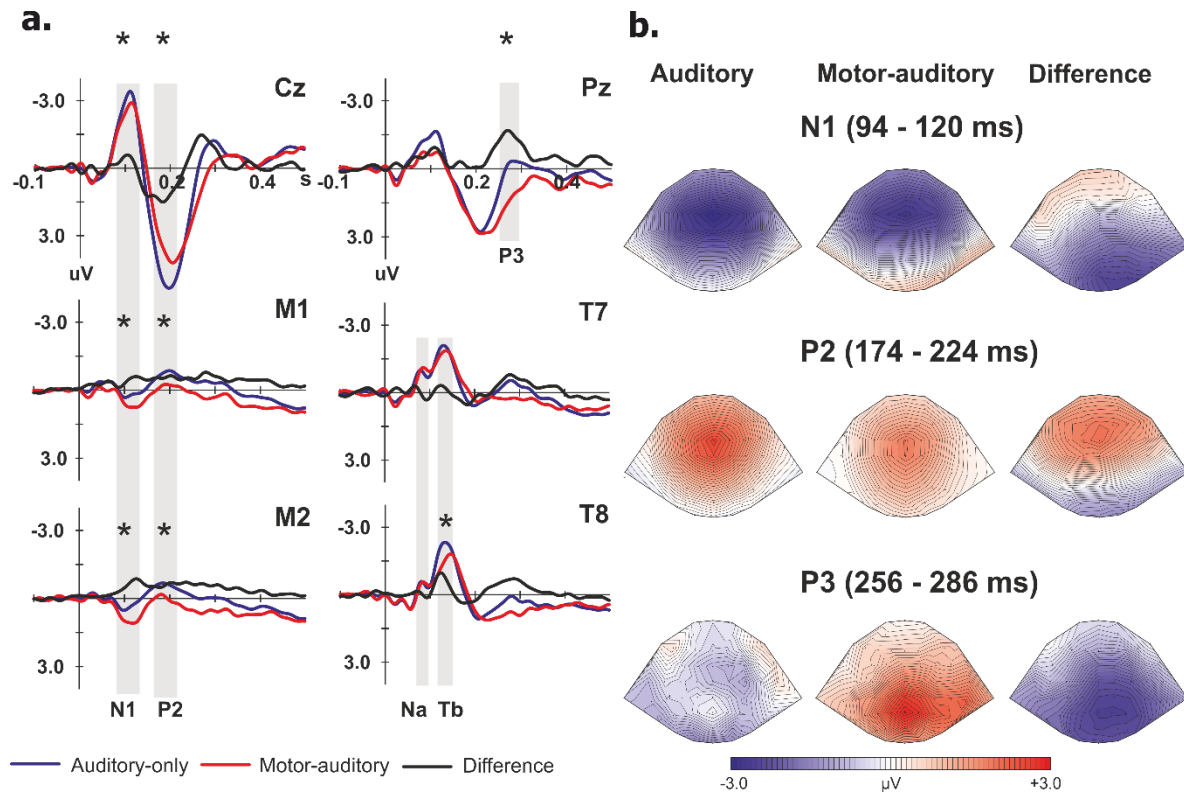
568 Next, we examined the attenuation effects at the N1 subcomponents at temporal sites,
 569 using a 2x2 ANOVA, with factors Sound Type (A vs. MA) and Laterality (T7 vs. T8) on
 570 Na and Tb (Figure 3a). For Na, only a significant main effect of Laterality was obtained,
 571 with lower amplitudes at T8 compared to T7, $F(1, 22) = 4.82, p = .039, \eta_p^2 = .18$, while the
 572 main effect of Sound Type and the interaction did not reach significance, $F(1, 22) = 0.05, p$

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573 = .828 and $F(1, 22) = 0.35$, $p = .563$, respectively. For Tb, however, we obtained
574 significantly lower amplitudes for sounds coinciding with a motor act compared to the
575 auditory-only ones, $F(1, 22) = 9.03$, $p = .007$, $\eta_p^2 = .29$, while the main effect of Laterality
576 did not reach significance, $F(1, 22) = 0.03$, $p = .871$. However, we also found a significant
577 interaction, $F(1, 22) = 8.63$, $p = .008$, $\eta_p^2 = .28$, reflecting that the attenuation for MA
578 sounds was only significant in T8 but not in T7 (post-hoc t-tests, $t(22) = -4.06$, $p < .001$, $d =$
579 -0.85 and $t(22) = -1.04$, $p = .311$, respectively).

580 Subsequently, we performed a one-sided *t*-test to test for possible differences in P2
581 amplitudes between A and MA sounds at encoding, with the hypothesis of attenuated
582 responses for the latter. We obtained a significant P2 attenuation at Cz, $t(22) = 3.98$, $p <$
583 $.001$, $d = 0.83$, with lower amplitudes for sounds that coincided with a motor act, compared
584 to those that were passively presented to the participants (Figure 3a-b). We also tested for
585 differences in this component (with reversed polarity) at the mastoids (P2_{mast}) using a
586 repeated measures ANOVA with factors Sound Type (MA vs. A) and Laterality (M1 vs.
587 M2). We observed a significant attenuation for the MA sounds, replicating the attenuation
588 observed at Cz, $F(1, 22) = 34.23$, $p < .001$, $\eta_p^2 = .61$, as well as a main effect of Laterality,
589 $F(1, 22) = 4.66$, $p = .042$, $\eta_p^2 = .17$, with more negative amplitudes at M1 compared to M2.
590 The interaction of Sound Type and Laterality on P2_{mast} did not reach significance, $F(1, 22)$
591 $= 0.54$, $p = .470$. Finally, we also tested for differences in P3 at Pz, which yielded a
592 significantly larger P3 amplitude for sounds coinciding with a motor act, $t(22) = -6.57$, $p <$
593 $.001$, $d = -1.37$ (Figure 3).

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594

595 **Figure 3. a)** Group-average event-related potentials across 23 participants for the corrected
 596 motor-auditory (red) and auditory-only (blue), analyzed in the corresponding electrodes.
 597 Difference waves (A-[MA-M]) depicting the self-generation effects are represented in
 598 black. Time windows used for the analyses are indicated in gray (Na: 72–92 ms, Tb: 120–
 599 150 ms, N1: 94–120 ms, P2: 174–224 ms, P3: 256–286 ms). Significant differences in the
 600 event-related potentials are indicated by asterisks. **b)** N1, P2, and P3 scalp topographies in
 601 the time windows for: (1) the auditory-only condition (left); (2) the corrected motor-auditory
 602 condition (middle); and (3) the (A-[MA-M]) difference waves, reflecting suppression (N1,
 603 P2) and enhancement (P3) effects.

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3.3. Electrophysiological responses at retrieval

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Next, we subdivided the retrieval data depending on whether the sound was encoded as A or MA and whether this sound was recalled or not and we assessed whether auditory evoked responses were affected by how the sound was encoded and whether it was remembered or forgotten. To this end, we ran an ANOVA with Sound Type (Encoded as MA vs. Encoded as A) and Memory (Remembered vs. Forgotten) as within-subject factors on N1/N1_{mast}, P2/P2_{mast}, Na, and Tb. An electrode factor (Laterality) was included in the ANOVA for the components identified in the mastoids and temporal electrodes. Figure 4 shows all the studied peaks for the remembered (a) and the forgotten (b) sounds at retrieval in the time windows

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615 72–92 ms, 120–150 ms, 94–120 ms, 174–224 ms, for the Na, Tb, N1/N1_{mast}, and P2/P2_{mast},
616 respectively at the relevant electrodes for each peak.

617 We did not observe any significant effects (all $ps > .05$) on the N1 at Cz and N1_{mast}.
618 However, significant results were obtained when we analyzed the modulatory effects of
619 Sound Type and Memory on the N1 subcomponents at temporal sites. We obtained a
620 significant main effect of Sound Type on Na, $F(1, 22) = 7.39, p = .013, \eta_p^2 = .25$, and Tb,
621 $F(1, 22) = 7.28, p = .013, \eta_p^2 = .25$, reflecting an enhanced amplitude for sounds that were
622 previously encoded as MA. Additionally, we found a significant interaction between Sound
623 Type and Memory on Na, $F(1, 22) = 5.08, p = .035, \eta_p^2 = .19$, where post-hoc comparisons
624 showed significantly larger Na amplitude for sounds that were Encoded as MA and were
625 remembered compared to sounds that were Encoded as A and were remembered, $t(45) =$
626 $3.73, p < .001, d = 0.55$. In contrast, the post-hoc comparisons did not show significant
627 differences for forgotten sounds as a function of how they were encoded, $t(45) = 0.67, p =$
628 $.504$. No significant differences were found between remembered and forgotten sounds that
629 were Encoded as A, $t(45) = -1.34, p = .187$, or between remembered and forgotten sounds
630 that were Encoded as MA, $t(45) = 1.64, p = .109$. Similarly, we obtained a significant
631 interaction between Sound Type and Memory on Tb, $F(1, 22) = 4.85, p = .038, \eta_p^2 = .18$.
632 Post-hoc comparisons showed significantly larger Tb amplitude for sounds that were
633 Encoded as MA and were remembered compared to sounds that were Encoded as A and were
634 remembered, $t(45) = 4.31, p < .001, d = 0.64$, which is in line with the differences we obtained
635 in the Na window. The post-hoc comparisons also showed lower Tb amplitudes for the
636 Encoded as A sounds when they were remembered compared to when they were forgotten,
637 $t(45) = -3.23, p = .002, d = -0.48$. Nevertheless, no significant differences were observed
638 between remembered and forgotten sounds that were encoded as MA, $t(45) = 0.64, p = .523$,
639 or between the Encoded as MA and Encoded as A sounds that were forgotten, $t(45) = 0.47,$
640 $p = .640$. For both Na and Tb, we did not observe any significant main effects of Laterality,
641 nor any significant interactions between Laterality and Sound Type and/or Memory (all $ps >$
642 0.05). Finally, we did not observe any significant effects on P2 at Cz and P2_{mast} (all $ps > .05$),
643 except for a significant main effect of Memory on P2_{mast}, $F(1, 22) = 7.65, p = .011, \eta_p^2 = .26$,
644 that showed lower amplitudes for sounds that were forgotten ($M_{Forgotten} = -2.08, M_{Remembered}$
645 $= -2.46, SD_{Forgotten} = 1.44, SD_{Remembered} = 1.56$).

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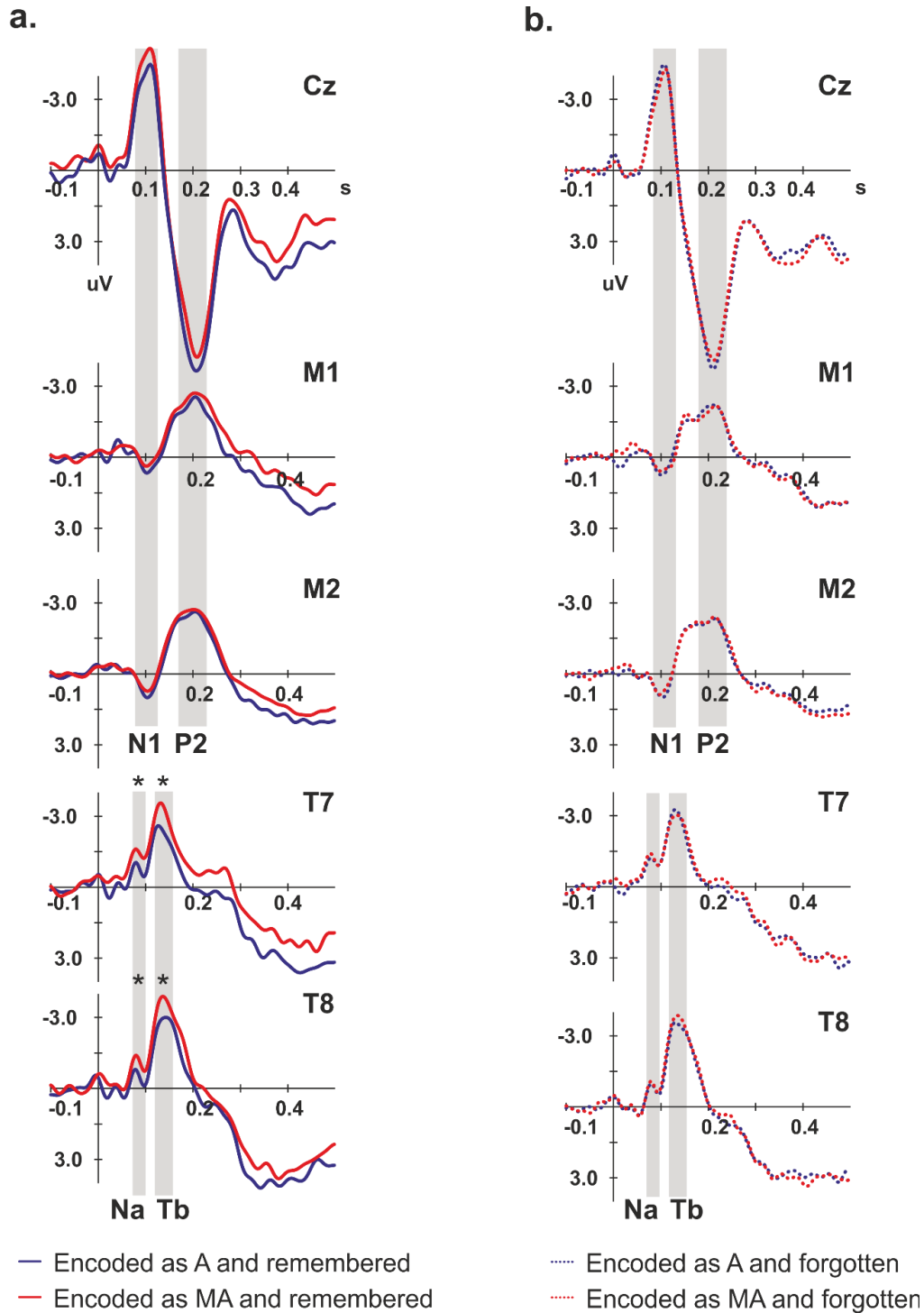
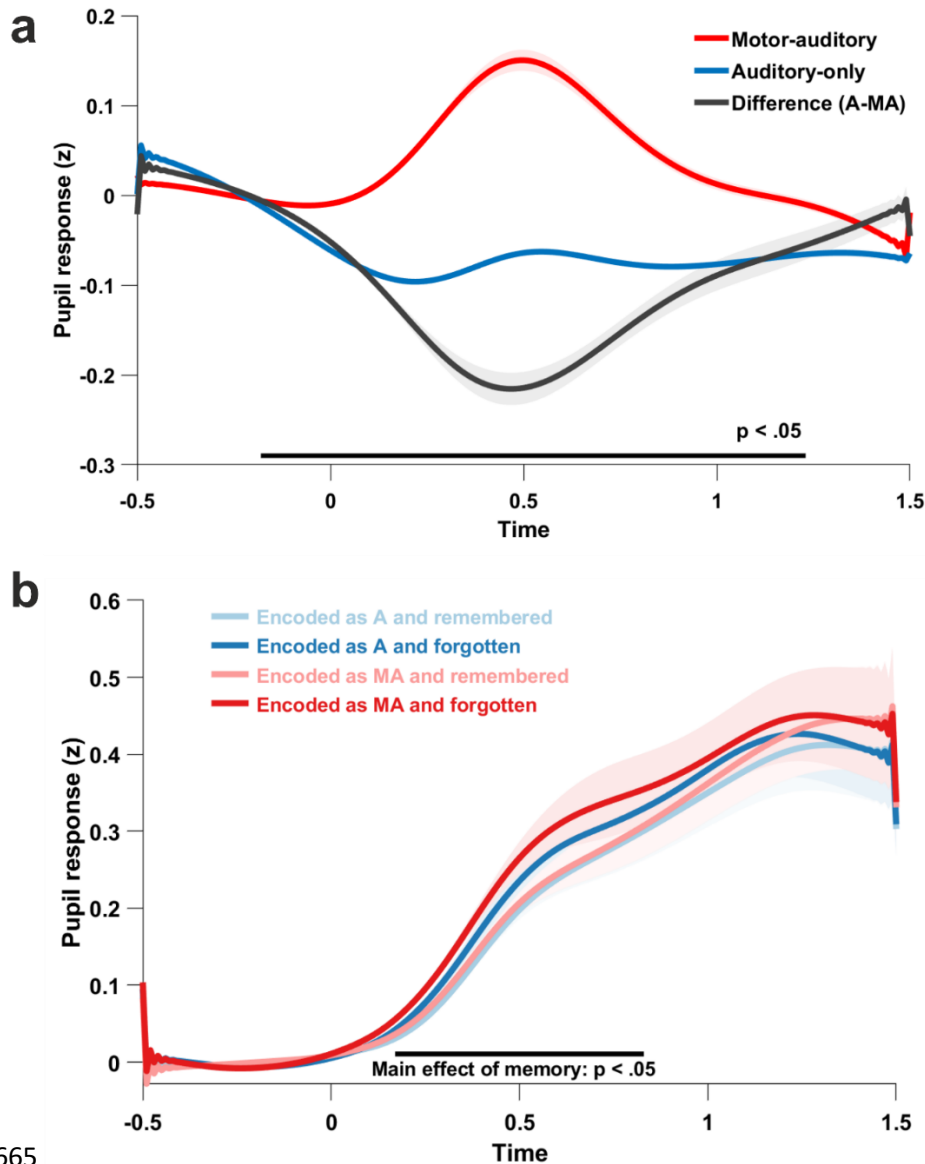


Figure 4. Group-average event-related potentials across 23 participants for the Encoded as MA (red) and Encoded as A (blue), analyzed in the corresponding electrodes and presented separately for the remembered (left) and the forgotten sounds (right). Time windows used for the analyses are indicated in gray (Na: 72–92 ms, Tb: 120–150 ms, N1: 94–120 ms, P2: 174–224 ms). Significant differences in the event-related potentials are indicated by asterisks.

652 **3.3. Pupil responses at encoding and retrieval**

653 Cluster-based permutation statistics were used to test for possible differences in pupil
654 diameter between the conditions of interest. First, we tested for differences in the pupil
655 response between motor-auditory and auditory-only events at encoding and we obtained
656 significantly larger pupil diameter for motor-auditory events (starting 180 ms before sound
657 onset and lasting up to 1,230 ms after sound onset; $p < .05$; Figure 5a) in line with previous
658 animal work (e.g., McGinley et al., 2015). Subsequently, we tested for possible main effects
659 of Sound Type (Encoded as A vs. Encoded as MA) and Memory (Remembered vs.
660 Forgotten), as well as for interactions between Sound Type and Memory on the pupil
661 responses at retrieval. This analysis showed only a significant main effect of Memory, with
662 larger diameter for forgotten sounds at retrieval compared to the remembered ones,
663 irrespective of how they were encoded (starting 170 ms after sound onset and lasting until
664 830 ms after sound onset ($p < .05$; Figure 5b).

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665

666 **Figure 5. a)** The group-average evoked pupil responses to auditory-only (blue) and motor-
667 auditory (red) events. The effect is depicted as the difference between auditory-only and
668 motor-auditory events (black). Black bar indicates a significant Auditory-only vs. Motor-
669 auditory effect in the window 180 pre-stimulus to 1,230 ms post-stimulus, $p < .05$ (cluster-
670 based permutation test). **b)** The group-average evoked pupil responses to encoded as auditory
671 (A) and encoded as motor-auditory (MA), separately for the remembered and forgotten
672 sounds. Black bar indicates a significant main effect of memory for Remembered vs.
673 Forgotten sounds in the window 170 – 830 ms post-stimulus, $p < .05$ (cluster-based
674 permutation test).

675 **3.4. Correlations**

676 Next, we tested for possible correlations between the behavioural performance,
 677 pupillometric and electrophysiological data. For the correlation analyses, we focused on the
 678 significant neurophysiological effects at encoding (i.e., ERPs and pupil diameter) and the
 679 significant behavioural effect on memory performance. The effects were introduced in the
 680 correlation analyses as the difference between A and MA events (see Methods). For the
 681 components identified in two electrodes, we calculated the mean amplitude across the two,
 682 except for the Tb at encoding, where we introduced only the amplitudes at T8 given the
 683 significant interaction between Sound Type and Laterality that showed that attenuation was
 684 lateralized. For the pupil data, we calculated the peak of the difference wave (A – MA) within
 685 the window of significance (180 ms pre-stimulus until 1,230 ms post-stimulus). All the
 686 planned correlations are reported in Table 2.

687

688 **Table 2.** Correlations between the significant self-generation effects. a) electrophysiological
 689 effects at encoding (N1, P2, N1_{mast}, P2_{mast}, P3, and Tb amplitudes) and memory performance
 690 (1T sequences), b) neuromodulatory effects at encoding (pupil diameter) and memory
 691 performance (1T sequences), c) electrophysiological (N1, P2, N1_{mast}, P2_{mast}, P3, and Tb
 692 amplitudes) and neuromodulatory (pupil diameter) effects at encoding.

693

<i>Correlations between</i>		<i>r</i>	<i>p</i>
(a) Memory performance (1T sequences)	N1	-0.43	0.041 *
	Tb (at T8 only)	-0.55	0.007**
	P2	-0.19	0.383
	N1 _{mast}	-0.41	0.055
	P2 _{mast}	-0.10	0.657
	P3	-0.35	0.098
(b) Memory performance (1T sequences)	Pupil diameter	0.46	0.029*
(c) Pupil diameter	N1	-0.36	0.091
	Tb (at T8 only)	-0.25	0.251
	P2	0.27	0.209
	N1 _{mast}	-0.23	0.291
	P2 _{mast}	-0.16	0.507
	P3	-0.08	0.702

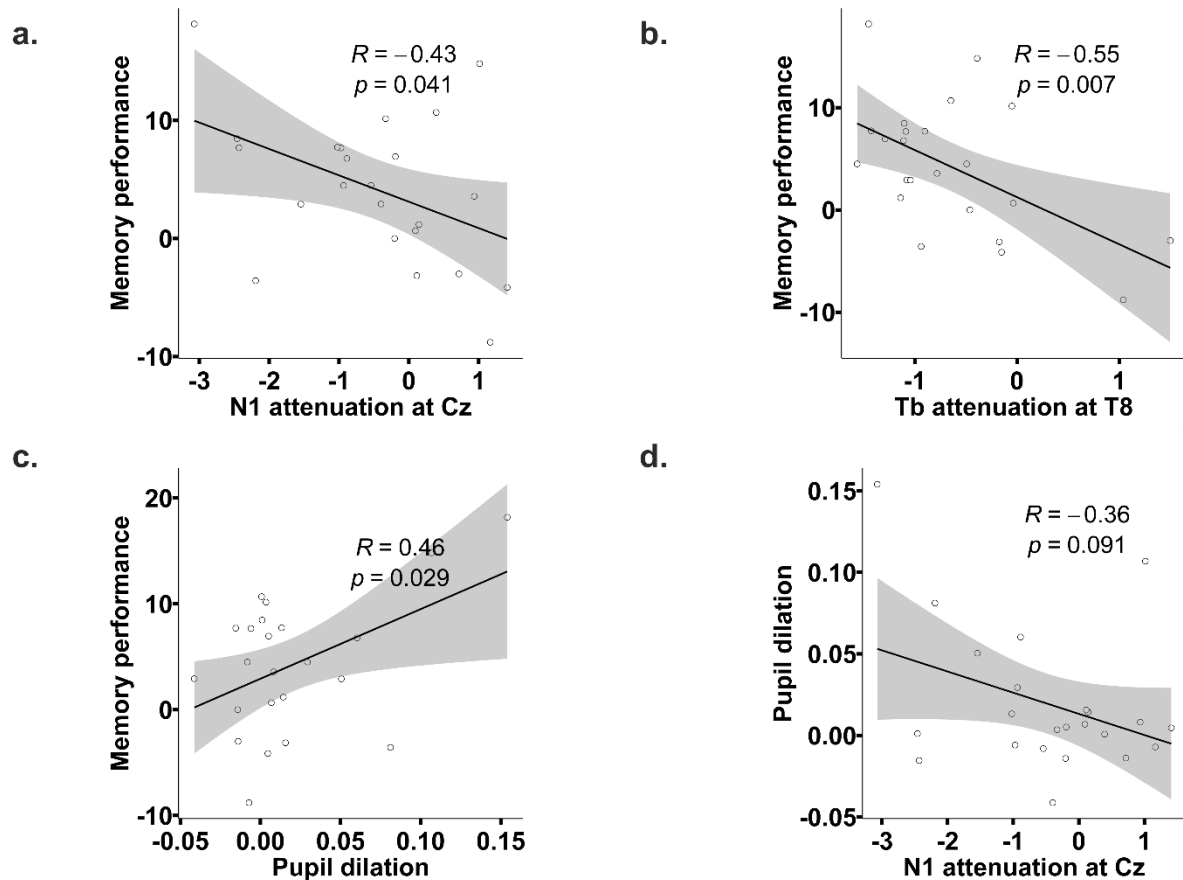
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695 First, we tested whether the significant self-generation effects at encoding (on N1, P2,
696 N1_{mast}, P2_{mast}, P3, and Tb amplitudes) correlated with the significant self-generation effects
697 on memory performance (1T sequences). This analysis showed a negative correlation
698 between N1 suppression and memory performance ($r = -0.43$, $p = .041$; Figure 6a), and a
699 negative correlation between Tb suppression (at T8) and memory performance ($r = -0.55$, p
700 $= .007$; Figure 6b), that is, the larger the N1 and Tb suppression, the greater the memory
701 impairment for motor-auditory compared to auditory-only sounds. The remaining
702 correlations did not reach significance (all $ps > .05$). Second, we assessed whether the
703 difference in pupil diameter between auditory-only and motor-auditory events was related to
704 memory performance and we obtained a significant positive correlation between the two (r
705 $= 0.46$, $p = 0.029$; Figure 6c), that is, the larger the pupil dilation for the motor-auditory
706 events, the greater the memory impairment for these sounds. Third, we tested for possible
707 links between the self-generation effects obtained in the ERP analyses (i.e., N1, P2, N1_{mast},
708 P2_{mast}, P3 and Tb) and the larger pupil diameter for motor-auditory events. None of these
709 correlations reached significance (all $ps > .05$), but we observed a non-significant trend
710 towards a correlation between N1 attenuation at Cz and pupil dilation for MA events (Figure
711 6d).

712 Finally, we performed an exploratory correlation analysis to test whether the significant
713 differences in sensory processing we obtained at retrieval between Encoded as A and
714 Encoded as MA sounds were related to the magnitude of the self-generation effects at
715 encoding. To this end, we performed a correlation analysis between the A – MA difference
716 in peaks of the Na and Tb amplitudes (only for the remembered sounds due to the significant
717 interaction) and the effects at encoding (for the N1, P2, N1_{mast}, P2_{mast}, P3, and Tb amplitudes).
718 We obtained a significant positive correlation between the P2 suppression at encoding and
719 the Na enhancement at retrieval for the remembered sounds, reflecting that the larger the
720 attenuation for P2 at encoding, the larger the Na enhancement for the Encoded as MA sounds
721 that were remembered at retrieval ($r = 0.51$, $p = .012$). Similarly, we also obtained a
722 significant negative correlation between Tb at encoding (at T8) and Na for the remembered
723 sounds at retrieval ($r = -0.42$, $p = .04$), showing that the larger the attenuation for Tb at
724 encoding, the greater the Na enhancement for motor-auditory sounds that were remembered
725 at retrieval.

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726

727 **Figure 6.** Planned correlations between the behavioural, electrophysiological, and pupil data
728 using the Pearson correlation coefficient. **a-b)** Significant negative correlations between N1
729 suppression (at Cz) and memory performance ($r = -0.43$, $p = .041$), and Tb suppression (at
730 T8) and memory performance ($r = -0.55$, $p = .007$), showing that the larger the N1 and Tb
731 suppression, the greater the memory impairment for motor-auditory compared to the
732 auditory-only sounds. More negative values indicate larger suppression effects for N1 and
733 Tb and worse memory performance for motor-auditory sounds. **c)** Significant positive
734 correlation between pupil dilation and memory performance ($r = 0.46$, $p = 0.029$), that is, the
735 larger the pupil dilation for the motor-auditory events, the greater the memory impairment
736 for these sounds. **d)** The correlation between N1 attenuation at Cz and pupil dilation at
737 encoding for the MA events did not reach significance ($r = -0.36$, $p = 0.091$). The shaded
738 gray areas represent the confidence interval (95% confidence level).

739 **4. Discussion**

740 In this study, we assessed the effects of motor actions on sensory processing and memory
741 encoding of concomitant, but unpredictable sounds, by employing a combination of a self-
742 generation and memory recognition task, while monitoring the brain's and the pupil's
743 responses to sounds that were either presented passively or that coincided in time with a
744 motor act. The aim of the present work was to assess how motor acts affect first sensory
745 processing and second memory encoding of concomitant sounds, and the possible
746 relationships between these two types of effects of actions. Related to the first aim, regarding
747 the effects of actions on sensory processing, we examined whether a) attenuation of sensory
748 processing (i.e., measured by ERPs) prevails even in the absence of a contingent action-sound
749 relationship (e.g., Hórvath et al., 2012), b) actions create a halo of subcortical
750 neuromodulation around them that could be reflected in the pupil diameter (e.g., McGinley
751 et al., 2015), and c) sensory processing (i.e., measured by ERPs) and subcortical
752 neuromodulation (i.e., measured by pupil diameter) were related. Our findings showed N1,
753 P2, P2_{mast}, and Tb attenuation for motor-auditory sounds even when they merely coincide
754 with the action, as well as enhancement of P3 and N1_{mast}. These findings suggest that self-
755 generation effects are at least partly stimulus-unspecific and driven by alternative
756 mechanisms to the cancellation of predicted sensory reafference via motor forward
757 modelling. Additionally, our data replicated previous animal work (e.g., McGinley et al.,
758 2015) showing that pupil diameter increases dramatically for motor-auditory compared to
759 auditory-only events providing evidence for an alternative stimulus-unspecific mechanism
760 that could underlie sensory suppression for self-generated sounds, namely the activation of
761 subcortical neuromodulation during motor actions. However, the data did not provide clear
762 evidence for a correlation between sensory attenuation and pupil dilation for motor-auditory
763 events. The second aim of the present study was to investigate how actions affect memory
764 encoding of concomitant sounds and whether the potential differences in the memory
765 encoding of motor-auditory and passively presented sounds correlate with sensory
766 suppression and/or subcortical neuromodulation. We found a significant impairment in
767 memory performance for sounds that were encoded as motor-auditory compared to the
768 auditory-only ones demonstrating that the mere presence of an action affects memory
769 encoding of simultaneously presented stimuli. Most importantly, worsened memory

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770 performance for motor-auditory events correlated with increased sensory suppression (i.e.,
771 N1 and Tb attenuation) and larger pupil dilation for motor-auditory events. These findings
772 fit well with the predictive coding framework suggesting that prediction errors (i.e., reflected
773 in ERPs) drive learning and memory and further support previous work showing that high
774 arousal (i.e., reflected in pupil diameter) may worsen behavioural performance.

775 The first aim of the present study was to assess the effects of actions on auditory
776 processing and subcortical neuromodulation, as well as the relationship between the two.
777 First, we replicate previous work showing that attenuation of N1 and Tb prevails even for
778 mere action-sound coincidences (Horváth et al., 2012, 2013b). Traditionally the N1
779 attenuation has been attributed to predictive processing driven by our actions that attenuate
780 responses in auditory areas when the stimulus can be indeed predicted by the action, implying
781 that attenuation should be specific to the predicted stimulus and thus, mediated by sensory-
782 specific cortices. The stimulus-specificity of the self-generation effects is supported by work
783 showing more pronounced suppression when predictions match more precisely with the
784 sensory input (Fu et al., 2006; Hashimoto & Sakai, 2003; Heinks-Maldonado, Mathalon,
785 Gray, & Ford, 2005; Houde, Nagarajan, Sekihara, & Merzenich, 2002; Baess et al., 2008).
786 However, attenuation of auditory responses occurs also for stimuli merely coinciding with
787 finger movements (Hazemann, Audin, & Lille, 1975; Horváth et al., 2012; Makeig, Muller,
788 & Rockstroh, 1996; Tapia, Cohen, & Starr, 1987) or for unrelated auditory inputs during
789 speech (Numminen, Salmelin, & Hari, 1999), reminiscent of the generalized attenuation
790 found in other sensory modalities during movements (e.g., saccadic suppression or
791 somatosensory gating; Crapse & Sommer, 2008; Williams, Shenasa, & Chapman, 1998;
792 Ross, Morrone, Goldberg, & Burr, 2001). The stimulus-unspecificity of the effects is at least
793 partly supported by evidence suggesting that the N1 and Tb attenuation is probably driven
794 by mere temporal contiguity (Horváth et al., 2012; Hazemann et al., 1975; Han et al., 2021)
795 or temporal predictability (Schafer & Marcus, 1973; Lubinus et al., 2020; Kaiser & Schütz-
796 Bosbach, 2018) and that it mostly reflects modulations of the unspecific component of the
797 auditory N1 (SanMiguel et al., 2013). In line with this evidence, our findings partly point to
798 the modulation of the unspecific component, since for the suppression to be specific to the
799 auditory cortex, N1 should be suppressed at vertex but also at the mastoids. Instead, here we
800 found N1 suppression at vertex, but enhancement on the mastoids for sounds coinciding with

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801 actions. Therefore, the effects cannot be entirely specific and action-related activity
802 enhancements – possibly of attentional origin – in auditory areas may take place
803 concomitantly (Horváth, 2015; Schröger et al., 2015; Flinker et al., 2010).

804 The effects on N1 were followed by attenuated P2 and enhanced P3 responses for the
805 sounds coinciding with actions. Although a functional interpretation of P2 is missing
806 (Crowley & Colrain, 2004), empirical evidence has shown that P2 attenuation is mediated by
807 secondary auditory areas (Bosnyak et al., 2004; Pantev et al., 1996), reflecting the processing
808 of the specific features of auditory stimuli (Shahin et al., 2005), and it correlates with the
809 sense of agency (i.e., the feeling of control over actions and their consequences; Gallagher,
810 2000) contrary to the N1 that does not (Ford et al., 2013; Kühn et al., 2011; Timm et al.,
811 2016). These characteristics along with our data showing P2 attenuation in both vertex and
812 mastoids may point to a functional dissociation between N1 and P2 as suggested by previous
813 work (Knolle, Schröger, & Kotz, 2013; Schröger et al., 2015; Chen et al., 2012). Following
814 the P2 attenuation, we found enhanced P3 amplitude at Pz for sounds coinciding with actions.
815 Interestingly, a P3 effect was also evident – although not discussed – in previous work with
816 action-sound coincidences (Horváth et al., 2012). Recently, this effect has been suggested to
817 reflect violations in action-related predictions (Darriba et al., 2021) which may occur in tasks
818 where the self-generated sound is unexpected (e.g., in coincidence tasks where the action
819 does not always result in a sound; Horváth et al., 2012). Although previous work has already
820 described P3 modulations in self-generation paradigms, the posterior distribution and later
821 peak of our effect differentiates it from the fronto-central P3a effect reported for unexpected
822 externally-generated sounds (Baess et al., 2011) or self-generated deviant sounds (Knolle et
823 al., 2013b). Based on previous theories, we speculate that the posterior P3 effect may be
824 related to context updating (Donchin & Coles, 1988), event categorization (Kok, 2001) or
825 decision making (Twomey et al., 2015) and may reflect an evaluative process of the stimulus
826 (i.e., self/external categorization) that ultimately updates the internal model about the sensory
827 consequences of the button press (Polich, 2007).

828 The present study demonstrates that neuromodulatory processes take place concomitantly
829 to the modulatory effects of action-sound coincidence on evoked electrophysiological
830 responses. We obtained pupil dilation measures that are known to track the activity of the
831 LC-NE system (Aston-Jones & Cohen, 2005, Murphy, O’Connell et al., 2014; Joshi et al.,

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832 2016) and we showed a remarkable increase in pupil diameter for the motor-auditory events
833 that started even before the action (cf. McGinley et al., 2015a), supporting previous work
834 reporting pupil dilation during finger movements (Lubinus et al., 2021; Yebra et al., 2019),
835 and locomotion (Reimer et al., 2014; Vinck et al., 2015; McGinley et al., 2015) even in the
836 absence of visual stimulation (Richer & Beatty, 1985; Hupe et al., 2009). We hypothesized
837 that these neuromodulatory processes might be behind the stimulus-unspecific effects of
838 actions on simultaneously presented stimuli. However, pupil dilation did not correlate with
839 the sensory suppression effects for self-generated sounds. Although this may suggest that
840 motor-induced sensory suppression and arousal-related neuromodulation during actions
841 operate independently, there was a non-significant trend towards a link between N1
842 attenuation at the vertex and pupil dilation, and both of these measures correlated
843 significantly with memory performance. These inconclusive findings raise the need of future
844 work to further test for relationships between action-induced suppression effects and
845 neuromodulatory mechanisms operating during movement. In fact, previous work has shown
846 that movement correlates with some effects attributed to arousal (Reimer et al., 2014; Vinck
847 et al., 2015), yet, motor signals and arousal-related neuromodulatory inputs have been
848 suggested to exert distinct influences on sensory processing (e.g., McGinley et al., 2015a;
849 Nelson & Mooney, 2016; Reimer et al., 2014; Vinck et al., 2015; for a review see Ferguson
850 & Cardin, 2020). Although we cannot exclude the contribution of other mechanisms, our
851 findings suggest that sensory suppression is not driven by noradrenergic-mediated
852 modulations that have been mainly observed in the sensory thalamus rather than the sensory-
853 specific areas (McBurney et al., 2019), supporting the idea of noradrenergic release from the
854 LC-NE as a “hub” switch for triggering temporally specific, but spatially widespread changes
855 throughout the entire cortex (Kim et al., 2016; Aston-Jones & Cohen, 2005).

856 The second aim of the present study was to assess how the differential processing for
857 sounds coinciding with actions might affect their encoding in memory. While the links
858 between sensorimotor processing of auditory stimuli and memory processes remain largely
859 unexplored, there is evidence that actions attenuate responses in areas supporting memory
860 processes (i.e., Rummell et al., 2016; Mukamel et al., 2010), raising the possibility of a link
861 between self-generation and memory. In our study, motor actions affected the memory
862 encoding of concurrent sounds, but the effects were reflected only in memory performance

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863 and not in memory bias. The null effects on memory bias might suggest that participants
864 could recognize that both test sounds at retrieval were presented before, which is supported
865 by the general high level of objective accuracy as well as by reports during an informal
866 debriefing suggesting that many participants thought that most times all sounds at retrieval
867 were presented before. The memory benefit for the more surprising externally-generated
868 sounds fits well with predictive coding theories postulating that items eliciting larger
869 prediction errors at encoding will be encoded better in memory (Henson & Gagnepain, 2010;
870 Greve et al., 2017, 2019; Heilbron & Chait, 2018; Henson & Gagnepain, 2010; Pine et al.,
871 2018; Krawczyk et al., 2018; Rescorla & Wagner, 1972; Exton-McGuinness et al., 2015).
872 Yet, one would expect to observe this effect only in contingent paradigms where self-
873 generated sounds are inherently more predictable than the externally-generated ones.
874 However, although in our study actions were not predictive of sound identity or occurrence,
875 they afforded better temporal predictability, which may have compromised the memory
876 encoding of motor-auditory sounds. In fact, the present work is the first human study – to our
877 knowledge – to show that the self-generation effects (i.e., N1 and Tb attenuation) are related
878 to the performance decrements for sounds produced by actions as suggested by previous
879 animal work (Schneider et al., 2018; McGinley et al., 2015; Schneider et al., 2020). These
880 findings support the idea that the larger prediction error responses to unexpected items (as
881 indexed by enhanced ERPs to A compared to MA events at encoding) initiate a cascade of
882 synaptic changes, allowing for more distinctive representations at encoding (Kirwan & Stark,
883 2007, Norman, 2010) and thus better recollection at retrieval. Consistent with this
884 framework, the hippocampus has been implicated as a novelty and match/mismatch detector
885 (Knight, 1996, Stern et al., 1996, Li et al., 2003; Duncan et al., 2012) and there is compelling
886 evidence for hippocampal involvement in learning from prediction errors (Schiffer et al.,
887 2012) and expecting upcoming events (Davachi & DuBrow, 2015, Hindy et al.,
888 2016, Schapiro et al., 2017). Collectively, our data supports the predictive account of
889 memory by showing that sensory attenuation, interpreted as reduced prediction error, is
890 related to decreased memory performance.

891 Memory performance correlated with pupil diameter as well, such that the larger the pupil
892 diameter for motor-auditory events the worse the memory performance for these sounds at
893 retrieval. To date, there have been no direct attempts to test for possible links between motor-

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894 induced pupil dilation and memory performance for stimuli triggered by actions. Some
895 interim evidence points to a negative relationship between pupil dilation and detection
896 performance during (McGinley et al., 2015), but also without (Murphy, Vandekerckhove, &
897 Nieuwenhuis, 2014) locomotion, suggesting that performance may follow the classically
898 described, inverted U-shaped dependence on arousal (Yerkes & Dodson, 1908): Intermediate
899 levels of arousal – as indexed by pupil diameter – occur in states of quiet wakefulness and
900 are characterized by optimal performance. In contrast, performance during high-arousal
901 states such as movement, or during quiescence, drops dramatically. Therefore, the observed
902 link between pupil dilation and memory performance in our study may provide yet another
903 piece of evidence supporting the detrimental effects of high arousal on behavioural
904 performance.

905 The present study had clear hypotheses about the effects of actions on sensory and pupil
906 responses at encoding, yet, exploratory analyses of the retrieval data revealed further effects.
907 First, we obtained higher Na and Tb amplitudes for the sounds encoded as motor-auditory
908 and remembered compared to the remembered and encoded as auditory-only ones. Since the
909 sounds encoded as motor-auditory were presented passively at retrieval (i.e., without the
910 motor representation that they were encoded with), the higher Na and Tb amplitudes may
911 reflect a form of contextual prediction error (Exton-McGuinness et al. 2015; Kim et al., 2014;
912 Sinclair & Barense, 2019) due to the mismatch between encoding and retrieval contexts for
913 these sounds. This interpretation can be partly supported by the exploratory correlation
914 analyses that showed that the larger the P2 and Tb attenuation for motor-auditory sounds at
915 encoding, the greater the Na enhancement for these sounds at retrieval when they were
916 remembered. Thus, the greater the effect of the action at encoding, the greater the contextual
917 prediction error when the sound is presented without the action at retrieval. Second, we found
918 larger pupil responses for the forgotten compared to the remembered sounds at retrieval
919 irrespective of how they were encoded. While previous work has reported an old/new pupil
920 effect (i.e., increased pupil responses for the remembered items; Kafkas & Montaldi, 2015;
921 Naber et al., 2013, but see Beukema et al., 2019 for the opposite effect), in our study both
922 sounds at retrieval were presented before. The increase in pupil diameter for the forgotten
923 sounds at retrieval could be instead related to selection or decision uncertainty (Geng et al.,

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924 2015; Richer & Beatty, 1987; Nassar et al., 2012; Preuschoff et al., 2011) when participants
925 experienced greater difficulty to decide whether a given sound was presented before or not.

926 In sum, the overarching aim of the present study was to investigate how motor acts affect
927 both sensory processing and the memory encoding of concomitant sounds. To the best of our
928 knowledge, there have been no previous attempts to simultaneously assess the specificity of
929 the self-generation effects and their possible link with neuromodulatory processes while also
930 looking into their possible effects on memory encoding. Here, in a combination of self-
931 generation and memory task, we show that actions affect auditory responses, pupil diameter,
932 and memory encoding of sounds. Actions suppressed sensory responses for concomitant
933 sounds and increased pupil diameter, but these effects were not related, pointing to
934 simultaneous, but probably independent processes. However, sensory suppression and pupil
935 dilation both correlated with memory performance independently, such that the memory
936 performance for sounds coinciding with actions decreased with larger sensory attenuation
937 and greater pupil dilation. Collectively, our findings show self-generation effects even in the
938 absence of a predictive action-sound relationship, replicate previous work showing that pupil
939 diameter increases during actions, and finally point to differentiated internal memory
940 representations for stimuli triggered by ourselves compared to externally presented ones.
941 More importantly, the present study shows that subcortical neuromodulatory systems, along
942 with cortical processes, simultaneously orchestrate auditory processing and memory
943 encoding.

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944 **CRedit authorship contribution statement**

945 **Nadia Paraskevoudi:** Conceptualization, Formal Analysis, Methodology, Software,
946 Investigation, Writing - Original draft preparation, Visualization. **Iria SanMiguel:**
947 Conceptualization, Formal Analysis, Methodology, Software, Writing - Original draft
948 preparation, Supervision, Project administration, Funding acquisition.

949

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