

Self-generation effects: beyond sensory processing

Marta Font Alaminos

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Self-generation effects: Beyond sensory processing

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Self-generation effects: beyond sensory processing

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en neurociència cognitiva

To those who bore with me

... specially myself

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ABSTRACT

Our actions shape our everyday experience: what we experience, how we perceive and remember it, is deeply affected by how we interact with the world. Performing an action to deliver a stimulus engages neurophysiological processes which are reflected in the modulation of sensory and pupil responses. Furthermore, research shows that the sensory modulation of those self-generated (SG) stimuli may have an impact on higher order cognitive processes such as memory and personality. The present thesis attempts to elucidate whether actions have an impact on memory encoding and retrieval as well as examining whether the self-generation effects correlate with personality traits. Study I tested whether actions alone are a pivotal part of the production effect, a widely studied phenomenon that shows an increase of memory performance through active learning. Participants (N= 19) listened to sounds presented either during or in between their actions while the event related potentials (ERP) to the sounds were recorded and memory performance was assessed. Results showed attenuation of ERP sensory responses for action-coinciding sounds. However, there was no significant effect on memory performance. Study II went a step further looking into contingent action-sound relationships discerning whether the self-generation of sounds shape memory encoding, parsing the experience by grouping self- and externally generated (EG) stimuli into differentiated events. Participants (N = 25) encoded short sound sequences, in which either the first or last few sounds were SG and the rest EG while ERPs, pupil dilation and memory performance were recorded. Recall of the sequential order of sounds that had originated from within the same event was not higher than from across events, suggesting that the memory representation was not structured by actions. Recall of the sequential order of sounds between EG and SG remained similar, not evidencing a production effect. However, during encoding, we replicated the wellknown electrophysiological response attenuation, together with increased pupil dilation for self-generated sounds. Moreover, we found that at the boundary between events, the pupil and electrophysiological responses to the first sound originating from the new source were determined by the direction of the source switch. The results suggest that introducing actions, acts as a stronger contextual shift than removing them, despite not directly contributing to memory performance. Finally, Study III ventured into the realm of individual variability exploring the relationship between personality traits and the self-generation effects. The analysis was performed using data from four experiments (N = 87) from our laboratory, including data from Study II. Electrophysiological measures of self-generation effects on various ERP components, pupil dilation and memory performance, were analyzed along with scores from four personality questionnaires that assessed schizotypal traits and sense of agency. Findings suggest that individuals with higher schizotypal traits exhibit reduced self-generation effects on the Tb ERP component. However, our results challenge previous findings showing a correlation of schizotypal traits with the N1 ERP component. There was no relationship of personality with the pupil response or the memory performance. The findings contribute to our understanding of how interacting with sensory input shapes our experiences, by addressing the unexplored relationships between action effects on sensory responses, pupil dilation and memory. This thesis concludes that: 1) low-level neurophysiological mechanisms tied to action execution do not seem to significantly contribute to the modulation of memory; 2) the introduction of actions appears to exert a more powerful contextual shift compared to removing them; 3) no direct relationship was found between the neuromodulatory mechanisms of action, as reflected by pupil dilation, and the electrophysiological self-generation effects; and 4) individuals with higher schizotypal traits demonstrate reduced self-generation effects in

electrophysiological sensory responses; however the N1 may not be the perfect candidate to mirror the underlying prediction deficit.

RESUM

Les nostres accions configuren la nostra experiència quotidiana: el que experimentem, com ho percebem i com ho recordem, està profundament afectat per com interactuem amb el món. Realitzar una acció per a generar un estímul posa en marxa processos neurofisiològics que es reflecteixen en la modulació de les respostes sensorials i de la pupil·la. A més, la recerca mostra que la modulació sensorial d'aquests estímuls autogenerats pot tenir un impacte en processos cognitius de nivell superior com la memòria i la personalitat. Aquesta tesi intenta esbrinar si les accions tenen un impacte en la codificació i la recuperació de la memòria, així com intenta examinar si els efectes d'autogeneració es correlacionen amb trets de personalitat. L'Estudi I va provar si les accions per si soles són una part cabdal de l'efecte de producció, un fenomen àmpliament estudiat que mostra un augment en el rendiment de la memòria mitjançant l'aprenentatge actiu. Els participants (N = 19) van escoltar sons presentats durant o entre les seves accions mentre es registraven els potencials evocats (PE) dels sons i es valorava el rendiment de la memòria. Els resultats mostren una atenuació de les respostes sensorials dels PE pels sons coincidents amb l'acció. No obstant això, no hi va haver un efecte significatiu en el rendiment de la memòria. L'Estudi II va anar un pas més enllà investigant les relacions d'acció-sons contingents, discernint si l'autogeneració de sons dóna forma a la codificació de la memòria, segmentant l'experiència agrupant els estímuls autogenerats (SG) i els generats externament (EG) en esdeveniments diferenciats. Els participants (N = 25) van codificar sequències curtes de sons, en què els primers o els darrers sons eren SG i la resta EG, mentre es registraven els PE, la dilatació de la pupil·la i el rendiment de la memòria. La memòria de l'ordre seqüencial dels sons que provenien del mateix esdeveniment no va ser més alta que la dels esdeveniments diferents, suggerint que la representació de la memòria no estava

estructurada per les accions. La memòria de l'ordre seqüencial dels sons entre EG i SG va romandre similar, sense evidenciar un efecte de producció. No obstant això, durant la codificació, es va replicar la coneguda atenuació de la resposta electrofisiològica, juntament amb una dilatació major de la pupil·la pels sons autogenerats. A més, vam trobar que en el llindar entre esdeveniments, les respostes de la pupil·la i electrofisiològiques al primer so que provenia de la nova font estaven determinades per la direcció del canvi de font. Els resultats suggereixen que introduir les accions actua com un canvi contextual més potent que eliminarles, tot i no contribuir directament al rendiment de la memòria. Finalment, l'Estudi III es va aventurar al món de la variabilitat individual explorant la relació entre els trets de personalitat i els efectes d'autogeneració. L'anàlisi es va realitzar amb dades de quatre experiments (N = 87) del nostre laboratori, incloent dades de l'Estudi II. Les mesures electrofisiològiques dels efectes d'autogeneració en diversos components dels PE, la dilatació de la pupil·la i el rendiment de la memòria, es van analitzar juntament amb les puntuacions de quatre qüestionaris de personalitat que avaluen trets esquizotípics i el sentit d'agència. Els resultats suggereixen que les persones amb trets esquizotípics més alts mostren efectes d'autogeneració reduïts en el component del PE Tb. No obstant això, els nostres resultats qüestionen les troballes anteriors que mostren una correlació dels trets esquizotípics amb el component del PE N1. No es va trobar una relació entre la personalitat i la resposta de la pupil·la o el rendiment de la memòria. Els resultats contribueixen a la nostra comprensió de com la interacció amb l'entrada sensorial dóna forma a les nostres experiències, abordant les relacions inexplorades entre els efectes de les accions en les respostes sensorials, la dilatació de la pupil·la i la memòria. Aquesta tesi conclou que: 1) els mecanismes neurofisiològics de baix nivell vinculats a l'execució d'accions no semblen contribuir significativament a la modulació de la memòria; 2) la introducció de les accions sembla exercir un canvi contextual més potent en comparació amb la seva eliminació; 3) no hi ha una relació directa entre els mecanismes neuromoduladors de les accions, tal com es reflecteix en la dilatació de la pupil·la, i els efectes d'autogeneració electrofisiològics; i 4) les persones amb trets esquizotípics més alts mostren efectes d'autogeneració reduïts en les respostes sensorials electrofisiològiques; no obstant això, l'N1 potser no és el candidat perfecte per reflectir un dèficit subjacent en la predicció.

FOREWORD

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ABBREVIATIONS

Α	Auditory-only
ANOVA	Analysis of Variance
В	Boundary
bB	before-boundary
BF	Bayes Factor
EEG	Electroencephalogram
EG	Externally-generated
ERP	Event-related potential
ICA	Independent Component Analysis
LC-NE	Locus coeruleus norepinephrine system
LOC	Locus of Control
Μ	Motor-only
MA	Motor-auditory
MIS	Magic Ideation Scale
PAS	Perceptual Aberration Scale
PDI	Peters et al. Delusion Inventory
PNR	Parietal Negative Response
SD	Standard Deviation

SEM	Standard error of the Mean
SG	Self-generated
SPQ	Schizotypal Personality Questionnaire

INDEX

Acknowledgements	ii
Abstract	iii
Resum	vi
Foreword	ix
Abbreviations	X
Introduction	1
Actions on sensory processing: self-generation effects	2
Actions on memory encoding and retrieval	6
Perception of actions: personality	10
The motivation behind this thesis	13
Objectives	17
Overview	17
Specific aims and hypotheses	17
Study I	17
Study II	18
Study III	20
Methodology	21
General methodology	21
Participants	21
Experimental procedure	21

Apparatus	22
Data Analysis	23
Specific methodology	26
Study I	26
Study II	33
Study III	44
Results	55
Study I: Action effects on auditory memory	55
Memory performance	55
Electrophysiological	56
Study II: Self-generation effects on structuring memory encoding	59
Order memory performance	59
Electrophysiological effects	60
Pupillometry effects	64
Correlations	66
Study III: Schizotypy, locus of control and the self-generation effects	68
Discussion	71
Discussion of Study I	71
Action and the production effect	72
Conclusion of Study I	73
Discussion of Study II	74
Effects of self-generation on memory structure	74

Self-generation and the production effects	77
The un-specificity of the self-generation effects	78
Limitations	80
Conclusion of Study II	81
Discussion of Study III	
The overlooked Tb	84
Limitations	85
Conclusion of Study III	86
General discussion	
Strengths, limitations and future research	
Conclusions	92
References	93

INTRODUCTION

At the heart of our subjective experience lies the intricate interplay between perception and selfhood, an essential construct for our adaptability and survival. Consider the scenario of wandering through a dense forest, where the boundary between oneself and the external world becomes paramount. In such an environment, one simultaneously processes the subtle crunch of their steps on leaves and twigs, the various inoffensive animals encircling them and the abrupt snap of a branch – an auditory signal that potentially foreboding danger or a merely benign occurrence caused by their own steps. This adept ability to attribute significance to imminent threats while attenuating one's presence in the surroundings is vital for survival.

However, individuals vary in their responses to such scenarios, as everyone's experiences, although similar, possess unique qualities. Some may choose to halt their journey and return home upon perceiving a potential threat, convinced that they are being followed, while others may dismiss it and continue their path. The objective truth in these situations becomes secondary, as both responses could be considered appropriate responses.

This dynamic interplay between perception and selfhood is not limited to matters of survival; it also manifests in scenarios where external stimuli coincide with self-initiated motor actions, leading to the attribution of outcomes to one's own agency. For instance, you may have had the childhood experience of playing a keyboard that produced pre-recorded tunes which may have temporarily created the illusion of an enhanced technical skill that you obviously didn't have. While persistent practice may eventually lead to genuine skill acquisition, the initial instances of "fake playing" raise intriguing questions. Do these seemingly mismatched motor actions facilitate memory recall between the tunes being played? These anecdotal examples underscore the profound role of attributing consequences to our own actions in the formation of memories and our sense of self (Hohwy, 2007a; Blakemore, et al., 1998; Claxton, 1975). Thus, there is no doubt that embedded within our perceptual engagement with the world is the profound influence of our actions.

ACTIONS ON SENSORY PROCESSING: SELF-GENERATION EFFECTS

The way we experience the world is fundamentally shaped by our actions. Stimuli generated by our own actions are processed differently than the inputs coming from external sources. The most well-known example arises from the fact that we cannot tickle ourselves (Weiskrantz et al., 1971). Numerous studies have demonstrated that self-generated (SG) stimuli elicit reduced subjective sensations and sensory responses compared to stimuli that are externally-generated (EG), across various domains, including auditory, visual and tactile (e.g. Blakemore et al., 2000; Crapse & Sommer, 2008; Cullen, 2004; Gentsch & Schütz-Bosbach, 2011; Hughes & Waszak, 2011; Kilteni et al., 2020; Mifsud et al., 2018; SanMiguel et al., 2013; Straka et al., 2018; for reviews see Horváth, 2015; Hughes et al., 2013; Schröger et al., 2015).

In the auditory domain, the effects of self-generation on sensory responses have been mainly studied on event-related potentials (ERPs), where an attenuation of the N1 component is consistently observed for SG sounds. Research often employs the self-generation paradigm, wherein participants generate sounds through button presses (SG), passively listen to computer-delivered sounds (EG), or perform button presses without generating sounds (motor-only control). By comparing responses to EG sounds with those to SG sounds, corrected for motor activity, researchers typically focused on the N1 and P2 components of the stimulus-evoked response to study sensory suppression to the SG simuli (Baess et al., 2008; Knolle et al., 2012; Sowman et al., 2012; Ott & Jäncke, 2013; Timm et al., 2013, 2014). This paradigm

has also been extended to participants' own speech, yielding similar sensory attenuation effects (Gunji et al., 2000; Kudo et al., 2004; Baess et al., 2011; Mock et al., 2011).

The self-generation effect has been mostly attributed to motor-driven predictive processes engaged via forward modelling (Blakemore et al., 1998; Frith et al., 2000; Wolpert et al., 1995) within the predictive coding framework of perception (Bastos et al., 2012; Dayan et al., 1995; Friston, 2005; Hohwy, 2007b; Rao & Ballard, 1999). These theories propose that copies of the motor commands, known as efference copies, serve to generate predictions through internal models. These internal models predict sensory outcomes of actions based on prior experiences. When the predicted and actual sensory inputs diverge a prediction error emerges and the incoming sensory information that was accurately predicted is cancelled, resulting in a reduction in neural responses.

The N1 ERP component typically manifests as a negative deflection approximately 100 ms after sound onset and has historically been linked to auditory cortex activity (Näätänen & Picton, 1987). However, the characterization of N1 as a single entity is nuanced. When confined to the vertex of the skull, at electrode Cz, it has been revealed to be a conglomerate of several underlying components (SanMiguel et al. 2013), with polarity inversion occurring when measured at the mastoids (with a nose reference). When N1 at the vertex and mastoids have been simultaneously examined, N1 suppression at the mastoids has not been found or it even showed enhancement to SG sounds suggesting that this attenuation is not specific to the auditory cortex (Horváth et al., 2012; Paraskevoudi & SanMiguel 2023a, 2023b, Timm et al., 2013).

Exhibiting latencies like the N1 in adults, the Na and Tb components, the first and second negative peaks of the "T complex", have recently been examined for modulations during self-generation. Despite the temporal alignment, the maturation of the T complex differs from that

of N1 (Tonnquist-Uhlen et al., 2003), making shared neural sources improbable. These components' generators have been traced to areas of the secondary auditory cortex situated on radial sources of the superior temporal gyrus (Ponton et al., 2002; Tonnquist-Uhlen et al., 2003). Investigations into Na and Tb have hinted at attenuations during self-generation mainly on the Tb component, primarily driven by temporal contiguity rather than precise stimulus predictions (Horváth et al., 2012; Horváth, 2013b; SanMiguel et al., 2013; Paraskevoudi & SanMiguel 2023a, 2023b). Consequently, if N1 attenuation is attributed to specific motor predictions influencing auditory activity, it likely reflects the modulation of sensory N1 components. Yet, research suggests that self-generation predominantly affects the stimulus-unspecific facet of N1, associated with a reticular process facilitating motor activity, signifying a diminished orienting response rather than intricate predictions about sound attributes (SanMiguel et al., 2013).

Finally, the P2 component emerges as a positive deflection around 200 ms post-sound onset with an origin in secondary auditory regions (Bosnyak et al., 2004; Pantev et al., 1996) reflecting the processing of specific auditory stimulus features (Shahin et al., 2005) and it is thought to index prediction error (Costa-Faidella et al., 2011). Moreover, P2 stands apart from N1 due to its correlation with the sense of agency, signifying the feeling of control over actions and their outcomes (Gallagher, 2000). Unlike the N1, the P2 is intimately linked to the sense of agency and is believed to encode the perception of control over actions and their consequences (Ford et al., 2014; Kühn et al., 2011; Timm et al., 2016).

Gathering the information reviewed regarding the ERP components that typically show the self-generation effect, the observed modulations in ERP components when stimuli are SG cannot be solely attributed to predictions. Compelling evidence suggests that the self-generation effects might, in part, be due to the temporal proximity between a movement and

the stimulus, as this modulation also occurs in situations lacking predictability (i.e. when actions and sounds coincide; Horváth et al., 2012; Horváth, 2013a, b; Paraskevoudi & SanMiguel, 2023a). This implies the involvement of other mechanisms in mediating sensory attenuation. These authors propose that N1-suppression effects could be driven by both specific (i.e., predictive mechanisms) and non-specific suppression mechanisms associated with the motor act. An example of non-specific suppression mechanisms was discovered in an animal study in which motor cortex neurons in mice suppressed excitatory neurons in the auditory cortex when the animals were in motion (Schneider et al., 2014). Additionally, further support for the idea that the modulation of the N1 component is driven by movement rather than sound predictability comes from studies observing N1 attenuation for SG sounds when comparing them to cued EG sounds (Lange, 2011; Sowman et al., 2012). However, P2 attenuation has been identified in cued externally generated sounds (Sowman et al., 2012), suggesting that predictive mechanisms not reliant on motor information could underlie this phenomenon.

Movement has indeed been demonstrated to modulate sensory processing (Schafer & Marcus, 1973; Roy & Cullen., 2001; Hesse et al., 2010; Kelley et al., 2010; Requarth & Sawtell, 2011; Schneider et al., 2014; Chagnaud et al., 2015; Kim et al., 2015; Pyasik et al., 2018). An intriguing possibility is that the suggested non-specific suppression mechanisms might stem from a "halo" of neuromodulation surrounding motor actions, potentially mediated by arousal-related non-specific modulatory mechanisms influenced by motor areas (Aston-Jones & Cohen, 2005). A prime candidate for mediating the non-specific regulation of stimulus processing surrounding motor acts is the Locus Coeruleus norepinephrine (LC-NE) system.

Numerous animal studies have demonstrated that auditory cortical neurons receive inputs from both the motor cortex and neuromodulatory areas (mainly originating from the caudal basal forebrain) that are simultaneously active during movement (Nelson & Mooney, 2016; see Schneider & Mooney, 2018). Basal forebrain neurons receive inputs from subcortical regions, including the Locus Coeruleus (LC), suggesting that the concurrent activity of motor and neuromodulatory inputs in auditory neurons may indicate a coexistence between specific and non-specific effects during movement (Nelson & Mooney, 2016).

The LC is a critical structure located in the brainstem housing norepinephrine (NE)synthesizing neurons (Wetzel et al., 2016). Supportive evidence linking LC activity to motor actions has been observed in both animal and human studies (Reimer et al., 2016; Strauch et al., 2020; Yebra et al., 2019). Numerous studies have also shown that LC-NE system activity can be measured physiologically using pupil diameter as a proxy for LC activity (Aston-Jones & Cohen, 2005; Gilzenrat et al., 2010; Murphy et al., 2014; Wetzel et al., 2016; Yebra et al., 2019), as activity in the NE system is positively correlated with pupil diameter (Larsen & Waters, 2018; Reimer et al., 2016). Recently, driven by the exposed findings, Paraskevoudi & SanMiguel (2023a, 2023b) have tested the notion that subcortical neuromodulation during motor actions (Aston-Jones & Cohen, 2005; Eggermann et al., 2014; McGinley et al., 2015; Vinck et al., 2015) could potentially regulate the observed sensory attenuation on selfgeneration paradigms and found that an increase in pupil dilation correlates with the attenuation of the SG sounds, however only when predictability about the outcome of the action is highest.

ACTIONS ON MEMORY ENCODING AND RETRIEVAL

The self-generation effect could have larger implications than the mere alteration of sensation and sensory responses. You have probably been told at least once to study aloud or while chewing gum to best prepare for an upcoming test. Like these, there are countless examples from daily life that suggest that actions could have an impact on memory performance. A related finding in scientific literature is the production effect. Several studies have collectively found that SG sounds (i.e. rehearsed piano melodies and spoken words) are better recalled from memory than their passively processed counterparts (Ekstrand et al., 1966; Hopkins & Edwards, 1972; Conway & Gathercole, 1987; Gathercole & Conway, 1988; MacDonald & MacLeod, 1998; MacLeod et al., 2010; Brown & Palmer, 2012; Mathias et al., 2015).

The production effect is frequently explained with the distinctiveness model, which proposes that items containing more distinct components have a higher probability of being recalled from memory than items with fewer components (Ozubko & Macleod, 2010). This distinctiveness is rooted in the notion that the retrieval of a memory event is facilitated when it is integrated within a network of associations, rather than being isolated in recollection (Bangert et al., 2006; Fiebach & Schubotz, 2006; Lahav et al., 2007). Furthermore, a recent study has linked memory enhancements resulting from overt actions to the activation of the LC-NE system, reflected in increased pupil dilation (Yebra et al., 2019). All in all, it is possible that the distinctiveness provided by the actions, along with the differential sensory encoding of SG sounds, could be contributing to the memory performance enhancement seen in the production effect.

Memory, a crucial aspect of human cognition, enables individuals to store and retrieve past experiences that significantly influence present and future behaviors. These experiences are not stored indiscriminately; rather, they are structured into discrete units or events through a process known as event segmentation (DuBrow & Davachi, 2013; Zacks & Swallow, 2007). Event segmentation allows for the effective organization and retrieval of episodic memories by breaking them down into meaningful units or events (Zacks & Swallow, 2007). These meaningful units are separated by event boundaries, identifiable moments where there is a noticeable change in the content, context, or purpose of an experience (Kurby & Zacks, 2008). Minor changes in the physical environment or in the ongoing task, such as on the background color or sound, can create these event boundaries, highlighting their importance in the organization of episodic memory (Kurby & Zacks, 2008; Newtson & Engquist, 1976; Speer et al., 2003; Swallow et al., 2010).

Event Segmentation Theory posits that individuals naturally construct schemas or mental models of the world to enhance memory retention as part of a hierarchical informationprocessing system (Zacks & Swallow., 2007). Event segmentation, as a spontaneous process, evolved as an adaptive mechanism to enhance predictive capabilities, allowing individuals to anticipate forthcoming information effectively (Kurby & Zacks, 2008). Moreover, segmentation plays a crucial role in updating working memory when a contextual change occurs, resulting in an increased prediction error when predictions are challenged (Fernández et al., 2016; Zacks & Swallow 2007). This prediction error triggers the updating of working memory representations, specifically the event models, signifying the inception of a new event or event boundary (Radvansky & Zacks, 2017; Swallow et al., 2009; Zacks & Swallow, 2007). One crucial impact of event segmentation on memory is enhancing memory for information occurring at event boundaries. Research has consistently shown that objects presented after an event boundary, referred to as boundary objects, are more effectively recognized than those within the same event (Clewett et al., 2020; Pettijohn et al., 2016; Richmond et al., 2017; Speer & Zacks, 2005; Swallow et al., 2009; Zacks & Swallow, 2007). Additionally, serial recall performance is superior for information within the same event compared to information presented across event boundaries (Clewett et al., 2019, 2020; DuBrow & Davachi, 2016; Pettijohn et al., 2016; Radvansky & Zacks, 2017; Speer & Zacks, 2005; Swallow et al., 2009; Zacks et al., 2009). Based on recent findings from human studies, brain activity synchronized with the offset of an event boundary may indicate a swift reactivation of the recently encoded sequence. This reactivation process exhibits substantial neural resemblance to the neural

patterns elicited during the initial encoding of the preceding episode (Sols et al., 2017; Silva et al., 2019). Memory reactivation following encoding has been found to be an inherent process that is specifically activated to facilitate the formation of memories for significant events (Wu et al. 2022, Wu & Fuentemilla, 2023).

Some anatomical neural structures that have an especial involvement in how the brain represents and tracks contextual information are the prefrontal cortex and the hippocampus. The prefrontal cortex, known for its role in higher-order cognitive functions, contributes to organizing, maintaining, and updating context information during events (Frank et al., 2001; Postle, 2006). On the medial temporal lobe, the hippocampus, is particularly engaged in recognizing and encoding contextual shifts that define event boundaries (Davachi, 2006; Diana et al., 2007; Eichenbaum et al., 2007; Ranganath, 2010). Although not in isolation, these are the main anatomical structures creating a neural network that underpins the memory-enhancing effects of event segmentation, facilitating the encoding and retrieval of information at event boundaries.

One neurophysiological response that reflects prediction error and memory updating is the P3 ERP component (Escera et al., 1998). The P3 exhibits a positive polarity and a peak latency of at least 300 ms around centro-parietal electrodes. Research has demonstrated that violations of expectancies, such as unexpected behaviors in sentences, evoke a larger P3 response compared to expected events, and these unexpected events are subsequently better remembered (Fabiani, 2006). The P3, is also linked to the ongoing updating of working memory (WM) and the revision of mental representations (Polich, 2007).

The LC-NE system is also believed to play a crucial role in memory processes (Fernández et al., 2016; Kafkas & Montaldi, 2011; Larsen & Waters, 2018; Naber et al., 2013). The LC-NE system is well-known for its essential role in reorienting and focusing attention, task

engagement, working and episodic memory, as well as retrieval from remote memory, among other functions (Aston-Jones & Cohen, 2005; Sara, 2015; Wetzel et al., 2016; Yebra et al., 2019; Zacks & Swallow, 2007). NE release is thought to improve the speed of processing new sensory information and memory retrieval, enhance memory formation and consolidation, and promote a reset of the active network in response to salient or unexpected events (Bouret & Sara, 2005; Dayan & Yu, 2006; Lemon et al., 2009; Sara, 2015; Zacks & Swallow, 2007).

Prior research in this domain has demonstrated that LC activity and pupil dilation increase with goal-directed actions, leading to enhanced memory for the resulting stimuli when greater pupil dilation occurs. These findings suggest a potential interaction between LC activity induced by actions and the encoding of stimuli into episodic memory (Yebra et al., 2019). Conversely, some authors have identified an inverse relationship between pupil response during encoding and the strength of subsequent memory, with more pupil dilation at encoding associated with later forgotten items (Kafkas & Montaldi, 2011; Naber et al., 2013). Furthermore, pupil dilation, as it is an indicator of autonomic arousal, it is notably more pronounced on boundary events compared to other events in the same sequence (Clewett et al., 2020).

PERCEPTION OF ACTIONS: PERSONALITY

Personality traits play a pivotal role in shaping an individual's approach to perceiving and interacting with the world around them. For example, as it is the scope of this thesis, the distinction in memory representation between SG and EG stimuli could be influenced by interindividual differences on sense of agency or personality characteristics. However, although this is not a surprise, the inter-individual differences associated with personality traits on the self-generation effects have not been largely explored beyond clinical populations. For instance, the self-generation effect variability has been largely studied under the umbrella of psychosislike symptoms. For example, individuals suffering from schizophrenia exhibit altered selfgeneration effects, particularly a significant reduction or complete absence of N1-suppression in response to self-generated sounds (Ford et al. 2014; Randeniya et al., 2018). This impaired N1-suppression has been linked to disruptions in self-perception characteristic of these individuals, potentially related to the delusion of attributing internal experiences to external sources due to an altered sense of agency. However, the precise relationship between these well-established self-generation effects and the sense of agency remains far from clear (Timm et al., 2014, 2016). The intermediate steps in the causal chain connecting modulated sensory processing of self-generated stimuli to high-level cognitive processes, such as the concept of self, remain largely uncharted.

This atypical processing of self-generated events has been particularly associated with specific first-rank symptoms of schizophrenia, which seem to reflect external attributions of internally generated phenomena (Fletcher & Frith, 2009), such as delusions of control and passivity experiences (Frith et al., 2000; Lindner et al., 2005; Shergill et al., 2005; Synofzik et al., 2010). It is conceivable that these symptoms observed in schizophrenia patients represent an extreme manifestation of a continuous phenotype distributed throughout the general population, potentially covarying with the magnitude of neurophysiological self-generation effects. Consequently, this may influence the clarity of the distinction between SG and EG sensory events within an individual's memory representation of everyday life experiences.

Under the general view that the population falls along a continuum of psychosis, this thesis will review schizotypy as a means to look into the phenotype of psychosis. Schizotypy, is a multifaceted personality construct associated with an array of perceptual and cognitive alterations resembling those found in schizophrenia and other related disorders (Meehl, 1962). Schizotypal personality is defined as a vulnerability to schizophrenia spectrum disorders,

encompassing a range of subclinical psychotic-like experiences including delusions and hallucinations (Ettinger et al., 2015). Unlike clinically high-risk individuals who seek help due to symptoms, those with high schizotypy scores often demonstrate similarities to high-risk individuals but lack the help-seeking behavior (Barkus et al., 2011), making them particularly intriguing subjects for investigation. Schizotypy is characterized by positive, negative, and disorganized dimensions (Raine, 2006). Positive schizotypy corresponds to unusual ideas and perceptual aberrations reminiscent of subsyndromal hallucinations, while negative schizotypy pertains to reduced emotional, physical, and social functions. The disorganized dimension involves thought disorder and bizarre behaviors.

Concerning perception, schizotypy encompasses diverse perceptual alterations across sensory modalities such as visual (Bedwell et al., 2013; Koychev et al. 2010; Luh & Gooding, 1999; Uhlhaas & Silverstein, 2005), auditory (Lagioia et al., 2010; Potter et al. 2006), olfactory (Park et al. 1997; Mohr, 2001), and somatosensory (Lenzerweger, 2000) domains. For instance, regarding audition, these alterations tend to be subtle in schizotypy: in the sensory ERPs, heightened schizotypy correlates with diminished amplitudes of P3b and N2, while the N1, P2, and P3a components remain unaffected (Klein et al., 1999; Nuchpongsai et al., 1999).

Among the various cognitive domains influenced by schizotypy, memory and mental imagery hold particular significance. Studies have indicated reduced attention, working memory, and memory performance in individuals with elevated schizotypal traits (Forbes et al. 2008; Lee & Park, 2005; Park & Holzman, 1992). Additionally, mental imagery, a process of active generation and manipulation of internal representations, has been associated with vivid imagery experiences in individuals with elevated schizotypal traits (Beaman & Williams, 2013).

In the healthy population, the inter-individual variability of self-generation effects remains largely unexplored. Under the general view that the population falls along a continuum of psychosis, previous studies have found a relationship between the diminished SG effect on the component N1 of the event-related potential and high scores in the Schizotypal Personality Questionnaire (SPQ; Oestreich et al., 2015, 2016). Nevertheless, at least two studies have reported significant correlations between the inclination to predict and attenuate the sensory consequences of self-generated actions and delusional ideation in healthy individuals, as assessed through questionnaires measuring schizotypy and delusion-like thinking (Malassis et al., 2015; Teufel et al., 2010), while a recent preprint found attenuated self-generation effects at N1 in individuals with hallucination proneness (Duggirala et al., 2023)

THE MOTIVATION BEHIND THIS THESIS

In the realm of memory, theories regarding the mechanisms underlying the production effect, which seems to be mainly explained by the distinctiveness account, have largely overlooked the potential contribution of mere movement to memory enhancement. Recent studies have sought to bridge this gap by integrating paradigms measuring self-generation effects with memory tasks, yielding intriguing yet conflicting results. Using slightly different memory tasks and action-sound relationships, these studies have found conflicting results from memory enhancement for predictable SG sounds (Paraskevoudi & SanMiguel, 2023b) to memory impairment for sounds coinciding with actions (Paraskevoudi & SanMiguel, 2023a) compared to EG sounds, despite the presence of reliable self-generation effects on auditory ERPs in both studies. Although results seem straightforward, pointing to an advantage in memory favoring predictability and not the actions per se, further research is needed to clarify the impact of actions on sensory processing and memory encoding and identify the critical variables responsible for the discrepancy in the observed effects and draw robust conclusions on the

direction of the effects. Consequently, both Study I and Study II aim to investigate whether movement, whether it occurs coincidentally (Study I) or congruently (Study II), influences memory performance and, if so, in what manner.

Moreover, Study I delves into the electrophysiological modulations during the retrieval of sounds encoded in conjunction with an action. The distinct processing that unfolds during encoding could potentially impact how items are stored in working memory, providing an advantage to self-produced items. This suggests that the memory trace of self-generated items may be neurally reflected when these items are presented for judgment regarding their presence or absence in a previously encoded sequence. This modulation of sensory responses during encoding could, for example, lead to a modulation of the old/new effect. The old/new effect is characterized by a more positive-going potential in response to correctly recognized old items compared to new ones, serving as an index of the quality of conscious recollection (Sanquist et al., 1980; Warren, 1980; Wilding, 2000; Kayser et al., 2007; Rugg and Curran, 2007; Mecklinger et al., 2016; MacLeod and Donaldson, 2017). This suggests that if a relationship exists between the self-generation effect and the production effect, it may exert a cascading influence on how memories are processed and subsequently recognized, potentially altering the electrophysiological signatures associated with memory retrieval.

An intriguing possibility is that actions may not simply modulate the strength of memory traces to specific items; they might also play a role in structuring memory storage itself. Remarkably, no prior studies have specifically explored the potential of actions per se to create event boundaries. Given the current scope of research on self-generation, encompassing sensory processing, neuromodulation, and memory, Study II aims to test the plausibility that actions might not only modulate the strength of memories for SG stimuli but also structure the encoding of sounds in memory, potentially generating distinct storage for SG and EG sounds. Regarding sensory processing, the self-generation effect, continues to intrigue researchers due to ongoing debates surrounding its underlying neural mechanisms. A promising avenue of investigation lies in the possibility that motor actions, by engaging broad neuromodulatory systems such as the LC-NE system, may influence sensory cortex responses, potentially modulating the self-generation effect (Paraskevoudi and SanMiguel, 2023b). While preliminary evidence has linked self-generation effects with pupil dilation during sound processing (Paraskevoudi & SanMiguel, 2023a, 2023b), there is a need of replication to understand the precise role of LC-NE activity, inferred through pupil dilation, in the self-generation effect. Study II within this thesis seeks to shed light on this relationship by measuring pupil diameter and investigating neuromodulatory effects associated with motor actions. The hypothesis is that greater pupil dilation will be observed for SG stimuli compared to EG stimuli during sound encoding and that this modulation will correlate with the self-generation effects (Paraskevoudi & SanMiguel, 2023a, 2023b).

Finally, regarding the influence of the self-generation effect on personality traits, earlier investigations have identified a link between reduced attenuation in the amplitude of SG sounds on the N1 ERP component and elevated scores on the SPQ (Oestreich et al., 2015, 2016). However, these findings have yet to be independently verified. Critically, the correlation between the self-generation effect and the SPQ was observed in Oestreich et al. (2015) when comparing participants' own speech with a listening condition. However, this correlation was not reported in the subsequent study (Oestreich, 2016), which involved self-initiated sounds via button presses, akin to the approach in the present thesis. Hence, Study III is structured to both attempt to replicate these prior findings and explore whether they hold across different experimental settings where self-generation effects have been identified. Going beyond previous research, Study III incorporates multiple measures of self-generation effects,

including sensory attenuation, pupil dilation, and memory performance. Additionally, given the potential connection between the N1 attenuation deficit in schizophrenia and alterations in sensory prediction, Study III expands upon previous research by collecting data from four additional personality questionnaires. These questionnaires have been utilized to explore the relationship between sensory prediction deficits, schizotypal traits, and the sense of agency (Teufel et al., 2010) and will aid to discern which traits are contributing to the observed variability.

OBJECTIVES

OVERVIEW

The present work examined, through three studies, the self-generation effects from the neurophysiological (i.e., electrophysiological and pupil responses) and high-order cognitive levels (i.e., memory encoding and personality traits). The overarching aim was to elucidate whether the impact that motor actions have on our sensory experience have further consequences on active learning and shape the way we perceive the consequences of our own actions.

SPECIFIC AIMS AND HYPOTHESES

STUDY I

- Investigate the impact of sensory response modulation on the ERP components N1, Na, Tb and P2 during movement on memory encoding for concurrent stimuli. We expect to replicate attenuation of the sensory components for sounds coinciding with actions compared to EG sounds.
- 2. Assess whether the P3 component is elicited during the encoding phase due to sound unpredictability. Although both passively presented sounds and motor-coinciding sounds will be equally unpredictable, the surprise for the sounds coinciding with a motor act will be higher and thus will elicit a P3 component.
- 3. Examine whether memory performance is affected by the coincidence of sounds with motor actions during the encoding phase. Memory performance for stimuli that coincide with actions should be enhanced compared to stimuli that are passively presented.

- 4. Explore potential neural indicators at retrieval of altered memory representation, specifically focusing on N1 and P2 attenuation. Although we don't have a specific hypothesis, we expect a modulation of those sensory responses at retrieval that have been modulated at encoding during the presentation of a sound previously encoded with a motor action.
- 5. Assess the modulation of the old/new effect at the neural level at retrieval, with a focus on a more positive-going potential for correctly recognized old items as an index of conscious recollection. We expect that sounds encoded with a concurrent motor action will be better remembered and thus will present an enhanced old/new effect when correctly remembered compared to passively heard sounds.

STUDY II

- Investigate whether motor actions structure memory encoding, leading to differentiated memory representations for pairs of sounds encoded within the same context (SG-SG or EG-EG) compared to across contexts (EG-SG or SG-EG). Based on event segmentation literature, within context pairs will have a higher memory performance than across context pairs.
- 2. Examine whether a memory advantage exists for SG sounds over EG sounds, specifically focusing on sequential order memory performance for SG pairs compared to EG pairs. Based on the production effect, within context pairs that are SG will have a higher memory performance than EG pairs.
- 3. Determine whether self-generation effects are present by assessing the presence of attenuated N1, Na, Tb and P2 amplitudes for SG sounds compared to EG sounds during

encoding. We expect to replicate previously reported attenuation effects to SG sounds on the sensory components.

- 4. Investigate the contribution of unspecific neuromodulatory mechanisms associated with motor actions, particularly by measuring pupil dilation and comparing the dilation for SG stimuli to that of EG stimuli during sound encoding. Pupil dilation elicited to SG sounds will be greater than for EG sounds.
- 5. Explore the formation of event boundaries in memory encoding and its relationship to motor actions. Based on current knowledge we expect an enhanced P3 amplitude to boundary sounds (occurring after an event boundary) compared to non-boundary sounds.
- Examine whether event boundaries lead to changes in arousal, as marked by pupil dilation. We expect a greater pupil dilation for boundary sounds compared to nonboundary sounds.
- 7. Assess whether self-generation effects on auditory ERPs at encoding are correlated with memory performance. If the self-generation effect impacts memory performance, we expect a positive correlation were higher attenuation (more self-generation effect) is associated with higher order memory performance for SG pairs and greater memory difference between across and within pairs.
- 8. Investigate potential correlations between differences in pupil dilation for SG and EG sounds and the magnitude of self-generation effects on auditory ERPs at encoding, shedding light on unspecific neuromodulatory contributions. We expect that self-generation effects will be associated with pupil dilation, i.e., higher pupil dilation for SG sounds with higher sensory attenuation.
9. Explore the relationship between the activity of unspecific neuromodulatory mechanisms, as indicated by differences in pupil dilation during encoding, and memory performance, providing insights into the role of neuromodulation in memory encoding. We expect that higher pupil dilation will correlate with better memory performance.

STUDY III

- Examine the inter-individual variability on the SG effects, under different experimental manipulations, and its relationship to schizotypal personality and internal or external locus of control in healthy individuals. We expect that individuals who score higher on schizotypal scales and have an external locus of control will have an attenuated selfgeneration effect:
 - a. Replicate previous findings that found a relationship between schizotypy, as reflected by the SPQ scale, and the N1 self-generation effect. We expect to find a negative correlation with high schizotypy and the N1 self-generation effect.
 - b. Conduct a factorial exploratory analysis on several psychological scales that measure schizotypy and locus of control to identify which specific personality traits are most strongly related to sensory attenuation or facilitation effects in the context of self-generation.
 - c. Explore the existence of a continuum of psychosis on other sensory components that exhibit a consistent self-generation effect, that is Tb and P2.
 - d. Explore the existence of a continuum of psychosis on the neuromodulation of SG sounds compared to EG sounds as reflected by pupil dilation.
 - e. Explore the existence of a continuum of psychosis on memory performance differences between SG and EG sounds.

METHODOLOGY

GENERAL METHODOLOGY

This section is a concise overview of the main methodology employed throughout the development of the present thesis. All three studies were conducted within the laboratory of the Brainlab - Cognitive Neuroscience Research Group at the University of Barcelona and are under the scope of a funded Ministry project (PSI2017-85600-P). Details regarding the methodologies specific to each study will be presented in the following sections.

PARTICIPANTS

Participants across all three studies were healthy individuals with normal hearing and no history of psychiatric or neurological disorders, mainly recruited from the University of Barcelona's student population. Participants in these studies were required to meet specific inclusion criteria, including not consuming drugs that affect the central nervous system 48 hours prior the start of the experiment, and falling within the age range of 18 to 45; additionally, for studies involving pupillometry (II and III), participants were also excluded if they wore glasses or contact lenses. All participants provided written consent, and ethical approval was obtained from the Bioethics Committee of the University of Barcelona (IRB00003099). Compensation was provided to participants in all three studies, with a payment of 10 euros per hour being the standard practice.

EXPERIMENTAL PROCEDURE

All studies were conducted in an electrically and acoustically shielded room appropriate for electroencephalography (EEG) recording. Additionally, for Studies II and III, participants sat

with their head positioned on a chinrest, maintaining approximately 60cm from the screen to record pupil dilation. To ensure participants were adequately prepared for the tasks, they were carefully instructed of the task they had to perform and were always provided with a practice block before commencing the experimental trials. To prevent participant fatigue, short breaks were introduced throughout the duration of the experiments. The overall duration of the experiments, with breaks, was kept under 90 minutes. Preparation usually took between 30 and 60 minutes.

APPARATUS

Auditory stimuli were uniformly delivered binaurally through over-ear headphones (Sennheiser, HD 558) to ensure a consistent listening experience. Participants' responses, including button presses and other task-related actions, were accurately recorded using a silent response pad (Korg nanoPAD2), minimizing interference with the auditory stimuli. Visual stimulation was delivered through an AT Radeon HD 2400 monitor. Experimental control and stimulus presentation were executed through MATLAB R2017a (The Mathworks Inc., 2017) in conjunction with the Psychophysics Toolbox (Brainard, 1997; Kleiner et al., 2007), providing precise control over experimental parameters and participant responses. EEG data acquisition was conducted using a Neuroscan SynAmps RT amplifier (NeuroScan, Compumedics) with a sampling rate of 500 Hz. A total of 64 Ag/AgCl electrodes were placed following the 10% extension of the International 10–20 system (Oostenveld and Praamstra, 2001) and inserted into a nylon cap (Quick-Cap; Compumedics), guaranteeing standardized electrode placement. Impedance levels for EEG electrodes were closely monitored throughout the recordings, with values kept below 10 k Ω , to ensure signal quality.

Study II, and the experiments that conform Study III, incorporated the EyeLink 1000 desktop mount with the Eyelink add-in toolbox for eye tracker control (SR Research; sampling rate: 1,000 Hz) to record pupil dilation along with horizontal and vertical eye movements during the experiment, whereas pupil recording was not present on Study I.

For Study III we employed five personality questionnaires, delivered through the Qualtrics platform. The Spanish versions of those questionnaires were the Schizotypal Personality Questionnaire (Raine, 1991; Spanish: Fumero et al., 2009 and Rabella et al., 2018), the Peters et al. Delusion Inventory (Peters et al., 1999; Peters et al., 2004; Spanish: López-Ilundain et al., 2006), the Perceptual Aberration Scale (Chapman et al., 1978; Spanish: Fonseca-Pedrero et al., 2009 and Ros-Morente et al., 2010), the Magic Ideation Scale (Eckblad & Chapman, 1983; Spanish: Fonseca-Pedrero et al., 2009 and Ros-Morente et al., 2009 and Ros-Morente et al., 2010) and the Rotter Internal-External Locus of Control (I-E scale; Rotter, 1966; Spanish: Tous, 1984 and Ferrando et al., 2011).

DATA ANALYSIS

Analyses of the EEG, pupil, and behavioral data were conducted employing MATLAB R2019a (The Mathworks Inc., 2019) and R (version 3.6.0). In terms of statistical examination R, SPSS and Jamovi (version 2.3; The jamovi project, 2022) were used. T-tests and ANOVAs were conducted as the main statistical method, with the analysis in Study I further supplemented by Bayesian t-testing. For the assessment of personality data, an exploratory factorial analysis was employed. Correlation analyses were executed utilizing the Pearson correlation coefficient. Cluster-based permutation statistics were adopted for both pupillometric and EEG data, for the pupil as the main analysis form and as an additional and exploratory analytical approach for the EEG.

Behavioral

As for behavioral data, in all three studies there was memory performance on the experimental tasks. The percentage of correct responses was calculated on all of them separately for each experimental condition and compared by using paired samples t-tests. Additionally for Study I, we conducted post-hoc Bayesian t-tests to assess the evidence supporting a difference calculating the Bayes factor (BF10) for the alternative hypothesis. To assess the bias in the responses of Study I, we calculated sensitivity and criterion measures. Specifically for the aims of Study III behavioral data was normalized (z-score) across experiments and experimental groups.

Personality

To analyze the questionnaire data for Study III, we conducted an exploratory factorial analysis. The factors that emerged from this analysis, along with their respective loadings, were employed to compute factorial scores. To categorize participants into two groups for subsequent analysis using repeated measures ANOVA, we applied a median split based on their scores on the derived personality measures.

Electrophysiological

All studies underwent a similar pipeline of EEG preprocessing. Data were processed and analyzed using EEGLAB, Fieldtrip and Eeprobe software. Manual artifact rejection was performed to eliminate non-stereotypical artifacts. Independent Component Analysis (ICA) was applied to identify and remove eye-movement-related components from the data. Afterward, the data was bandpass filtered (0.5 or 1 to 25 Hz), and interpolation was applied to channels marked as broken during recording. Epochs were extracted relative to event onsets and underwent baseline correction. Rejected epochs with voltage range exceeding 75 μ V were

discarded. The studies examined auditory ERPs, including in all of them the N1, P2, and N1 subcomponents (Na and Tb) at encoding. Before statistical analysis, data for Study III was normalized (z-score) across experiments and experimental groups. Paired sample t-tests were used for statistical analysis on Study I and II and repeated measures ANOVAs for Study III. Additionally, Bayesian factors were calculated only for Study I. An exploratory analysis was conducted for Study II to uncover potential effects that may not have been evident through our focused ERP analyses. To manage the challenge of multiple comparisons and identify clusters showing significant group differences across various dimensions (combining electrode and time samples), we employed a non-parametric cluster-based permutation approach (Maris & Oostenveld, 2007). This involved creating clusters by grouping neighboring sensors using a Delaunay triangulation in a 2D representation of the electrode arrangement. We ensured each cluster included a minimum of two nearby electrodes. For each experimental comparison, we performed a two-tailed t-test on the values extracted from individual electrode-time samples within the epochs. To determine the significance of these clusters, we utilized the nonparametric Monte Carlo method, conducting 10,000 random partitions. Clusters were formed by grouping adjacent electrode-time samples that surpassed a predefined significance level of 0.05. To obtain a cluster-level statistic, we summed the individual t-statistics within each cluster. The significance level (p-value) was calculated using the non-parametric Monte Carlo method, providing a robust assessment of the identified clusters' statistical significance.

Pupillometry

In both Study II and the independent studies that comprise Study III, pupillometry data were processed and analyzed following a similar pipeline (Paraskevoudi & SanMiguel, 2023a), using Fieldtrip (Oostenveld et al., 2011). The EyeLink software detected missing data and blinks, which were linearly interpolated within a time window of -100 to 100 ms. Blinks

occurring less than 250 ms apart were joined as a single blink (Urai et al., 2017). A bandpass filter (0.05–4 Hz third-order Butterworth) was applied to the interpolated pupil data to reduce noise. To remove the effects of blinks and saccades on pupil responses, a deconvolution analysis was conducted, and the responses were eliminated from the data using linear regression (Knapen et al., 2016; Urai et al., 2017). The processed pupil data, after z-scoring per trial, were epoched, baseline corrected by subtracting the mean pupil diameter 500 ms before the event onset, and resampled to 100 Hz. The average evoked response for the main events of interest was computed for each participant.

To assess statistical significance, cluster-based permutation tests were employed (Urai et al., 2017). These tests were conducted to account for multiple comparisons and determine whether there were statistical differences between contrasting conditions within participants. Clusters were defined by consecutively passing a specified threshold (sample p-value of 0.05). Cluster statistics were computed as the sum of paired t-values for all samples within the cluster. The permutation procedure involved randomly switching labels of individual observations between paired sets of values, repeated 10,000 times. The p-value was calculated as the fraction of permutations that exceeded the observed difference between the means, indicating two-sided dependent samples tests.

SPECIFIC METHODOLOGY

STUDY I

Participants

Twenty-two healthy subjects provided written consent and participated in the study. The sample size was selected based on previous studies reporting robust self-generation effects (e.g. Horváth et al., 2012). Three participants were excluded from the analysis due to low signal-to-

noise ratio on the electrophysiological data. Thus, the final sample consisted of 19 participants (6 males, mean age 22.74 years, range 18 - 29).

Stimuli

We generated a total of 100 different environmental, natural, complex and non-identifiable sounds. Samples selected from the McDermott were (http://mcdermottlab.mit.edu/svnh/Natural-Sound/Stimuli.html) and the Adobe (https://offers.adobe.com/en/na/audition/offers/audition_dlc.html) sound libraries. Nonidentifiable sounds were selected to avoid, or at least minimize, semantic activation and instead focus the identification on the physical properties of the sounds. Sounds were sliced to a duration of 250 ms, ramped (0.01 s, exponential) and presented at 44.1 kHz, 16 bit and mono. The sound intensity was normalized across sound samples and adjusted to a comfortable hearing level. The 50 least identifiable sounds, according to an independent rating of 3 subjects, were used in the main experiment and the next 50 in the training.

Experimental design

The general design of the experiment was a Delayed-Match-to-Sample Task (DMTS), which consisted of 3 phases: encoding, retention, and retrieval. During the encoding phase, we exposed the subjects to auditory stimuli which they had to memorize. Half of the sounds were presented coinciding with a button press of the participant and constitute the Motor-auditory (MA) condition. The other half of the sounds were not related to any action of the participant and constitute the Auditory (A) condition. After a short retention period, we presented a test sound at retrieval. Participants responded whether the test sound was one of the sounds presented during the encoding and, thus, an old sound (Old condition) or a new sound (New condition, Figure 1).



Figure 1. Schematic description of a trial depicting the Visual (Vis), Auditory (Aud), and Motor (Mot) occurrences taking place, and highlighting an example event for each Condition (Con): motor-auditory (MA), auditory (A), and motor (M). Time in seconds, t(s): the timepoints mark the beginning of each phase of the trial. ITI: inter-trial interval. Finger used to generate sounds was the thumb.

Encoding

At the beginning of each trial, the screen displayed 6 horizontally aligned and randomly spaced grey rectangles and a perpendicular, horizontal line that proceeded from left to right. Subjects pressed a button with their right thumb every time the line intersected a rectangle. Meanwhile, 6 sounds were presented which they had to memorize. On 50% of the presses, a sound was immediately presented after the press and the remaining sounds were presented between presses. Subjects were not told that some of the sounds will be generated by their actions. This resulted in 3 different event types: 3 x Motor condition (M): The subject pressed the button, but no sound was presented, 3 x A condition: A sound was presented without any action of the subject, 3 x MA condition: A sound was presented the moment the subject pressed the button. If subjects failed to press the button when indicated, an error message was presented, and the trial was aborted.

The total duration of the encoding phase was 12.8 s. The 9 encoding events occurred pseudo randomly within this time, with the following limitations: The event-to-event onset asynchrony varied randomly between 0.8 s and 2.4 s. However, the minimum sound-to-sound onset

asynchrony was 1.6 s. The last event occurred latest at 12 s, and it was always a sound event (MA or A). M events were always separated by at least one sound event.

Retention

After the encoding phase, a fixation cross was presented for 1.2 s. This was estimated as the minimum duration that would engage short term memory while minimizing echoic memory contributions (Crowder, 1976; Lu et al., 1992).

Retrieval

The test sound was presented 14 s after trial onset. A "Yes/No?" replaced the fixation cross on the screen 0.8 s after test sound onset, prompting participants to answer whether the test sound was old or new. The response window was 1 s. Once the participant responded, or after the response window ended, the question on the screen was replaced with a fixation cross until the onset of the next trial. The intertrial interval was 2 s.

Each of the 50 unique sounds used in the experiment served as the test sound in 4 trials. In these 4 trials, the sound sequences were composed of the same 6 encoding sounds and one test sound. However, two of these trials belonged to the Old condition, where the test sound was part of the encoding sequence, once presented coinciding with a button press (MA condition) and once presented without any action (A condition). The other two trials represented the New condition. These were identical to the Old condition, except that the test sound was replaced by another sound both at encoding and retrieval. The rest of the events of the trial (i.e., the other encoding sounds and the participant's actions) were identical across the 4 trial versions generated for each unique sound.

The position of the test sound within the encoding sequence was chosen randomly for each unique sound. The positions could be from the second to the fifth, avoiding the first and last encoding sound positions to avoid primacy and recency effects (Mondor & Morin, 2004). However, to ensure that subjects did not learn to ignore those positions, 20 Catch-trials were added to the experiment with either position 1 or 6 for the encoding-test sound. The Catch-trials were not part of the analysis.

Procedure

The experiment started with a progressive training where the participants learned how to perform the experiment in several short blocks of 5 trials each. First, they learned how to press the button on time whenever the line hit one of the rectangles, without auditory input. The word "error" appeared instantly on the screen every time they did not press the button on time. At the end of each block, feedback was presented on how many presses they missed and how many presses were not on time. Subsequently, auditory input was added, and subjects were instructed to perform the memory task. Here, the feedback screen at the end of each block also showed the "Misses" indicating unanswered questions or answers out of the required time window. Each part of the training was repeated until the subject could perform within minimal errors and misses.

After the successful training the experiment began which consisted of 22 blocks of 10 trials each, presented in randomized order. Total experimental time without pauses was 65 minutes. Subjects took short breaks between blocks to avoid fatigue.

Apparatus

The experiment was performed in an electrically shielded chamber. The center of the screen was positioned at eye height, at 1.2 m. The EEG was recorded at a sampling rate of 500 Hz

using Neuroscan 4.4 software via a SynAmps RT amplifier (NeuroScan, Compumedics). We used 64 Ag/AgCl electrodes inserted in a nylon cap (Quick-Cap; Compumedics) following the 10% extension of the International 10–20 system (Oostenveld & Praamstra, 2001). The EOG was recorded with NAS and one electrode under each eye (Schlögl, 2007). The reference was set at the tip of the nose and the AFz electrode served as the ground. Impedances were kept below 10 k Ω . Auditory stimuli were delivered binaurally via over-ear headphones (Sennheiser, HD 558). Participants' button presses and responses were recorded with a silent response pad (Korg nanoPAD2). The setup was controlled and performed via MATLAB (The MathWorks, www.mathworks.com) with the Psychophysics Toolbox (Brainard, 1997; Kleiner et al., 2007).

Behavioral analysis

We calculated the percent of correct responses for sounds encoded as A and MA as well as for Old (both A and MA) and New sounds and performed a two-tailed paired samples t-test for each of the two comparisons (A-MA, Old-New). To complement our frequentist analysis, we conducted post-hoc Bayesian t-tests to assess the evidence supporting a difference. We calculated the Bayes factor (BF10) for the alternative hypothesis (i.e., the difference of the means is not equal to zero), which was specified as a Cauchy prior distribution centered around 0 with a scaling factor of r = 0.707. The null hypothesis was specifically matched to an effect magnitude with a standardized effect size $\delta = 0$ (Rouder et al., 2009). Data were viewed as moderate support for the alternative hypothesis if the BF10 was larger than 3, whereas values close to 1 were considered only weak evidence and values below 0.3 were viewed as supporting the null hypothesis (Lee & Wagenmakers, 2013). Finally, to assess the bias in the responses we calculated sensitivity (as d' = z(Hit) - z(False Alarm)) and criterion (c = -0.5 * (z(Hit) + z(False Alarm)); Roussel et al., 2013).

EEG preprocessing and analysis

EEG analysis was performed with EEGLAB (Delorme et al., 2004) and Eeprobe (ANT Neuro) was used for visualization. Data was high pass filtered at 0.5 Hz and non-stereotypical artifacts were manually rejected. We then applied Independent Component Analysis (ICA) decomposition using the binary version of the Infomax algorithm. After manual identification of the eye-movement artifactual components, the ICA weights of those components (mean components: 2.8) were removed from the raw data, already high pass filtered at 0.5 Hz. Subsequently, data was low pass filtered at 25 Hz and channels marked as broken at recording were interpolated.

Epochs were extracted from -0.1 to 0.5 s around the onset of each event of interest using the prestimulus period for baseline correction. At encoding epochs were defined for Auditory (eA) and Motor-auditory (eMA) sounds and Motor (eM) events; and at retrieval for encoded as Auditory (rA) and encoded as Motor-auditory (rMA) sounds. At retrieval, we also extracted epochs for correctly rejected New sounds, and for correctly recognized Old sounds, both as a whole and separately for those encoded as Auditory (rAcorrect) and Motor-auditory (rMAcorrect). Epochs with a voltage range exceeding 75 μ V were rejected.

To test for the effects of actions on neural responses to sounds, we compared the auditory ERPs between MA and A events at encoding (eA vs eMA) and between encoded as MA and encoded as A at retrieval (rA vs rMA). At encoding, MA responses were corrected subtracting the ERP elicited by Motor events (eMA-eM) prior to this comparison. Both at encoding and retrieval, specifically, we tested for differences in the amplitude of the auditory N1 and P2 components at electrodes Cz and mastoids, and the N1 subcomponents Na and Tb at the collapsed electrodes T8 and T7, all identified and measured following SanMiguel et al. (2013). Given that P3 modulations have been reported (but not discussed) in previous work (e.g. Horvath et al. 2012),

we decided to analyze P3 at encoding identified as the peak of the difference wave (A –[MA–M]) in the P3 window range based on previous work (e.g., Baess et al., 2008). At retrieval, the P3 component window served to test the old/new effect comparing responses between the correct New and correct Old (as a whole and separately for rAcorrect and rMAcorrect). We compared the mean amplitude of the components of interest in the identified time-windows at each electrode with two-tailed paired samples t-tests (Cz, Pz, collapsed mastoids and temporal electrodes) and with the BF10 for consistency with the behavioral analysis.

STUDY II

Participants

The sample size for Study II was determined based on previous similar studies (Silva et al., 2019). Initially, a total of 28 healthy participants were recruited to take part in the experiment. However, 3 participants had to be excluded due to a low signal-to-noise ratio in the EEG data. As a result, the final sample consisted of 25 participants (mean age: 21 years old; 8 males).

Study Design

We designed an electrophysiological and pupillometry experiment with a temporal order memory task to investigate how self-generation affects event segmentation. The order memory task had three phases: encoding, retention, and retrieval (Figure 2). During the encoding phase, participants were presented with a sequence of nine sounds that included both SG and EG sounds. Critically, all SG or EG sounds at encoding appeared consecutively, creating two different events based on the source of the sounds within the nine-sound sequence. Immediately after, there was a short retention period to memorize the sequential order of the sounds. During the retrieval phase, participants were presented with a pair of sounds, and they had to indicate whether they appeared in the same order as during encoding. The test sounds belonged either to the same event (within condition) or to different events (across condition) but were nonconsecutive in the sequence. We used visual stimuli to structure the task and indicate participants when to perform actions to generate sounds. To ensure participants understood the task, they underwent at least five practice trials using a simplified version of the task before the start of the experiment (see page 39).



Figure 2. Schematic description of the temporal order memory task with externally-generated (EG) and self-generated (SG) sounds. This example trial corresponds to the across-events condition. The timepoints mark the duration of each phase of the trial. ITI corresponds to the inter-trial interval.

Encoding phase

At the beginning of each trial, participants were presented with a row of vertical lines on the screen. The number and distribution of vertical lines varied from trial to trial as determined by the experimental manipulations. Throughout the encoding period (14.85 s), a horizontal line moved steadily across the screen from left to right, passing over each vertical line in its path. Participants were instructed to press the bottom-right button on a response pad with their right index finger whenever the horizontal line crossed a vertical line. This action produced a sound immediately after the button press. In each trial, the encoding set consisted of nine sounds,

some of which were delivered consecutively after each button press (SG), while others were presented passively (EG) either before or after the sequence of button presses. This manipulation created two events in a sequence, each event formed by SG or EG sounds. The change in the source that generated the auditory stimuli, either EG or SG, acted as the contextual shift, and the first sound delivered by the new source was the boundary sound. Participants were instructed to pay attention to the order of all the sounds regardless of the motor task. The sound onset asynchrony was set between 1.3 to 2 s semi randomly in steps of 0.05 s.

Retention and Retrieval phase

Following the encoding phase, participants were given a short retention period of 2 s to retain the sequence's order. During the retrieval phase, a pair of two non-consecutive sounds of the encoding phase were presented, with a 2 s onset separation interval. The pair of test sounds could appear in the correct or in the inverse order of presentation and could both be from the same encoding event (within condition) or could be one sound from each of the two encoding events (across condition). After 0.8 s following the onset of the second test sound, participants were asked if the pair's order of presentation was the same as at encoding. They had unlimited time to respond on the response pad YES or NO using the middle and index fingers of their left hand. The identity of the two buttons, either YES or NO, was counterbalanced across participants. The inter-trial interval was set to 2 s after the participant's response.

Visual Stimuli

The use of visual stimulation was necessary to ensure participants followed instructions and maintained fixation during the experiment, which allowed us to record their pupil response accurately. We presented a fixation cross at the center of the screen throughout the experiment,

to indicate where participants should focus their gaze. The moving horizontal line from left to right and the stationary vertical lines appeared just below the fixation cross to indicate the progress of each trial and the appropriate time to press the button. These visual stimuli appeared within a small area on the center of the screen (visual angle 2.3°) to eliminate any effects of gaze position on pupil diameter (Gagl et al., 2011).

Auditory stimuli

We developed a set of unique auditory stimuli for our experiment by sourcing identifiable sounds from several freely available sound databases (Adobe; FreeSound; Belin et al., 2000; Gygi & Shafiro, 2010; Hocking et al., 2013; Norman-Haignere et al., 2015). Initially, we extracted 1110 different sounds, which we edited to have a duration of 250 ms and 10 ms exponential onset/offset ramp. To ensure the task's feasibility, we manually selected sounds that were still recognizable after editing (i.e., not noise) and categorized them into distinct semantic groups. We grouped similar sounds into the same category to create as many different categories of sounds as possible, resulting in 15 semantic categories with 24 sounds each from animal, environmental, human, and music sounds (e.g. high pitch animal vocalizations, drums, alarms, aspirated vowels, etc.). During practice trials, we presented participants with pure tones of different frequencies ranging from 300 to 3700 Hz in 100 Hz steps instead of experimental sounds. All sounds were played at a sampling rate of 44.1 kHz, 16 bits, mono, and an intensity of 75 db.

We generated 24 unique sound sequences for each participant, consisting of 9 different sounds randomly selected without replacement from 9 of the 15 semantic categories to ensure variability. These unique sound sequences were presented 9 times each with different experimental manipulations (see next section). In each unique sound sequence, seven of the sounds were presented only in the encoding phase (encoding-only sounds), while the remaining two encoding sounds were also test sounds, presented again during the retrieval phase. To prevent sequential presentation of the 9 repetitions for each unique sequence, we distributed the 216 trials into 24 blocks, each containing a single repetition of a unique sound sequence.

Experimental manipulations

We manipulated several variables across each repetition of a unique sound sequence. At encoding, we used two sound sources: SG and EG, with half of the encoding sounds overall in the experiment belonging to each type. We counterbalanced the order of the two events within each sequence, thus half of the sequences began with EG sounds and then SG sounds and vice versa. Additionally, we manipulated the position of the test pairs at encoding. In half of the trials the test sounds appeared in the third and sixth positions of the encoding sequence, and the other half had them in the fourth and seventh positions. We also varied the length of the events, which ranged from 2 to 7 sounds. The varied lengths allowed us to counterbalance the appearance at encoding of both retrieval test pair conditions (within and across) in each test position. However, we included 24 catch trials (one for each block) where we asked about the fifth and eighth positions, to ensure that participants didn't notice that we were asking about the same positions repeatedly. The retrieval phase of these catch trials was not included in the analysis.

At retrieval, we created two test pair conditions: within and across. In the within condition, half of the trials featured a SG-SG pair, while the other half featured an EG-EG pair. In the across condition, half of the trials presented a SG sound followed by an EG sound, and the other half presented an EG sound followed by a SG sound. Finally, we presented the test sounds in either the correct sequential order or the inverse order, with each version used in half of the trials.

Motor-only blocks

In self-generation studies, to be able to assess the effects of actions on auditory ERPs, it is standard procedure to eliminate the motor-related activity from the SG sound ERPs prior to comparing the auditory responses between SG and EG sounds (SanMiguel et al., 2013). To subtract the motor component from the SG sound responses in the ERP analysis, we added motor-only (M) blocks. These blocks were equal to the first 4 blocks of experimental trials but without a retrieval phase and without auditory stimuli. This ensured that the M evoked potentials were elicited by similar conditions to the SG sounds. These sequences were presented in 4 separate blocks of 9 sequences each, creating a total of 36 motor sequences which gave us a mean of 162 M items per participant (2 to 7 M items per sequence). Before the beginning of each motor block, we warned participants that they were in a motor only block and that, consequently, no question or sounds would appear.

Apparatus

Binaural presentation of auditory stimuli was achieved using over-ear headphones (Sennheiser, HD 558). Participants' button presses and responses were recorded using a silent response pad (Korg nanoPAD2) to avoid interference with the auditory stimuli. The instructional visual stimulation was delivered through an AT Radeon HD 2400 monitor. The experimental setup and control were conducted using MATLAB R2017a (The Mathworks Inc., 2017) in conjunction with the Psychophysics Toolbox (Brainard, 1997; Kleiner et al., 2007) and the Eyelink add-in toolbox for eye tracker control (SR Research).

To record the EEG activity, we used a Neuroscan SynAmps RT amplifier and CURRY 8 software (NeuroScan, Compumedics). We recorded data from 64 channels placed according to the international extended 10–20 electrode system (Chatrian et al., 1985) by means of 64 Ag/AgCl electrodes inserted in a nylon cap (Quick-Cap, Compumedics). The reference

electrode was placed at the nose, and we placed 4 additional electrodes above and below the left eye and in the outer canthi of the eyes to record the electrooculogram. We continually recorded the EEG activity at a sampling rate of 500 Hz. Impedance levels were maintained below 5 k Ω to ensure proper signal quality.

To obtain the pupillometry, we recorded the pupil's area from the left eye along horizontal and vertical gaze position at 1000 Hz sampling rate using an EyeLink 1000 desktop mount (SR Research). Pupil area was assessed using a center-of-mass algorithm in the centroid mode of the eye tracker.

Procedure

We conducted the experiment in an electrically and acoustically shielded room. Participants sat with their head placed on a chinrest approximately 60cm from the screen. To ensure that participants were adequately prepared for the task, they were given a practice block consisting of five trials of a modified version of the task where the sounds were pure tones, the encoding phase had only six sounds and test sounds were separated only by one sound. They were allowed to repeat this block as many times as needed to ensure they understood the task. The main experiment consisted of 24 blocks of experimental trials and four blocks of motor-only trials, with the first motor block presented before the first experimental block, and every six blocks thereafter. To prevent participant fatigue, short breaks were included at least every seven blocks. The experiment lasted approximately 90 minutes without preparation or breaks.

Behavioral analysis

To evaluate participants' order memory performance, we calculated the percentage of correctly answered retrieval questions ("is this the correct order?") for pairs of sounds that were presented either within or across events, and for each specific combination of sound source (EG-EG, SG-SG, SG-EG, EG-SG) separately. We conducted two-tailed t-tests to compare the percentage of correct responses between conditions and sound source combinations.

EEG preprocessing

We measured electrophysiological activity to retrieve event-related potentials (ERPs) in response to the encoding sounds and button presses in the motor-only (M) trials. The raw EEG data was bandpass filtered from 1 to 25 Hz using a Kaiser window (Kaiser β 5.653, filter order 1812) and manually examined to remove continuous atypical artifacts and to identify faulty electrodes. We then applied Independent Component Analysis (ICA) using the logistic infomax ICA algorithm (Onton & Makeig, 2006) to identify the eye-movement related components. The ICA weights of those components were subtracted from the raw bandpass filtered data. Remaining artifacts were rejected by applying a threshold of 75 µV maximal signal-change per epoch and malfunctioning electrodes were interpolated spherically. Participants with excessive artifacts in their EEG recordings (> 60% of epochs meeting the rejection criteria) were excluded. All the catch trials and the encoding trials with incorrect button presses were removed from the analysis. Epochs of -200 to +600 ms relative to sound or button press onsets, with a baseline correction from -200 to 0 ms, were extracted for each encoding item (EG, SG, and M) and for encoding sounds that occurred in the last position before a boundary (bB) and the boundary sounds (i.e. after a switch in the sound source, the first sound elicited by the new source, B), separately for EG (EGbB, EGB) and SG sounds (SGbB, SGB). All SG epochs were corrected for motor activity (SG-M) by subtracting the M epochs' averages to remove the activation resulting from motor actions. For simplicity, however, we will from now on refer to SG-M as SG.

ERP analysis

In order to investigate the self-generation effects, we compared the responses to EG sounds and the SG sounds by extracting the mean amplitudes of the N1 component (window: 80-120 ms) at Cz and joined mastoids (N1mast), the P2 component (window: 150-250 ms) at Cz, and the N1 subcomponents Na (window: 80-100 ms) and Tb (window: 110-150 ms) at the joined temporal electrodes (T8 and T7), following the methodology described in SanMiguel et al. (2013). We used two-tailed t-tests to compare the amplitudes of EG and SG on all the defined components: N1, N1mast, P2, Na and Tb.

To examine the potential boundary effect, we evaluated the sensory response to boundary sounds by extracting the mean amplitudes of the N1 and P2 components at Cz. To assess context change we planned to extract the mean amplitude in the P3 window at its maximum midline electrode (Pz). However, contrary to our expectations, we observed a negative instead of positive response at this spatiotemporal location. Moving forward, we will refer to this component as the parietal negative response (PNR, window: 392-432). We used 2x2 repeated measures ANOVAs with the factors Source (EG vs. SG sounds) and Position (B vs. bB sounds) to compare the amplitudes on all the defined components: N1, P2, and PNR.

We conducted a data-driven analysis to explore the possibility of detecting further effects that may not have been captured by the targeted ERP analyses (Maris & Oostenveld, 2007). To control for multiple comparisons and identify clusters with significant group differences in multiple dimensions (electrode-time samples), we used a non-parametric cluster-based permutation analysis. We defined neighboring sensors using a Delaunay triangulation over a 2D projection of the electrode montage and set a minimum of 2 nearby electrodes per cluster. This analysis was performed for all comparisons, and for each comparison, a two-tailed t-test was performed on the extracted values of each electrode-time sample of the epochs. The resulting amplitude values were assessed using the non-parametric Monte Carlo method with 10000 random partitions. Clusters were created by grouping adjacent electrode-time samples exceeding a significance level set to 0.05. The sum of individual t-statistics was calculated within each cluster to obtain a cluster-level statistic, and the significance level (p-value) was calculated using the non-parametric Monte Carlo method.

We used EEGLAB (Delorme & Makeig, 2004) for EEG preprocessing and ERP analysis, Eeprobe (ANT Neuro) for ERP visualization and mean amplitude extraction, and Fieldtrip (Oostenveld et al., 2011) for the data-driven analysis.

Pupillometry preprocessing

We measured the pupil diameter in response to all the encoding items following a similar pipeline as described in (Paraskevoudi & SanMiguel, 2023a), using Fieldtrip (Oostenveld et al., 2011). The EyeLink software detected missing data and blinks which were linearly interpolated using a time window from -100 to 100 ms. Missed blinks were identified using peak detection on the velocity of the pupil signal (Urai et al., 2017). If they occurred less than 250 ms apart they were joined as a single blink and the resulting blinks were then linearly interpolated. To reduce measurement noise not likely to originate from physiological sources, the interpolated pupil time series were filtered using a 0.05-4 Hz third-order Butterworth filter. The effect of blinks and saccades on the pupil response was estimated through a deconvolution analysis and removed from the data using linear regression (Knapen et al., 2016; Urai et al., 2017). We used the residual bandpass filtered pupil time series (z-scored) for the evoked analyses (Slooten et al., 2019). The data was downsampled to 100 Hz and epoched from -0.5 to 1.5 ms with a baseline correction of 500 ms before the sound onset. The average evoked response for each participant was obtained for all the EG and SG sounds at encoding, and for the boundary and the before boundary sounds separated by sound source (EGB, EGBB, SGB,

SGbB). To further explain the boundary pupil data we decided a posteriori to conduct an exploratory (not pre-registered) analysis to assess the overall pupil response for each event type, depending on the event order within a sequence (1st or 2nd). For this additional analysis, we aggregated all preprocessed (except for baseline correction) sound epochs belonging to the same event and calculated the overall mean pupil diameter for the event. We then calculated the grand average for all first events (sounds before the boundary) and all second events (sounds after the boundary), separately for EG events and SG events. It is important to clarify that we did not perform any motor correction in the pupillometry analysis because our goal was to evaluate the impact of motor actions on the pupil response.

Pupillometry analysis

Non-parametric permutation statistics were used to test for group-level significance of the individual averages, following the same procedure as for the EEG data except that for pupillometry the clusters were defined based on the time dimension only. We tested for possible differences in evoked pupil responses computing t-values of the difference between the conditions of interest and thresholded these t values at a p value of .05. We tested for the main effects of Source (EG vs. SG sounds) and Position (B vs. bB sounds) as well as their interaction (performed on the difference waves EGB-EGbB vs SGB-SGbB). Adjacent time-samples that passed the threshold of the p-value (< .05) were constituted as clusters. The sum of individual t-statistics was calculated within each cluster to obtain a cluster-level statistic, and the significance level (p-value) was calculated using the non-parametric Monte Carlo method with 10000 random partitions. Additionally, to evaluate the effects in the overall event pupil response depending on event order we performed a 2x2 repeated measures ANOVA on Source (EG vs. SG) and Order (1st vs 2nd) of the two events that formed each sequence.

Correlations

To investigate our hypotheses on the relationship between the behavioral, electrophysiological, and pupillometry results we tested the possible correlations between these effects, considering only the physiological effects that were significant in the previous analyses. For the ERP responses and pupil data we included the self-generation effect (amplitude difference of EG minus SG) and the boundary effect separately by source (EGB minus EGbB; SGB minus SGbB) for each significant component or cluster. To obtain one value to perform the correlations on the significant clusters, we extracted the mean amplitude of the significant time window at its maximal electrode for the ERPs, and the peak of the difference wave for the pupil data. We then correlated the electrophysiological and neuromodulatory (pupil dilation) effects with the hypothetical production effects (the difference in temporal order memory performance between across and within), and directly with the memory performance in each combination of sound sources (EG-EG, SG-SG, SG-EG, EG-SG) using Pearson's correlation coefficients.

STUDY III

Participants

The data for Study III were obtained from 87 healthy participants with normal hearing who took part in one of the four prior experiments from the same project this thesis belongs to (PSI2017-85600-P; Study II, Paraskevoudi & SanMiguel 2023a, 2023b, and Sturm et al. 2023). The exclusion criteria used in the four experiments were consistent, and detailed information can be found in the section Participants in the General Methods (see page 21 or Study II, Paraskevoudi & SanMiguel 2023a, 2023b, Sturm et al. 2023). Data from three participants in the original studies were excluded due to incomplete responses on the personality questionnaires. Participants provided written consent for the use of their data in Study III and were compensated accordingly during the original sessions.

Study design

Besides the experimental data from each participant, acquired across four experiments exploring self-generation effects under various experimental conditions, we utilized personality data that had been previously gathered but not analyzed as part of these studies to probe the relationship between personality traits and the observed self-generation effects. The distribution of these questionnaires was facilitated through the Qualtrics platform, ensuring a standardized and efficient data collection process. The chosen questionnaires were selected to provide an insightful evaluation of psychosis proneness in non-pathologic population and the perception of locus of control, thereby enabling a comprehensive examination of their potential associations with the distinct self-generation effects observed within the dataset. The employed self-report questionnaires were the Spanish versions of the Schizotypal Personality Questionnaire (Raine, 1991; Spanish: Fumero et al., 2009 and Rabella et al., 2018), the Peters et al. Delusion Inventory (Peters et al., 1999; Peters et al., 2004; Spanish: López-Ilundain et al., 2006), the Perceptual Aberration Scale (Chapman et al., 1978; Spanish: Fonseca-Pedrero et al., 2009 and Ros-Morente et al., 2010), the Magic Ideation Scale (Eckblad & Chapman, 1983; Spanish: Fonseca-Pedrero et al., 2009 and Ros-Morente et al., 2010) and the Rotter Internal-External Locus of Control (I-E scale; Rotter, 1966; Spanish: Tous, 1984 and Ferrando et al., 2011).

Regarding the experimental data, the dataset encompasses electrophysiological, pupil dilation, and memory responses to both self- and externally generated sounds. These responses were all recorded utilizing the apparatus delineated in the General Methods (see page 22). Nevertheless, pupil dilation data for one of the experiments (Sturm et al., 2023) was not possible to analyze due to task constraints related to eye movements. While all these responses were captured under akin conditions, substantial disparities exist within the experimental designs that elicited these

responses to external and SG sounds. An overview of these variations is provided in the summary table (Table 1).

	Paraskevoudi &	Study II	Paraskevoudi &	Sturm et al., 2023	
	SanMiguel 2023a		SanMiguel 2023b		
Action	Button press	Button press	Button press	Eye movement	
	externally paced	externally paced	self-paced	self-paced	
Stimuli	250 ms non-	250 ms identifiable	500 ms identifiable	500 ms consonant-	
	identifiable sounds,	natural sounds,	natural sounds,	vowel syllables	
	unpredictable identity	unpredictable identity	predictable category		
Action-sound Delay	0 ms	0 ms	150 ms	750 ms	
Conditions	Motor-auditory vs	SG vs EG	SG vs EG	Self-controlled vs	
	Auditory			externally controlled	
Control	Coincidence (50%)	Contingent SG	Contingent SG and	Contingent SG and	
	on SG sounds,	sounds and EG	EG sounds	EG sounds	
	unpredictable EG	sounds unpredictable	predictable in timing		
	sounds	in timing	and category		

Table 1. Summary table of the main experimental differences that characterize each elicited responses to the SG and the EG sounds across the four experiments.

In the study conducted by Paraskevoudi & SanMiguel (2023a), akin to Study I of this thesis, the aim was to explore the effects of the mere action-sound relationship on memory encoding. For this purpose, the authors employed a coincidental self-generation paradigm, wherein nonidentifiable sounds (with a duration of 250 ms) were triggered either through a guided button press (SG) or, alternately, initiated semi-randomly by the computer (EG). Crucially, only half of the button presses resulted in an immediate sound following the action, while the remaining half had no auditory consequences, thereby creating a context of coincidental self-generation. Subsequent to each trial, participants were presented with a pair of sounds (termed in the original study as the 1T condition), and they had to discern which sound from the pair had been present during the encoding phase by a two-alternative forced-choice (2AFC) response. In Study II, the experimental paradigm incorporated identifiable natural sounds, each lasting 250 ms. These auditory stimuli were introduced in response to a series of button presses, either occurring immediately after each press (SG) or interposed before/after the sequence of SG sounds (EG). This fully contingent paradigm informed participants about the expected timing of sound presentation upon their actions, while the identity of the forthcoming sound remained unpredictable. Although participants could anticipate the occurrence of externally generated sounds, the exact timing of these auditory events remained uncertain. Following the trial sequence, participants were presented with a pair of non-consecutive sounds, and they had to answer a Yes/No question of whether the order of the sound pairs was correct or incorrect. In the context of Study III, we focused on comparing order performance differences between SG sound pairs (SG-SG) and externally generated sound pairs (EG-EG).

Data from Paraskevoudi & SanMiguel (2023b) were gathered using a self-generation approach that manipulated predictability of the upcoming sounds' category and the time delay before the sounds occurred after an action or a visual cue. For Study III, to maintain the similarity with the other studies' data, our main focus was on the data collected from the predictable sound category condition, where there was a short delay of 150 ms after participants performed an action following a visual cue (SG) or simply after seeing the visual cue (EG). These sounds, taken from the same sound collection used in Study II, were made longer (lasting 500 ms) to ensure that participants could correctly recognize and categorize them, which was important to make the sounds' identity predictable. During the retrieval phase, participants passively listened to 20 sounds and had to decide whether each sound was one they heard during the initial learning phase or completely new to them.

	Parask	cevoudi &	St	udy II	Parask	evoudi &	Sturm	et al.,
	SanMi	guel 2023a			SanMig	guel 2023b	202	23
Ν	20		24		19		24	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Age (Years)	24.1	3.32	22.8	3.40	24.7	6.46	21.0	4.08
Sex (M/F)	5/15		9/15		9/10		10/14	
SPQ	11.8	8.92	23.8	12.0	19.7	8.72	22.5	12.8
LOC	10.7	4.91	12.5	4.10	13.3	3.38	12.4	4.78
PDI	1.60	1.64	4.83	3.52	3.26	2.13	5.00	4.85
PAS	3.00	1.72	5.63	4.65	3.26	1.97	6.33	7.11
MIS	4.35	3.88	8.38	4.53	7.42	4.35	8.08	5.34
N1 amplitude (µV)								
EG	-3.20	1.90	-3.75	1.8	-4.73	2.78	-2.51	1.20
SG	-2.71	2.10	-1.96	1.99	-3.25	2.56	-2.42	1.28
Tb amplitude (μV)								
EG	-2.27	1.46	-1.38	0.992	-2.63	1.93	-2.53	4.38
SG	-1.68	1.60	-0.925	0.923	-2.19	2.07	-1.05	4.48
P2 amplitude (µV)								
EG	4.89	2.66	4.17	1.63	3.87	2.30	1.58	1.64
SG	3.85	2.09	2.42	1.29	0.873	2.28	2.10	2.23
Pupil (z)								
EG	-0.0413	0.0299	0.0142	0.0512	0.181	0.130		
SG	0.177	0.111	0.165	0.0871	0.382	0.209		
Memory (% correct)	1							
EG	0.801	0.0967	0.711	0.107	0.684	0.112	0.583	0.136
SG	0.759	0.111	0.700	0.119	0.702	0.103	0.724	0.135

 Table 2. Demographic data, personality test scores and experimental measures of the participants of each experiment

Notably distinct among the four experiments featured in Study III, Sturm et al.'s (2023) study employed a self-generation paradigm that significantly deviated from the others. This paradigm was characterized by the use of eye movements instead of button presses as the motor action, with eye movements playing a central role in both the SG and EG conditions. Their study adopted an oculomotor paradigm for an associative learning task. In this setup, participants controlled the movement of a cursor on the screen to deliver the sounds by directing their eye movements (SG), or they followed the cursor movements displayed on the screen which triggered the sounds (EG). This distinction between the agent (SG) and observer (EG) conditions was rooted in the perception of agency associated with the movements. The direction of the eye movement determined the specific consonant-vowel syllable (lasting 500 ms) that was elicited, and participants were tasked with retaining the connection between movement direction and sound. Spanning seven stages, the memory task progressively established the associations between movement and sound. For Study III, we focused on the memory performance comparison of SG and EG sound during the initial learning stage, which had the minimal exposure to the sounds, as the other studies. For reference, on Table 2 there is a summary of the raw measures that come from each experiment.

Personality questionnaires

The Schizotypal Personality Questionnaire (SPQ), formulated by Raine (1991), focuses on the appraisal of schizotypal personality traits in alignment with DSM-III-R criteria. Presented in a dichotomous response format, the SPQ encompasses 74 items, and its total score spans from 0, signifying low schizotypy, to 74, representing high schizotypy. Raine (1991) identified a 10% cut-off score of 41 among college students, demarcating individuals with high schizotypy. Notably, 55% of those exceeding this threshold received a Schizotypal Personality Disorder (SPD) diagnosis following clinical assessment. In addition to the total score, the questionnaire encompasses nine subscales that align with the diagnostic criteria of SPD. These subscales encapsulate concepts such as ideas of reference, odd beliefs or magical thinking, unusual perceptual experiences, paranoid ideation/suspiciousness, excessive social anxiety, lack of close friends, constricted affect, odd or eccentric behavior, and odd speech. This instrument not only offers an overarching evaluation but also delineates higher-order factors encompassing cognitive perceptual, interpersonal, and disorganized traits.

The Peters Delusion Inventory (PDI), developed by Peters et al. (1999, 2004) serves as a selfreport tool for evaluating delusional symptoms in the general population. Comprising 21 dichotomously formatted items, this inventory's higher scores (max. 21) correspond to heightened delusional symptoms or proneness to paranoia, a lower score (0) means no delusional symptoms. Although these qualitative data were not considered for the present analysis, the PDI's assessment extends to the degree of conviction, preoccupation, and distress associated with delusional symptoms.

The Perceptual Aberration Scale (PAS), developed by Chapman et al. (1978), assesses perceptual distortions associated with body image and related phenomena commonly observed in experiences resembling those of individuals with schizophrenia. With its dichotomous True/False format and 35 items, PAS provides insight into the degree of perceptual aberrations experienced by individuals. A score of 35 indicates a high level of self-reported perceptual distortions, while a score close to 0 suggests the absence of such aberrations.

Similarly, the Magic Ideation Scale (MIS), also developed by Eckblad and Chapman (1983), explores superstitious and magical beliefs, as well as tendencies related to mind reading or thought broadcasting. Comprising 30 dichotomously formatted items, MIS helps in understanding individuals' inclinations toward these cognitive phenomena. As with the other questionnaires, a score of 30 signifies a high level of superstition and magical beliefs, while a score close to 0 indicates a more sceptical and rational perspective.

Finally, the Rotter Internal-External Locus of Control (LOC) assesses an individual's perception of control over situations and events, distinguishing between internal and external attributions over 23 items. Originally conceptualized by Rotter (1966), this forced-choice paradigm examines whether individuals perceive circumstances as influenced by their own actions or external forces. Although contemporary perspectives on Locus of Control propose a multidimensional construct, Rotter's measure, which gauges a more generalized internal-external disposition, remains widely employed. The score on this measure can range from 0 to 23, with higher scores indicating a more external locus of control and lower scores reflecting a more internal locus of control.

Analysis

Personality measures

We employed the SPQ total score to ensure the replication of existing findings. Additionally, we opted for an exploratory factorial analysis instead of relying exclusively on the total scores of each of the five questionnaires for several reasons. We sought a more nuanced understanding of the relationships between schizotypal traits, locus of control dimensions, and other related psychological attributes. To accomplish this, we conducted a factorial exploratory analysis that encompassed not only the SPQ subscales but also the subscales of locus of control (LOC), as well as scores from the PDI, PAS, and MIS questionnaires. This multifaceted approach allowed us to unravel potential underlying structures and relationships within the data that might not have been apparent with a total score-based analysis alone. As a result of this analysis, three distinct factors emerged (see factor loadings in Table 3) explaining cumulatively the 50.5% of the variance. The correlations between factors were 0.275 between Factor 1 and Factor 2, 0.4408 between Factor 1 and Factor 3, and 0.0840 between Factor 2 and Factor 3. The model exhibited a good fit with Root Mean Square Error of Approximation (RMSEA) of 0.0257, indicating a close fit between the model and the data. The Tucker-Lewis Index (TLI) of 0.982 suggests a high degree of model fit, and a Bayesian Information Criterion (BIC) value of -299 indicates that the model is a good fit for the data and is relatively parsimonious. Bartlett's test indicated significance ($\chi^2 = 662$, df = 136, p < .001), confirming that the correlations among variables are not due to chance, and the Kaiser-Meyer-Olkin (KMO) measure suggested adequate sampling adequacy (Global KMO = 0.843), indicating that the data is suitable for factor analysis. Consequently, we calculated factorial scores for each of these factors. To categorize participants effectively, we divided them into two groups based on a median split

according to their scores on the resulting personality measures: SPQ total score (median: 19),

Factor 1 (median: 15.4), Factor 2 (median: 8.24), and Factor 3 (median: 6.52).

		Uniqueness		
	1	2	3	
% Variance	26.2	11.9	12.3	
LOC				
General luck		0.737		0.472
Political control		0.569		0.624
Interpersonal control		0.569		0.684
Academic situations		0.407		0.808
Success via initiative		0.710		0.445
SPQ				
Ideas of reference	0.751			0.457
Odd beliefs or magical thinking	0.571			0.580
Unusual perceptual experiences	0.800			0.336
Paranoid ideation	0.582			0.416
Excessive social anxiety			0.541	0.654
No close friends			0.907	0.222
Constricted affect			0.662	0.450
Odd speech			0.363	0.642
Odd or eccentric behavior	0.462			0.610
PDI	0.832			0.249
PAS	0.815			0.389
MIS	0.789			0.398

Table 3. Results from the Factorial Exploratory Analysis of the four different questionnaires exploring schizotypal personality traits and internal-external locus of control.

To summarize Table 2, Factor 1, primarily encompasses the cognitive perceptual facet of schizotypy or positive dimension. In detail, Factor 1 includes SPQ subscales like Ideas of Reference, Magical Thinking, Unusual Perceptions, Paranoid Ideation, and, to a lesser extent, Odd or Eccentric Behavior. Additionally, it encompassed scales like PDI, PAS, and MIS, omitting the internal-external LOC scale and the negative dimension or social aspect of the SPQ that constituted Factor 2 and 3, respectively.

Self-generation effects

To address the specific preprocessing of the self-generation effects investigated in Study III, we direct readers to the pertinent studies that constitute this extensive dataset (Study II, Paraskevoudi & SanMiguel 2023a, 2023b, and Sturm et al., 2023). For the self-generation measures that we aimed to correlate with personality traits, we extracted the mean amplitudes of SG and EG sounds for the ERP components N1, Tb, and P2, in addition to pupil dilation and memory performance. To mitigate potential disparities arising from inter-experiment variations (Table 2), we employed a normalization approach akin to the methodology employed by Oestreich et al. (2016). Normalization was done through z-scoring, both across conditions (EG and SG) and between high and low personality trait groups (SPQ total score, Factor 1, Factor 2, and Factor 3). From these normalized variables, we calculated the attenuation index, indicating the degree of attenuation between active and passive conditions, for the ERP negative components N1 and Tb ((EG-SG) -1) and for the positive component P2 (EG-SG), ensuring positive values consistently indicated greater attenuation toward active sounds. Additionally, the facilitation index was computed for both pupil dilation and behavioral memory performance (SG-EG), with positive values denoting heightened responses during the active conditions. This methodology allowed us to systematically examine the interplay between self-generation effects and personality traits across diverse experimental contexts.

Statistical Analysis

A series of one-way repeated measures ANOVA tests were conducted for each experimental measure (N1, Tb, P2, Pupil, Memory) and each personality measure (SPQ total score, Factor 1, Factor 2, and Factor 3). Source (EG, SG) was employed as the repeated measures factor, while Group (high, low) served as the inter-subject factor. In cases where a significant

Source*Group interaction was observed, subsequent correlational analyses were undertaken to explore the connection between the respective attenuation or facilitation index and personality scores.



Figure 3. Depiction of the neurophysiological and behavioral self-generation effects for each of the four experiments. The first two rows present the electrophysiological results comparing the externally-generated (EG) and self-generated (SG) stimuli at encoding for the amplitudes of the N1 and the P2 components at electrode Cz and the Tb component at electrode T8. The third row depicts the evoked pupil responses at encoding to EG and SG stimuli. The last row represents the memory performance, as reflected by the percentage of correct responses, for EG and SG sounds. Error bars depict the Standard Error of the Mean (SEM).

RESULTS

STUDY I: ACTION EFFECTS ON AUDITORY MEMORY

MEMORY PERFORMANCE

The overall memory performance was 70.57 % (SD: 7.23). Accuracy for Old sounds did not differ based on how they were encoded ($t_{(18)} = -0.578$, p = 0.571, d = -0.129, $BF_{10} = 0.276$; Figure 4, left; see Table 4). However, participants were better at recognizing old sounds than correctly rejecting new sounds ($t_{(18)} = 2.716$, p = 0.014, d = 0.963, $BF_{10} = 3.901$; Figure 4, right).



Figure X. Behavioral results. Bar plots with individual data points comparing the memory performance for the encoded as motor-auditory and encoded as auditory (left) and for the Old and New (right) sounds at retrieval. Individual data points are connected by a discontinuous line in each comparison. Error bars display the standard error of the mean (SEM).

D-prime did not differ between Old and New ($t_{(18)} = 0.164$, p = 0.872, d = 0.008, $BF_{10} = 0.240$) nor between the A and MA conditions ($t_{(18)} = 0.621$, p = 0.543, d = 0.112, $BF_{10} = 0.282$). The Criterion measure differed between the Old and New ($t_{(18)} = -2.645$, p = 0.016, d = -1.191,
$BF_{10} = 3.450$). However, it was similar for the A and MA conditions ($t_{(18)} = -0.621$, p = 0.543, d = 0.086, $BF_{10} = 0.282$). This reflects a more conservative strategy when judging new stimuli, however, the presence of an action does not affect the judgment strategy of old stimuli.

Behavio	oral				
			% Correct	D-prime	Criterion
		Condition		Mean (SD)	
		А	0.75 (0.10)	1.26 (0.37)	-0.09 (0.27)
		MA	0.77 (0.10)	1.30 (0.44)	-0.11 (0.25)
		Old	0.76 (0.09)	1.27 (0.37)	-0.10 (0.25)
		New	0.65 (0.14)	1.27 (0.39)	0.22 (0.28)
Electro	physiological				
			Encoding	Retrieval	
ERPs	Electrodes	Condition	Mean (SD)	Condition	Mean (SD)
N1	Cz	А	-4.03 (1.68)	rA	-4.85 (2.61)
		MA	-3.46 (1.45)	rMA	-4.44 (2.06)
	Mastoids	А	0.39 (0.89)	rA	0.52 (1.07)
		MA	0.40 (0.94)	rMA	-0.07 (1.29)
Na	Temporal	А	-0.71 (1.07)	rA	-0.74 (1.08)
		MA	-0.87 (0.86)	rMA	-0.58 (1.31)
Tb	Temporal	Α	-1.69 (1.02)	rA	-2.12 (1.65)
		MA	-1.09 (0.91)	rMA	-1.93 (1.25)
P2	Cz	Α	3.04 (1.75)	rA	1.73 (2.54)
		MA	1.43 (1.18)	rMA	1.94 (2.18)
	Mastoids	Α	-0.63 (0.89)	rA	-0.91 (1.18)
		MA	-0.44 (0.71)	rMA	-1.17 (1.22)
P3	Pz	А	0.02 (0.88)	rAcorrect	2.27 (2.97)
		MA	0.64 (0.91)	rMAcorrect	2.48 (2.35)
				Old	2.40 (2.45)
				New	0.88 (2.23)

Table 4. Mean amplitudes and standard deviations of the results

ELECTROPHYSIOLOGICAL

Encoding

To assess the effect of action on sensory responses, we contrasted the ERPs for the A and the motor corrected MA conditions (eA vs. eMA-eM; Figure 5). First, we identified the time-windows for the components N1 (80-110 ms) and P2 (140-200 ms) at the Cz electrode and at the mastoids, the N1 subcomponents Na (74-94 ms) and Tb (102-132 ms) at T7 and T8, and the P3 at Pz (276-306 ms). The analysis of the mean amplitudes (see Table 4) of the selected time-windows revealed a significant attenuation at Cz of N1 ($t_{(18)}$ = -2.452, p = 0.025, d = -

0.56, $BF_{10} = 2.487$) and P2 ($t_{(18)} = 5.993$, p < 0.001, d = 1.37, $BF_{10} = 1957.803$) for the MA condition. At the mastoids there were no differences on N1 ($t_{(18)} = -0.126$, p = 0.901, d = -0.012, $BF_{10} = 0.239$) nor P2 ($t_{(18)} = -1.625$, p = 0.122, d = -0.235, $BF_{10} = 0.723$) between conditions. Examining the temporal electrodes we found a significant attenuation of Tb for the MA condition ($t_{(18)} = -3.313$, p = 0.004, d = -0.617, $BF_{10} = 11.50$), and no significant effects for Na ($t_{(18)} = 1.090$, p = 0.290, d = 0.165, $BF_{10} = 0.399$). At Pz, the P3 component revealed larger amplitudes for the MA condition ($t_{(18)} = -3.934$, p = 0.001, d = -0.690, $BF_{10} = 37.888$).



Figure 2. Electrophysiological results comparing the auditory and motor-auditory (motor corrected) stimuli at encoding. A) ERPs on the analyzed electrodes. At Cz, M1 and M2 the analyzed components are N1 and P2, at T7 and T8 the N1 subcomponents Na and Tb, and at Pz the P3 component. The grey shading marks the time windows of the amplitude analysis. Asterisks mark significance. B) Topographical plots of each component of interest.

Retrieval

First, we assessed whether the source of the stimuli at encoding had an effect when presenting passively the same stimuli at retrieval by comparing the Old of the A and MA conditions (rA vs. rMA; Figure 5A). Then, we analyzed whether the old/new effect was modulated by the action effect comparing the correct Old for both A and MA with the correct New. To this end, we identified the time-windows for the components N1 (90-120 ms) and P2 (170-210 ms) at Cz and at the mastoids and the N1 subcomponents Na (60-90 ms) and Tb (120-150 ms) at T7 and T8. Additionally, to assess the memory old/new effect we identified the time-window for the P3 component at Pz (300-350 ms) for the correct responses at retrieval Old and New. The analysis of the mean amplitudes (see Table 4) of the selected time-windows for the contrast rA vs rMA remained not significant for N1 ($t_{(18)} = -0.939$, p = 0.360, d = -0.175, $BF_{10} = 0.350$) and P2 ($t_{(18)} = -0.433$, p = 0.670, d = -0.088, $BF_{10} = 0.258$) at Cz. The P2 at the mastoids was in concordance with the findings on Cz ($t_{(18)} = 0.799$, p = 0.435, d = 0.211, $BF_{10} = 0.315$) however the N1 ($t_{(18)} = 2.671$, p = 0.016, d = 0.500, $BF_{10} = 3.604$) revealed a significant enhancement for the sounds encoded as MA. Given that we did not obtain a significant N1 attenuation for the active condition at the Cz electrode, this mastoid attenuation should be treated with caution. As for the N1 subcomponents, we found no significant effects on Na ($t_{(18)} = -0.674$, p = 0.509, d = -0.135, $BF_{10} = 0.291$) nor Tb ($t_{(18)} = -0.589$, p = 0.563, d = -0.126, $BF_{10} = 0.277$). Finally, the P3 old/new effect was significantly present at Pz between the Old and New ($t_{(18)} = 3.764$, p = 0.001, d = 0.650, $BF_{10} = 27.289$), however it did not differ between the rAcorrect and rMAcorrect condition ($t_{(18)} = -0.437$, p = 0.667, d = -0.079, $BF_{10} = 0.259$; Figure 5B).



Figure 5. Electrophysiological results at retrieval. A) ERPs comparing the encoded as auditory and motorauditory sounds, passively presented at retrieval on the analyzed electrodes. At Cz, M1 and M2 the analyzed components are N1 and P2, at T7 and T8 the N1 subcomponents Na and Tb. The grey shading marks the time windows of the amplitude analysis. Asterisks mark significance. B) Top figure: ERPs at Pz comparing the Old and the New conditions. Auditory and motor-auditory conditions are displayed here for visualization purposes. Bottom figure: topographical plots in the P3 time-window showing the distribution of the Old/New effect.

STUDY II: SELF-GENERATION EFFECTS ON STRUCTURING MEMORY ENCODING

ORDER MEMORY PERFORMANCE

Study II examined the accuracy of participants' order memory by analysing the mean percentage of correct responses to the retrieval question ("is this the correct order?") for sound pairs encoded within or across events, and for each sound source pair combination (EG-EG, SG-SG, SG-EG, EG-SG, Figure 6). Two-tailed t-tests revealed no significant difference in performance between sound pairs encoded within versus across events, $t_{(24)} = -.966$, p = .344. Examining the within condition, there was no significant difference in performance for sound pairs comprised of two encoded EG sounds versus two encoded SG sounds, $t_{(24)} = .536$, p = .536, p = .566, p = .56

.597. Additionally, for the across pairs, there was no significant difference in performance depending on whether the first sound was EG or SG, $t_{(24)} = .324$, p = .748). These findings indicate that the participants' order memory performance was not influenced by the sound source at encoding nor by the presence of two encoding events.



Figure 6. Behavioral performance on temporal order memory. Bar plots illustrate both the within- and acrosscondition, while considering each pair combination of sound sources, externally-generated (EG) and selfgenerated (SG), during the encoding phase. Specifically, the across-condition is represented by the combinations SG-EG and EG-SG, while the within-condition is represented by EG-EG and SG-SG. Individual data points are depicted alongside the bar plots and connected by discontinuous lines.

ELECTROPHYSIOLOGICAL EFFECTS

Results of the targeted ERP analysis on the self-generation effects showed significant differences between EG and SG on several components (Figure 7). Specifically, the



Figure 7. Electrophysiological results comparing the externally-generated (EG) and self-generated (SG) stimuli at encoding. The top section shows ERPs recorded on the analyzed electrodes. At Cz, M1, and M2, the analyzed components are N1 and P2, while at T7 and T8, the N1 subcomponents Na and Tb are examined. Significance is indicated by asterisks. The bottom section displays topographical plots representing three significant clusters identified through the ERP data-driven analysis comparing the EG vs the SG stimuli. The gray shading indicates the time windows corresponding to each cluster, the highlighted cluster electrodes indicate whether a cluster is negative (white) or positive (black) dots.

amplitude of the N1 component at Cz was significantly suppressed for SG compared to EG $(t_{(24)} = -6.671, p < .001, d = .101)$. Conversely, N1_{mast} did not differ significantly between EG and SG $(t_{(24)} = .791, p = .437)$. The Na and Tb components were also significantly modulated, with SG enhancement for Na and attenuation for Tb $(t_{(24)} = 2.556, p = .017, d = .310$ and $t_{(24)} = -2.597, p = .016, d = .397$, respectively). Moreover, the P2 amplitude at Cz was significantly

suppressed for SG compared to EG ($t_{(24)} = 6.985$, p < .001, d = .984). The cluster-based analysis showed more negative values over frontocentral electrodes for the EG compared to SG from 0 to 114 ms (t = -2.453, p = .025) and more positive values over frontocentral electrodes from 158 to 254 ms (t = 3.784, p = .001) and parietal electrodes from 528 to 598 ms (t = 3.181, p =.007), for the EG compared to SG. Thus, the negative cluster (0 to 114 ms) encompassed the Na (80-100 ms) and N1 (80-120 ms) components, and the first positive cluster (158 to 254 ms) encompassed the P2 (150-250 ms) component.

To examine the boundary effect, we examined responses to the boundary (B) and beforeboundary (bB) sounds and performed 2x2 repeated measures ANOVAs (Source x Position) on N1 and P2 (at Cz), as well as on PNR at Pz to test for possible interactions between selfgeneration and boundary effects (Figure 8). Related to the N1, we obtained a main effect of Source $(F_{(1,24)} = 38.184, p < .001, \eta_p^2 = .614)$ but no main effect of Position nor an interaction, thus reflecting the self-generation effect formerly reported, that is, a reduction of the N1 amplitude for SG sounds regardless of position. For the P2, we obtained a main effect of Source $(F_{(1, 24)} = 20.201, p < .001, \eta_p^2 = .457)$, as expected, and Position $(F_{(1, 24)} = 22.657, p > .001, p < .001)$ $\eta_p^2 = .486$), which we did not predict, but no interaction. This indicates that P2 was significantly enhanced for boundary sounds maintaining the P2 attenuation for the SG sounds regardless of position. Finally, for the PNR there was a significant interaction between Source and Position $(F_{(1,24)}=8.417, p=.008, \eta_p^2=.260)$. The post-hoc comparisons showed a significant effect of Position only for the SG sounds ($t_{(24)} = -2.274$, p = .032, d = 1.276), indicating that the PNR was enhanced for the boundary SG sounds. However, there was no effect of Position for the EG sounds ($t_{(24)} = .994$, p = .330). Thus, in terms of modulation of the PNR, starting to perform actions seemed to mark a clear boundary while stopping to perform actions did not. The clusterbased analysis revealed a significant interaction



Figure 8. Electrophysiological results comparing the boundary effect (boundary, B, minus before-boundary, bB) on externally-generated (EG) and self-generated (SG) stimuli at encoding and the interaction between boundary and self-generation effects. The top section displays the recorded ERPs on the analyzed electrodes. At Cz, the N1 and P2 components were analyzed, while at Pz, the PNR was examined. The left-most and middle columns depict the boundary effect for the EG and SG sounds, respectively. In the rightmost column the difference waves depicting the boundary effects are compared between the SG and EG sounds (interaction). Asterisks indicate significant effects. The bottom section exhibits topographical plots representing the two significant clusters identified through the ERP data-driven analysis. The gray shading indicates the time windows corresponding to each cluster, and the electrodes included in each cluster are highlighted with dots, the color indicating whether the cluster is negative (white) or positive (black).

temporally overlapping the N1-P2 complex (window: .084 to .198 s, t = 4643.049, p = .009). Post-hoc comparisons revealed that SG sounds differed significantly depending on Position, where the boundary SG sounds elicited more positive responses compared to the beforeboundary SG sounds (window: .084 to .198 s, t = 6237.125, p < .001); contrary, EG sound responses were not modulated by Position. The significant results from the cluster-based analysis overlapped with the N1 and P2 windows from the targeted ERP analysis, however, the cluster showed a posterior scalp distribution.

PUPILLOMETRY EFFECTS

The pupil analysis amongst all the encoding sounds showed a significant difference in pupil diameter between EG and SG sounds (Figure 9). Specifically, cluster-based permutation t-tests revealed a larger pupil diameter for SG sounds compared to EG sounds in the time window spanning from -.130 to .890 s (t = -750.562, p < .001).

Regarding the boundary effect, the pupil response cluster-based permutation t-tests revealed that the interaction between Position and Source was significant, (window: -.230 to 1.500 s, t = -1170.038, p < .001). Further analysis on the significant time window showed a simple main effect of Position on EG sounds (window: .790 to 1.100 s, t = -590.941, p < .001). This indicated that the phasic pupil response to EGB sounds was smaller than the response to EGbB sounds. Similarly, we found a simple main effect of Position on SG sounds (window: -.240 to 1.100 s, t = 990.362, p < .001). However, this indicated the opposite effect; the phasic pupil response to the SGB sounds was larger than to the SGbB sounds. Regarding Source, there was a simple main effect on before-boundary sounds (window: .010 to .620 s, t = -310.524, p < .001). This goes in accordance with the previous analysis amongst all the encoding sounds, showing enhanced pupil diameter for SGbB compared to EGbB sounds.



Figure 9. Pupil responses during encoding. The top panel shows the evoked pupil responses at encoding to all externally-generated (EG) and self-generated (SG) stimuli. The bottom right panel shows the evoked pupil responses for EG and SG depending on whether they were the last stimulus before a boundary (bB) or the boundary stimulus (B). The bottom left panel displays the overall mean pupil response of the entire events, separately for EG and SG events depending on order of presentation within a sequence (1st event or 2nd event). Error bars show the standard error of the mean (SEM). Significance is marked by a black line encompassing the significant time window.

Finally, there was a simple main effect of Source on boundary sounds (window: -.220 to 1.100 s, t = -1131.452, p < .001), indicating the same pattern of effect on the Position on SG sounds, that is, larger phasic response for the SGB compared to the EGB sounds. Overall, these findings suggest that both position and source play a significant role in the boundary effect on the pupil response. Additionally, the cluster-based analysis identified a difference on the baseline period (window: -0.490 to -0.260 s, t = 169.787, p = .021). However, due to the limited duration of the baseline period, we deemed it insufficient for drawing meaningful conclusions. Instead, considering that boundary effects on the baseline period of the boundary sound might relate to

the direction of the boundary (from EG to SG or from SG to EG), to further explore this, we examined the differences in the overall pupil response for each event type taking event order into account, by conducting a 2x2 repeated measures ANOVA on Source (EG vs. SG) and Order (1st vs. 2nd event) of the two events comprising each sequence. The analysis revealed a significant interaction between Source and Order ($F_{(1, 24)} = 10.619$, p = .003, $\eta_p^2 = .307$), main effect of Source ($F_{(1, 24)} = 50.755$, p < .001, $\eta_p^2 = .679$) and Order ($F_{(1, 24)} = 39.074$, p < .001, $\eta_p^2 = .619$). In terms of the simple main effects of Source, the overall event response was found to be larger for the SG events compared to the EG events during both the 1st event ($t_{(24)} = -4.674$, p < .001, d = .363) and the 2nd event ($t_{(24)} = -8.915$, p < .001, d = .241) of the sequence. Regarding the simple main effects of Order, 2nd events had significantly lower pupil dilations than 1st events both for EG events ($t_{(24)} = 8.691$, p < .001, d = .145) and for SG events ($t_{(24)} = -4.553$, p = .048, d = .240).

CORRELATIONS

Table 5 displays the correlations conducted in Study II to explore the possible relationships between the electrophysiological (ERPs) and neuromodulatory (pupil dilation) effects of actions at encoding and the memory performance effects at retrieval on the one hand; and the possible relationships between the two physiological effects of actions at encoding. The results indicate that the ERP SG effects (EG-SG) on each significant component did not exhibit correlations with the effect of actions on pupil dilation (EG-SG) or the effect of source on the performance of within pairs (EG-EG and SG-SG). Additionally, the pupil dilation effects did not demonstrate correlations with memory performance. Regarding the boundary effect, we examined the correlation between each significant physiological effect of the boundary (B-bB) and the corresponding associated memory performance for that boundary type. In cases where an interaction was present, we explored separately the boundary effect for each sound source (EG and SG). Notably, we discovered a significant negative correlation between the boundary effect on memory performance (within minus across) and the modulation of P2 for boundary sounds (r = -.425, p = .034). This finding suggests that larger performance differences between across and within events were associated with a smaller boundary effect at P2. However, no correlations were found between the behavioral boundary effect and the pupil, nor between the pupil and the ERP.

Table 5. Correlations between the memory performance, the significant self-generation and boundary effects on ERP components and the significant self-generation and boundary effects on pupil responses.

		r	р
SG effects			
	N1 (EG - SG)	099	.638
	Na (EG - SG)	.133	.526
Memory performance for within pairs	Tb (EG - SG)	.035	.870
(EG_EG - 5G_5G)	P2 (EG - SG)	.204	.328
	Pupil (EG - SG)	.313	.127
	N1 (EG - SG)	007	.972
	Na (EG - SG)	.070	.741
Pupil (EG - SG)	Tb (EG - SG)	061	.773
	P2 (EG - SG)	.040	.848
Boundary effect			
Memory performance (Within – Across)	P2 (B - bB)	425	.034
Memory performance (Within - Across $EG \rightarrow SG$)	Parietal cluster (B - bB for SG)	260	.209
´	PNR (B - bB for SG)	.030	.886
	Pupil (B - bB for SG)	209	.315
Memory performance (Within – Across SG→EG)	Pupil (B - bB for EG)	287	.164
Pupil (B - bB for EG)	P2 (B - bB)	218	.296
Pupil (B - bB for SG)	Parietal cluster (B - bB for SG)	256	.216
	P2 (B - bB)	.055	.792
	PNR (B - bB for SG)	236	.256

Correlations

STUDY III: SCHIZOTYPY, LOCUS OF CONTROL AND THE SELF-GENERATION EFFECTS

Based Study III specific hypothesis, we conducted twenty one-way repeated measures ANOVA for each of the five experimental measures (N1, Tb, P2, Pupil, Memory) and all four personality measures (SPQ total score, Factor 1, Factor 2, and Factor 3), considering Source (EG, SG) and Group (High, Low) as factors. Upon identifying a significant Source*Group interaction, we proceeded with correlational analyses between the variable effects (attenuation or facilitation) and the corresponding personality scores. Notably, all four personality groupings exhibited a substantial source effect (p < .05), mirroring an overall significant difference between SG and EG sounds on the experimental measures across the four experiments. Overall, all groupings revealed attenuated N1, Tb and P2 amplitudes, as well as enhanced pupil dilation and memory performance for the SG sounds compared to the EG sounds.

In the context of SPQ-based grouping, the Tb component displayed a noteworthy Source*Group interaction ($F_{(2,85)} = 6.75$, p = .011, $\eta_p^2 = .074$; Figure 10, top). In the Low group, meaning those with low schizotypy, we observed significant attenuation of Tb responses to SG sounds compared to EG sounds ($t_{(42)} = -3.84$, p < .001, d = -.586), while no such attenuation was evident for the High group ($t_{(43)} = -0.665$, p = .510), that is, individuals who scored high on the SPQ had no sensory attenuation at Tb for the SG sounds. This phenomenon was accompanied by a negative correlation between SPQ scores and the Tb attenuation index, indicating that higher SPQ scores correlated with reduced sensory attenuation on the Tb component (r = -0.240, p = .025; Figure 10, bottom). No other experimental measures exhibited a significant Source*Group interaction.



Figure 10. Top Panel: Residual plots resulting from the repeated measures analysis of variance (rmANOVA) interactions between inter-subject variables (high and low scorings on the personality measures) and intrasubject variables (self-generated sound, SG; externally-generated sound, EG) across five measures for the intrasubject variables (N1, Tb, P2, Pupil, and memory performance) and four personality groupings for the intersubject variables (SPQ, Factor 1, Factor 2, Factor 3). Bottom Panel: Dispersion plots displaying linear fits of the correlations observed in the significant ANOVA interactions. The y-axis represents the normalized (z) selfgeneration effect on Tb, while the x-axis corresponds to scores on personality measures SPQ and Factor 1. Dotted boxes indicate statistical significance.

Similarly, grouping based on Factor 1 revealed a significant Source*Group interaction for the Tb component ($F_{(2,85)} = 11.6$, p = .001, $\eta_p^2 = .116$; Figure 10, top). Analogous to the SPQ-based classification, the Low group demonstrated significant attenuation of Tb responses to SG

compared to EG sounds ($t_{(42)} = -4.06$, p < .001, d = -.619), while no such attenuation was observed for the High group ($t_{(43)} = -0.250$, p = .804). However, Factor 1 scores did not exhibit a significant negative correlation with the Tb attenuation index (r = -0.182, p = .092; Figure 10, bottom). Once more, no other experimental measures exhibited a significant Source*Group interaction.

Lastly, in the case of grouping by Factor 2 and Factor 3, no significant interactions emerged from our analysis. This implies that the personality traits that conform Factors 2 and 3 are not associated with variations in the experimental self-generation effects.

DISCUSSION

DISCUSSION OF STUDY I

The goal of Study I was to investigate whether actions alone could account for the production effect. Behavioral research has shown abundant evidence that sounds produced by oneself are better remembered than those just passively processed (Ekstrand et al., 1966; Hopkins & Edwards, 1972; Conway & Gathercole, 1987; Gathercole & Conway, 1988; MacDonald & MacLeod, 1998; MacLeod et al., 2010; Brown & Palmer, 2012; Mathias et al., 2015). However, since memory is a higher order process, it can be challenging to disentangle which lower-level processes are contributing to this complex effect. Normally, several co-occurring processes determine an outcome, thus, modulations of sensory responses could affect how action-revolving inputs are encoded in the memory stream.

In the auditory domain, self-generation effects refer to the attenuation of the sensory responses to a stimulus that has been produced by the same individual who is hearing the sound (SanMiguel et al., 2013; Saupe et al., 2013). Surprisingly, this effect persists even in the absence of contingency, that is, when the act performed does not actually generate the stimulus but occurs in the same time window (Horváth et al., 2012; Horváth, 2013a, 2013b). Looking at the electrophysiological response during the encoding phase of our study we have replicated this result. The attenuation we measured for N1, Tb and P2 during encoding for sounds coinciding with actions is in line with well-established literature (Horváth, 2015; Schröger et al., 2015). At encoding we also observed an increased P3 amplitude at Pz which may reflect the surprise of the sound that coincides with an action (Darriba et al., 2021), as in our experiment only half of the actions were accompanied by a sound (cf. Paraskevoudi & SanMiguel, 2023a; Horváth et al., 2012). The surprising nature of the motor-auditory event

could be obscuring the hypothetic memory encoding enhancement, and thus, result in the absence of memory improvement found for the motor-auditory sounds.

ACTION AND THE PRODUCTION EFFECT

Could the action effects described at encoding contribute to the memory advantage observed in the production effect? We examined whether a non-contingent action-sound relationship affected memory performance on a task where old items could be either encoded coinciding with an action or not (i.e., motor-auditory and auditory sounds here). Our measurements showed evidence against an effect on auditory memory for action-coinciding stimuli. This indicates that actions alone do not facilitate the production effect. In line with our behavioral results, as the test sound was always EG, we could not find the typical self-generation effects at retrieval. However, our aim was to detect if there was any modulation in the sensory processing at retrieval dependent on the condition of the test sound at encoding.

Previous ERP research has reported the old/new effect, that is, correctly recognizing a previously heard sound elicits a more positive potential (onset at 300ms) compared to hearing a new sound (Sanquist et al., 1980; Warren, 1980, Wilding; 2000; Kayser et al., 2007; Rugg & Curran, 2007; Mecklinger et al., 2016; MacLeod & Donaldson, 2017). In our study, this enhancement for the "Old" sounds at retrieval did not differ between previously encoded as motor-auditory and encoded as auditory sounds, indicating that the quality of recollection was also not affected by the presence of an action during encoding.

All in all, while we found a robust modulation of sound processing by actions during encoding, this did not seem to affect memory retrieval of these sounds, as we could not find any effects on the responses to the test sounds at retrieval. Hence, our data does not support a relationship between unspecific action effects of the coincidence of a sound with an action and memory accuracy. The null effect at retrieval could be related to the specific conditions of our experiment. We did not have sufficient trials to perform a remembered vs forgotten analysis that could reveal the slight differences in performance that a coincidental action could be mediating. Interestingly, the only two studies to date that tried to relate the memory advantage present on the production effect to the modulatory effects of motor activity surrounding auditory stimuli revealed conflicting results, finding improved (Paraskevoudi and SanMiguel 2023b) and worsened memory performance to sounds coinciding with actions (Paraskevoudi and SanMiguel, 2023a). One apparently minor difference between Study I results and Paraskevoudi and SanMiguel's (2023a) study, which otherwise had an identical paradigm, is the type of question at retrieval. Both the yes/no and two-alternative forced-choice (2AFC) are formats often utilized in the recognition memory literature. In the yes/no format, used in Study I, the target stimulus was presented for a decision in isolation. This is known to require higher memory strength than the decision making between two stimuli (Jang et al. 2009). It could be possible that in Paraskevoudi and SanMiguel (2023a) the 2AFC's inherently greater performance made it easier to uncover the subtler differences between the two research conditions.

CONCLUSION OF STUDY I

The absence of significant behavioral findings suggests that the production effect is not dependent on the presence of an action per se. We considered examining coincidental action was a logical first step to elucidate the role of action in the production effect. However, as we have evidenced, the surprise surrounding a coincidental action could be masking a co-occurrent memory enhancement. Future research with fully contingent paradigms will help clarify if there could be a memory advantage. We conclude the presence of an action alone is not sufficient to enhance auditory memory on a behavioral level and elicit a production effect.

DISCUSSION OF STUDY II

The primary aim of Study II was to explore the possible influence of motor actions to structure auditory memory. To do so, we manipulated the presence or absence of actions during the encoding of sound sequences and examined memory recall for the temporal order of presentation of sound pairs from the encoded sequences. We recorded electrophysiological and pupillary responses during the sound sequence encoding, aiming to relate the known physiological effects of actions during sensory processing to the possible effects of said actions on memory. We hypothesized that the neurophysiological processes engaged by actions, and the ensuing action-related modulation of sensory processing during encoding would promote the differentiated storage of self- and externally generated sounds in memory.

EFFECTS OF SELF-GENERATION ON MEMORY STRUCTURE

At the physiological level, we observed distinct modulations in both ERPs and pupil diameter in relation to the sounds encoded at the position coinciding with a change in sound source (SG or EG). This suggests that indeed the presence or absence of actions acted as a meaningful context for the sound encoding, and that specific neurophysiological mechanisms marked the processing of boundaries between the two different contexts. However, in contrast to our initial hypothesis, memory performance was not affected in any way by the actions performed during encoding as we did not find any significant differences in temporal order memory performance between the across and within conditions.

In principle, this finding indicates that actions did not structure the encoding sequence in two differentiated events. However, recent research by Pu et al. (2022) tested principles of event

segmentation manipulating several variables such as the length of events and position of the test items on a task where boundaries were defined as the change of color frame on a list of grey scaled pictures. Based on one of their observations they proposed the concept of the local primacy effect, which suggests that memory improvements, either across or within events, are strongest at the beginning of an event and gradually decrease as event positions move away from the event boundary. In our experiment, due to the need to control for the distance between the two test sounds in the encoding sequence, pairs of test sounds pertaining to the within event condition were primarily positioned at later local event positions, while pairs pertaining to the across events condition were positioned at earlier positions. This discrepancy in event position distribution may potentially explain our lack of differences between conditions. Furthermore, our findings are consistent with the results reported by Raccah et al. (2022) for the middle positions of temporal order memory as a function of serial position during encoding. In their study, where boundaries were defined as a change in male/female speaker over a list of spoken words, they also found no significant difference between across and within conditions on middle sequence positions. However, when they modeled for serial position to account for primacy and recency effects, they observed the expected segmentation effects.

Although we did not find differences in temporal order memory that could indicate event segmentation based on actions, our analysis of the electrophysiological data did reveal a boundary effect on the P2 component for both SG and EG boundary sounds, and additional boundary effects were observed only for SG boundary sounds (at EG \rightarrow SG boundaries), specifically, an increased positivity over parietal cortex temporally overlapping the N1-P2 complex, followed by an increased late parietal negative response (PNR). This suggests that the processing of SG sounds is more sensitive to modulations on sensory processing related to changes in source-context within an encoding sequence. In other words, introducing actions,

and engaging the associated neurophysiological effects, potentially acts as a stronger contextual shift than removing them. Interestingly, our analysis of pupil diameter showed an opposing pattern of boundary effects between sources (i.e., depending on the direction of the boundary), with SG boundary sounds (at EG \rightarrow SG boundaries) eliciting the highest pupil diameter, EG boundary sounds (at SG \rightarrow EG boundaries) eliciting the lowest, and both SG and EG sounds at the position immediately before the boundary falling in the middle range. Upon investigating the possible reasons for these contrasting effects, we observed EG boundary sounds were associated with larger pupil diameters at baseline compared to SG boundary sounds.

According to the law of initial values (Lacey, 1956), the magnitude of a physiological response to a stimulus is influenced by the baseline level of the response. In the case of EG boundary sounds, it is possible that the pupil did not dilate significantly because, coming from a sequence of SG sounds, it was already relatively dilated, reaching a physiological limit that hindered further dilation. Hence, when the baseline pupil size is larger, an equivalent dilatory response may have a reduced effect on the diameter, causing the dilation to appear smaller in comparison (Gilzenrat et al., 2010). To further understand these directional effects, we investigated the overall pupil response of the two events conforming a sequence. Although our paradigm and the exploratory analysis we performed does not exactly allow us to estimate the tonic response, previous literature on tonic and phasic pupil activity clearly shows an inverted U-shaped pattern, where the optimal phasic response is obtained at intermediate levels of tonic activity (McGinley et al., 2015; Yerkes & Dodson, 1908). Here, the boundary clearly occurs in contexts of different activity levels for one direction and the other, indicating an interaction between boundary and source which suggests that initiating actions marks more clearly the boundary than ceasing them which could explain why we didn't observe differences in temporal order memory.

Finally on memory structure, examining the relationship between electrophysiological, neuromodulatory, and behavioral responses in relation to self-generation on boundary effects, we observed that only the ERP P2 component's boundary effect exhibited a correlation with the performance difference between within and across conditions. Nevertheless, we did not find any associations between pupil response and EEG indicating that although both demonstrated distinct boundary-related effects, they may be reflecting different underlying processes in terms of providing sequential structure. In conclusion, these findings imply that a change in context was indeed processed at the sensory level by the participants, however, it did not result in significant performance differences on temporal order memory.

SELF-GENERATION AND THE PRODUCTION EFFECTS

Additionally, Study II contributes to our understanding of the role of motor actions in modulating the strength of memory traces, more directly relating to the production effect literature. Previous studies testing the influence of actions on auditory memory encoding have reported either impaired, equal, or enhanced single-item recognition memory for sounds encoded concurrently to the execution of an action compared to sounds in isolation (Study I; Paraskevoudi & SanMiguel, 2023a, 2023b). Importantly, in some of these studies, there was no contingent relationship between actions and sounds (Study I; Paraskevoudi & SanMiguel, 2023a). Their findings suggest that the presence of action alone during sound encoding does not reliably contribute to the production effect, and thus that beyond action-sound coincidence, action-sound predictability may play a fundamental role in the memory advantage for SG sounds.

In Study II, we aimed to create conditions that more closely resemble those of studies reporting the production effect. This resulted in SG sounds being fully predictable in time, while EG sounds remained unpredictable, resembling natural conditions where external inputs are inherently unpredictable, but SG ones are not. This setup also resembles more closely the paradigms in which the production effect has been reported, where stimuli that receive a memory advantage are generated in the context of well-established action-effect relationships, such as using one's own voice (MacLeod, 2011), or playing a musical instrument (Brown & Palmer, 2012). Nevertheless, in Study II the sound's identity remained equally unpredictable for SG and EG sounds. Moreover, while the previous studies (Study I; Paraskevoudi & SanMiguel, 2023a, 2023b) tested for effects of actions on single-item recognition memory, here, we explored possible effects on sequence memory, testing memory recall for sequential order. Despite these changes, we still could not demonstrate any effects of the presence of actions during sound encoding on memory performance.

THE UN-SPECIFICITY OF THE SELF-GENERATION EFFECTS

To delve into the specificity of the effects of self-generation during encoding, we examined sensory ERP components. Consistent with well-established findings on predictable SG sounds, our study replicated the attenuated sensory responses to SG sounds on N1, Tb and P2 (Fu et al., 2006; Houde et al., 2002; Paraskevoudi & SanMiguel, 2023b). These results reinforce the notion that SG stimuli are processed differently at the sensory level compared to EG stimuli. Notably, the absence of N1 attenuation at the mastoids suggests that, if any, the modulation of sound responses in areas located on the superior temporal plane (i.e., primary auditory cortex, which should be reflected at the mastoids, Horváth et al., 2012) is rather weak. Thus, the consistent lack of modulation at the mastoids (Study I; Paraskevoudi & SanMiguel, 2023a,

2023b) supports the idea of concurrent modulation of sensory-specific and -unspecific components of the auditory N1 during the SG effect (Horváth et al., 2012; SanMiguel et al., 2013).

Furthermore, we investigated the neuromodulatory effects surrounding motor actions by measuring pupil diameter during sound encoding. Our results revealed greater pupil dilation for SG stimuli compared to EG stimuli, indicating differential activity of the LC-NE system. This finding is in line with recent research highlighting the distinct modulation of pupil responses during the execution of goal-directed motor actions (Lubinus et al., 2022; Paraskevoudi & SanMiguel, 2023a, 2023b; Yebra et al., 2019). All in all, the physiological data shows the clear engagement of distinct neurophysiological processes during the processing of SG sounds, that could have substantial impact on perceptual and memory processes.

However, we did not observe any significant correlations between the electrophysiological, neuromodulatory effects and any memory performance differences between EG and SG sounds. This suggests that the observed modulations in sensory processing, as reflected by the attenuated sensory ERP components and the pupil dilation for SG sounds, are not meaningfully modulating the strength of memory traces. Regarding the relationship between the different physiological effects observed during encoding, it is worth noting that previous research has demonstrated that larger pupil diameter for highly predictable self-produced sounds significantly correlates with greater suppression of the Tb component (Paraskevoudi & SanMiguel, 2023b). We could not replicate this correlation between the pupil and EEG measures. Although the two studies were similar in terms of temporal predictability conditions of SG and EG sounds, notably a significant correlation between Tb suppression and pupil dilation was found only when participants could have an additional sense of control over the

stimulation, as they could choose out of several sound categories which one they wanted to produce on each instance (Paraskevoudi & SanMiguel, 2023b).

LIMITATIONS

Study II had several limitations that may explain the lack of significant behavioral results observed in the context of event segmentation paradigms on the visual modality and shed light on the complexity of event segmentation paradigms on auditory stimuli, particularly SG sounds. Firstly, the predictability of boundaries may have influenced participants' perception of events. We expected the motor act to be sufficient to signal a change in context and elicit an event boundary that could have consequences on memory. Event segmentation is an automatic process that occurs with little conscious control (Zacks & Swallow, 2007). However, it has been suggested that heightened attention is directed towards event boundaries due to their association with unpredictability and the optimization of information uptake (Kosie & Baldwin, 2019; Kurby & Zacks, 2008). Thus, the predictable nature of our paradigm's boundaries, as the sequence of actions to be performed was displayed at the beginning of the trial, may have hindered the necessary attentional engagement required to create distinct event boundaries.

Secondly, the length and repetition of events in our study could have impacted the results. Due to the constrains of designing an auditory temporal order memory task, we only utilized two repetitive event patterns, which limited the complexity and variability of the events. It remains unclear whether repeated pairing of two event types can lead to their integration into a more complex event type or if they are perceived as separate entities (Shin & DuBrow, 2021). Furthermore, while previous research demonstrated a robust (visual) boundary effect even with decreasing event length (Pu et al., 2022), we were not able to explore longer event lengths since

pilot behavioral testing indicated a sharp drop on auditory memory performance overall for longer events. Therefore, including more varied event patterns could yield different results.

Another divergence from previous sequential order memory tasks was the absence of a specific task to assess associative memory for the source of the items. Unlike other studies, our focus was just on examining the effects of the change in context in the form of a motor action. Thus, the inclusion of an associative memory task could have biased our results due to the increased attention on the contextual environment. Future research should explore this aspect to gain a more comprehensive understanding. Additionally, the dual task nature of our experiment, with participants simultaneously performing a motor task to generate sounds, may have acted as a distractor. Divided attention between the motor task and memory encoding can interfere with episodic memory processes, particularly memory for temporal order. Previous studies have demonstrated that memory for individual items (Mangels et al., 2001; Troyer & Craik, 2000).

CONCLUSION OF STUDY II

In conclusion, Study II investigated the influence of motor actions on memory encoding by examining order memory performance and electrophysiological and pupillary responses during sequence encoding. While the behavioral findings did not reveal significant differences in order memory performance based on event segmentation, we observed distinct modulations in sensory processing and pupil dilation related to motor actions. These findings contribute to our understanding of the production effect and suggest that factors beyond motor actions, such as the feeling of agency, may play a crucial role in memory enhancement for SG stimuli. Furthermore, the study's limitations, highlight the complexity of event segmentation on auditory paradigms and the need for future research to deepen our understanding of the underlying mechanisms and the role of motor activity in shaping our experiences.

DISCUSSION OF STUDY III

In Study III, we explored the inter-individual variability concerning self-generation effects, aiming to unravel potential links to schizotypal personality traits and the locus of control in healthy individuals. First and foremost, the results revealed an interaction between the amplitude on the Tb component elicited to SG and EG sounds and grouping individuals based on high or low schizotypy, which meant that individuals with high schizotypy had no attenuated sensory responses to SG sounds. Furthermore, we found a negative correlation between SPQ scores and the self-generation effect on the Tb component leading to a continuum expression of deficits in sensory attenuation the higher the scores on the SPQ.

However, counter to our initial expectations, our findings failed to validate the proposition that individuals with high schizotypal traits, as indicated by the SPQ questionnaire scores, would exhibit reduced self-generation effects in the N1 component compared to those with low SPQ scores. Notably, prior studies (Oestreich et al., 2015, 2016) that reported such associations primarily relied on fully contingent experimental designs, possibly confining the generalizability of their conclusions to specific instances of the N1 self-generation effect modulation.

Furthermore, we conducted a factorial exploratory analysis to gain deeper insights into the intricate interplay between schizotypal personality traits and locus of control and the modulation of the different experimental self-generation effects. Surprisingly, akin to the SPQ results, the groupings derived from the identified three factors failed to reveal significant interactions between high and low groups when comparing SG and EG sounds. This absence

of significance was observed not only for ERP components N1 and P2 but also for pupil dilation and memory performance. In accordance with the SPQ results, the most pronounced difference emerged on the Tb component within Factor 1, primarily encompassing the cognitive perceptual facet of schizotypy or positive dimension.

The lack of differences in Factor 3 appears logical, as it stands apart from the other two factors as it does not delve into perceptual, positive aspects, but in the negative aspects of schizotypy that translate to reduced emotional, physical, and social functions. However, our exploration of Factor 2, which directly relates to the internal or external locus of control, yielded no significant interactions between groups, contrary to our preliminary hypothesis. To support our findings, a behavioral study by Teufel et al. (2010) employing a force matching task similarly discovered no evident correlation between LOC scores and decreased predictive attenuation with SG and EG force instead, they found a correlation with the PDI.

It's important to highlight that the LOC scale primarily addresses the abstraction of perceiving internal or external control, which could theoretically differ from the delusions of control often experienced in psychosis-related instances. Hence, although there exists a certain logic in the hypothesis that these two might be related, it's a substantial leap to generalize perceptual anomalies to cognitive attributions of control, especially considering that numerous other aspects could contribute to having an internal or external locus of control beyond sensory perception. Notably, studies examining LOC and related dimensions in different paranoid patient groups have stressed that characteristics like LOC are not fixed traits in schizophrenia patients; rather, they fluctuate in response to symptoms and life events (Appelbaum, 2004; Bentall & Kaney, 2005). Negative events can lead to an increased perception of externality, observed both in patients with paranoid schizophrenia and individuals experiencing depression (Melo, et al, 2006).

THE OVERLOOKED TB

The absence of sensory attenuation for SG sounds on the ERP component Tb, as opposed to the N1, within individuals with high schizotypal traits compared to their low-trait counterparts, presents a compelling avenue for comprehending the intricate interplay between sensory processing and personality traits. The Tb component, as part of the T-complex, is known to emanate from radial-oriented sources in the superior temporal gyrus, situated in the secondary auditory cortex (Ponton et al., 2002; Tonnquist-Uhlen et al., 2003), contrary to the N1 and P2 which arise from tangentially oriented sources presumably stemming from the primary auditory cortex on the superior temporal plane. Distinct from the N1, the T-complex, and particularly the Tb component, has an early maturation, remaining stable after the age of 5 (Gomes et al., 2001; Pang and Taylor 2000; Tonnquist-Uhlen et al., 2003). The divergence in maturation profiles between N1 and the T-complex raised questions about their underlying sources and functions. Recent research indicates that attenuation of the Tb component can be driven by temporal contiguity or predictability, rather than exclusively by stimulus-specific predictions. Paraskevoudi & SanMiguel (2023b) proposed that the driving factor behind Tb attenuation isn't solely motor predictions but an overall heightened predictability for SG sounds compared to the EG sounds. This aligns with a more generalized predictive account (Friston, 2005) that doesn't exclusively hinge on motor-specific predictions to attenuate responses, further supporting the notion of distinct underlying mechanisms for N1 and Tb effects.

Moreover, seminal studies have dissociated the sense of agency from motor predictions, revealing the Tb component's sensitivity to shifts in the sense of agency even excluding the effect from motor actions (Han et al., 2021; Sturm et al., 2023). This suggests that the Tb component might not rely purely on efference copy or corollary discharge mechanisms linked to motor actions, but perhaps more on the sense of control over impending stimuli. Intriguingly,

the observed lack of SG effects on the Tb component in individuals with high schizotypal traits could indicate a disconnection between mechanisms governing the sense of agency or control and motor actions.

If future research consistently finds that the Tb component indeed reflects the predictability of the upcoming stimuli and remains unmodulated in high schizotypal populations, it could potentially serve as a robust biomarker for detecting disparities in aberrant perception from an early age. Additionally, this stability could align with the notion of psychosis existing as a continuum, highlighting a chore mechanism that distinguishes attributions of control across individuals.

LIMITATIONS

Study III adopts an exploratory and replication-focused approach, representing the initial stride towards validating prior assertions about the N1 component and its relationship with the SPQ across diverse experimental self-generation paradigms. Subsequent research directions should delve into the specific nuances of each experimental paradigm, investigating how they interplay with schizotypal traits. In its current form, the analysis employs mean peaks from ERP components to derive individual amplitudes, serving as an initial approximation. However, a more refined approach involves extracting individual components's amplitudes for each participant, rather than relying on the group average peak. It's vital to underscore that drawing meaningful conclusions necessitates a comprehensive understanding of the exact correlations at play, given the widespread misconceptions surrounding self-generation effects. In this context, our study fundamentally challenges the prevailing assumption that self-generation effects on the N1 component intrinsically align with the psychosis continuum as measured by schizotypal personality traits.

CONCLUSION OF STUDY III

In conclusion, the intricate interplay between sensory processing, personality traits, and cognitive functions is gradually unfolding. The divergent behaviors of N1 and the Tb component among individuals, along with their distinct relationships with schizotypal traits, provide insights into the complex mechanisms that govern self-generation effects and their potential implications for understanding individual differences in sensory perception and cognitive processing.

GENERAL DISCUSSION

Our current understanding of how humans perceive and process information to shape their unique experiences is still in its early stages. The phenomenon of self-generation is just one of the many inquiries stemming from the realm of perception. Whether we find ourselves traversing a forest, conjuring imaginative scenarios, or engrossed in a computer, attuned to the sounds of our keystrokes, our experiences are invariably intertwined with the outcomes of our actions. This thesis aims to illuminate the significance of actions in our daily encounters, endeavoring to deepen our comprehension of their role in shaping our lived realities. While it is undeniable that our cognitive processes extend far beyond the mere interpretation of sounds triggered by a button press, be it contingent or not, there is intrinsic value in exploring these finer nuances. Our surroundings may not typically present us with meticulously crafted sequences that challenge our memory by prompting recollection of seemingly unrelated sounds. Yet, for us to advance our limited understanding of the intricate orchestration of conscious experiences, it becomes imperative to engage with these subtleties that can wield a profound impact. This motivation underscores the fundamental purpose driving the present thesis. Numerous studies on the production effect point us to the direction that actions could play an important role on the memory advantage for SG sounds (Ekstrand et al., 1966; Hopkins and Edwards, 1972; Conway and Gathercole, 1987; Gathercole and Conway, 1988; MacDonald and MacLeod, 1998; MacLeod et al., 2010; Brown and Palmer, 2012; Mathias et al., 2015). However, the literature to date that investigated the role of actions on memory from a neurophysiological view has found conflicting results (Paraskevoudi & SanMiguel 2023a, 2023b). Using slightly different memory tasks and action-sound relationships, now there are four studies that have found conflicting results ranging from no difference in memory in Studies I and II from the present thesis to memory enhancement (Paraskevoudi & SanMiguel, 2023b) and memory impairment (Paraskevoudi & SanMiguel, 2023a) for SG compared to EG sounds, despite the presence of reliable self-generation effects on auditory ERPs in all four studies.

However, the question arises: does the act itself hold any significance? Based on our experimental outcomes, when combined with prior research findings (Paraskevoudi & SanMiguel 2023a, 2023b), we are beginning to validate the notion that actions in isolation, along with their associated neurophysiological regulatory mechanisms, do not constitute the foundation for, nor substantially contribute to, the production effect. While the absence of significant behavioral findings on Study I suggests that the production effect is not dependent on the presence of an action per se, Study II with a fully contingent paradigm evidenced that self-generation alone is not sufficient to grant a memory advantage.

This suggests that factors beyond the mere occurrence of motor actions play a pivotal role in augmenting memory for SG stimuli. It is noteworthy to mention that the results from Study III indicate a substantial improvement in memory encoding for SG compared to EG stimuli. However, when examining the individual studies that conform Study III (Figure 3), it becomes evident that this comparison is primarily influenced by the substantial effect observed in the study by Sturm et al. (2023). In their study, an active learning paradigm was employed where the sense of agency was the primary distinction between EG and SG sounds. In essence, action-sound predictability may play a fundamental role in the memory advantage for SG sounds, also, possessing a sense of control or agency over a situation has been shown to facilitate the process of memory encoding (Hon & Yeo, 2021). This assertion gains further support from the observation that motor activities lacking a connection to strategic control over the learning process fail to enhance memory performance (Voss et al., 2011).

Considering the lack of feeling of control reported by several participants in both Study I and II, but specially the latter where there was full contingency, the feeling of agency and control over the stimuli may be a key factor contributing to memory improvement, rather than the mere generation of a sound by a motor action during encoding. Recent studies have demonstrated that the presence of agency enhances the ability to remember the temporal order of events (Houser et al., 2022) and that voluntarily initiating the onset of stimuli improves working memory and speeds up visual and attentional processes (Loyola-Navarro et al., 2022). These findings suggest that the cognitive aspect of control and agency may play a crucial role in memory enhancement for SG stimuli (Sturm et al., 2023).

Regarding the un-specificity of the self-generation effects, sufficient converging negative evidence (Paraskevoudi & SanMiguel, 2023a; and the present thesis) is starting to accumulate indicating that 1) actions alone, and the associated sensory attenuation reflected on ERPs and engagement of neuromodulatory mechanisms are not the basis for the production effect; and 2) an increase in LC-NE activity engaged by making overt actions does not meaningfully contribute to attenuation of SG sound ERPs.

Another point towards the importance of the sense of agency or control to the longer-term implications of the self-generation effect comes from the findings from Study III. Trying to validate previous findings relating the lack of N1 attenuation in highly schizotypal individuals we found that that precise correlation is not that easily well established under different experimental paradigms. Instead, the association with the Tb component with the cognitive perceptual or positive dimension of schizotypy appears more in line with the concept that perception of control and the ability to predict forthcoming stimuli are the underlying mechanisms affected by both concepts. Collectively the present thesis suggests that actions themselves, while undeniably influential in shaping our immediate perceptual encounters, might not wield the same enduring influence on memory or holistically shape our experiential journey as previously postulated.

STRENGTHS, LIMITATIONS AND FUTURE RESEARCH

The three studies presented herein collectively contribute to our understanding of the intricate relationships between sensory processing and cognitive functions, such as memory and personality traits. Each study offers unique insights and approaches, shedding light on the complexity of these phenomena. In this section, we delve into the strengths and limitations of each study and potential avenues for future exploration.

Study I aimed to investigate the relationship between the production effect and coincidental motor activity during encoding, and subsequent memory retrieval. The strength of Study I lies in its meticulous control over experimental conditions, ensuring that memory performance differences were attributed to the manipulation of motor actions. The findings provided valuable insights into the potential cognitive implications of coincidental motor activity during memory encoding. However, despite its strengths, Study I encountered limitations that warrant

consideration. The null effect at retrieval could be attributed to specific experimental conditions, potentially impacting the ability to unveil subtle performance differences influenced by coincidental actions. The limited number of trials might have hindered the examination of remembered vs. forgotten differences that could shed light on the underlying mechanisms. Moreover, the choice of retrieval question format, while common in recognition memory literature, might have influenced the ability to detect nuanced performance variations. Further exploration is needed to ascertain the conditions under which coincidental motor activity may influence memory retrieval.

Study II delved into event segmentation paradigms to explore whether SG sounds aid into structuring memory encoding. A notable strength of Study II was its attempt to extend the findings of event segmentation to the auditory domain, considering the unique challenges posed by SG sounds. The study's meticulous design ensured controlled manipulations, providing valuable insights into the interplay between motor activity and event perception. However, Study II design was not absent on constraints. The predictable nature of event boundaries in the paradigm could have impacted participants' engagement and attention, potentially affecting the establishment of distinct event boundaries. Additionally, the limited event patterns used in the study might have restricted the complexity and variability of events, impacting the outcomes. The exclusion of an associative memory task focused solely on the contextual change due to motor actions, and the dual-task nature of the experiment could have affected memory processes. Future research should explore these factors to gain a more comprehensive understanding of event segmentation's intricate dynamics.

Finally, Study III adopted an exploratory approach to probe the association between selfgeneration effects and schizotypal personality traits. By examining the relationship between these variables across multiple experimental paradigms, the study highlighted the complexity of the self-generation effects. Furthermore, the inclusion of factorial exploratory analysis allowed to disentangle which traits from the SPQ are more closely linked to the self-generation effects. Yet, the exploratory nature of the study, while insightful, underscores the need for further validation and replication of the findings. The sample size and peak identification methodology could be optimized in future studies. Additionally, the complexity of self-generation effects demands a cautious interpretation of results. Despite these limitations, Study III challenged prevailing assumptions, and future research should confirm whether the Tb component is more linked to schizotypal traits than the well-known N1 component.
CONCLUSIONS

- The presence of an action alone, while initially hypothesized as a potential key contributor in the production effect, does not appear to significantly influence auditory memory on a behavioral level. Contrary to the distinctiveness account, predictability and sense of agency seem to play a fundamental role in the memory enhancement seen on the production effect.
- Introducing actions potentially acts as a stronger contextual shift than removing them. However, the mere presence or absence of overt actions during sound sequence encoding, and the neurophysiological processes engaged by them, does not meaningfully structure auditory memory representations.
- The modulation of the LC-NE system around actions, as reflected by an increase in pupil dilation, is not directly connected to the observed electrophysiological self-generation effects. Therefore, a "halo" of neuromodulation around actions is probably not regulating the attenuation of sensory responses of self-generated stimuli as hypothesized.
- Finally, the present thesis challenges the prevailing perspective that the N1 selfgeneration effect is a good index to reflect the continuum of psychosis in the healthy population. Instead, the Tb and other agency related components should be carefully considered as potential biomarkers to study sensory prediction deficits causing perceptual alterations of self-produced consequences. Encouraging further investigations into the complexities of the self-generation effects interactions with aberrant perception, will ultimately contribute to the advancement of research on psychosis-related conditions.

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